REFERENCE ONLY

UNIVERSITY OF LONDON THESIS

Degree PhD Year 2005 Name of Author KATTEY G. J.

COPYRIGHT

This is a thesis accepted for a Higher Degree of the University of London. It is an unpublished typescript and the copyright is held by the author. All persons consulting the thesis must read and abide by the Copyright Declaration below.

COPYRIGHT DECLARATION

I recognise that the copyright of the above-described thesis rests with the author and that no quotation from it or information derived from it may be published without the prior written consent of the author.

LOAN

Theses may not be lent to individuals, but the University Library may lend a copy to approved libraries within the United Kingdom, for consultation solely on the premises of those libraries. Application should be made to: The Theses Section, University of London Library, Senate House, Malet Street, London WC1E 7HU.

REPRODUCTION

University of London theses may not be reproduced without explicit written permission from the University of London Library. Enquiries should be addressed to the Theses Section of the Library. Regulations concerning reproduction vary according to the date of acceptance of the thesis and are listed below as guidelines.

A. Before 1962. Permission granted only upon the prior written consent of the author. (The University Library will provide addresses where possible).

B. 1962 - 1974. In many cases the author has agreed to permit copying upon completion of a Copyright Declaration.

C. 1975 - 1988. Most theses may be copied upon completion of a Copyright Declaration.

D. 1989 onwards. Most theses may be copied.

This thesis comes within category D.

☑ This copy has been deposited in the Library of UCL

☐ This copy has been deposited in the University of London Library, Senate House, Malet Street, London WC1E 7HU.

C:\Documents and Settings\lproctor.ULL\Local Settings\Temporary Internet Files\OLK36\Copyright - thesis.doc

Cladocera in mountain lakes: their potential role in reconstructing climate change

Thesis submitted for the degree of
Doctor of Philosophy
in the University of London

Giri Raj Kattel

University College London

May 2004

UMI Number: U592950

All rights reserved

INFORMATION TO ALL USERS
The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript
and there are missing pages, these will be noted. Also, if material had to be removed,
a note will indicate the deletion.



UMI U592950
Published by ProQuest LLC 2013. Copyright in the Dissertation held by the Author.
Microform Edition © ProQuest LLC.
All rights reserved. This work is protected against
unauthorized copying under Title 17, United States Code.



ProQuest LLC
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106-1346

Abstract

Research on climate change is becoming increasingly important to understand its multifaceted impacts on ecosystems at the present day and to identify patterns of natural climate variability and their impact in the past. Many remote Northwest European mountain lakes are undisturbed by air pollution and land-use change and can potentially be used for studies of climate change. Climate change influences the mountain lake ecosystem directly via changes in patterns of ice-cover, seasonality, stratification and hydrology and indirectly via changes in alkalinity, nutrient dynamics and habitat structure. Cladocera can be used as one of the significant indicators of such change since they have well-defined taxonomy, life history behaviour, and clear ecological preferences, and the fossil remains of these fauna are well preserved in lake sediments. In this thesis, first, sampling of contemporary and surface sediment assemblages of Cladocera along various transects in Loch Coire Fionnaraich (LCFR), Scotland was carried out to understand the response of Cladocera to temporal and spatial variables at the site and to assess the patterns of fossil representation in the loch. Cladoceran assemblages varied with micro-habitat structure and seasons, while a taphonomic study indicated changes in the patterns of fossil representation in the sediments with respect to seasonality, time, lake morphometry and the source habitats. Secondly, a calibration training set was developed for surface sediment assemblages of Cladocera and major physico-chemical variables from 72 mountain lakes of Scotland and Norway. In a direct gradient analysis and the associated Monte Carlo permutation tests, summer lake surface water temperature (LSWT) explained the maximum variation for the species-environment relationships in the data-set. A Cladocera-based PLS-transfer function for summer LSWT was then developed. A transfer function model with RMSEP=1.80^{0}C and r^2=0.71 allowed the past summer LSWT of LCFR to be reconstructed. The results of Cladocera-inferred summer LSWT reconstructions were compared with the local instrumental air temperature records over the last 20 years and the Central England Temperature series over the last 110 years. Reconstruction was also assessed for taphonomic bias. Although the reconstructed summer LSWT showed a relatively similar pattern to the local instrumental temperature records, the relationship between the longer CET series and reconstructed LSWT was poor indicating either the insensitivity of the loch to temperature change prior to the recent warming of the last few decades or that the Cladocera response to temperature predominantly a more complex, indirect one. For the most recent period a rapid decline in species diversity and in the relative abundance of littoral Cladocera and a reciprocal increase in total planktonic Cladocera together with changes in loss-on-ignition of the sediment appears to be associated with the impact of recent climate warming. Again the predominant mechanisms may be indirect involving changes in trophic status and in the habitat architecture of the loch. In conclusion, it is essential to understand further the factors controlling the community dynamics of Cladocera and the overall ecological complexity of mountain lakes before reliance can be placed on simple Cladocera-temperature transfer function for climate change reconstruction.

Acknowledgements

I have pleasure in extending my gratitude to my supervisor, Prof. Rick Battarbee. He taught me about the role of lacustrine sediments in global environmental change research, and showed great sincerity in helping with every step of my life, from household to academic, while being in UCL. I am also grateful to my co-supervisor, Dr. Anson Mackay for his untiring help, mainly on the data analyses of my PhD and to my previous co-supervisor, Dr. Laurence Carvalho, who directed the very early plan for a PhD.

I had great joy in meeting with Prof. John Birks. He, along with his colleagues in the Botanical Institute, University of Bergen provided the surface sediment samples and environmental variables from Norwegian lakes. He also taught me the techniques of numerical analyses. I am grateful to the EU-EMERGE programme for providing the surface sediment samples and the environmental data of Scottish lochs, used to develop a joint Scottish-Norwegian mountain lakes training set. I would like to thank the Scottish Meteorological Office for providing the past instrumental temperatures of Scottish sites. Prof. Peter Appleby in the University of Liverpool is thanked for dating the core from LCFR. A number of people within and outside UCL have contributed to my work directly and indirectly. I am grateful to those working for the ENSIS Ltd, ECRC and the Department of Geography especially, Dr. Simon Patrick, Dr. Martin Kernan, Don Monteith, Dr. Roger Flower, Ewan Shilland, James Shilland, Dr. Chris Curtis, Dr. Neil Rose, Dr. Gavin Simpson, Dr. Handong Yang, David Seamark, Mike Hughes, Dr. Sergi Pla, Elanor McBay, Daryl Lloyd, Helene Coleman, Gail Crick, Janet Hope, Tula Cloke, Ian Patmore, Nick Mann and Paul Schooling.

I am very grateful for an ORS Award, the ENSIS Trust Fund, the UCL Graduate School Research Scholarship and the UCL Department of Geography Scholarships for financial support. I am grateful to the Mead Scholarship and the Friend's Programme Hardship Funds, the UCL Graduate School Conference Awards and ENSIS Ltd. for supporting my academic career while being in UCL.

Finally, I would like to dedicate this thesis to my parents and my family, my wife, Roshani, daughter, Astha and son, Avash. This work was not possible without their love, patience and continuous encouragement.

TABLE OF CONTENTS PAGE

TITLE i

FRONTISPIECE ii

ABSTRACT iii

ACKNOWLEDGEMENTS iv

TABLE OF CONTENTS v

LIST OF TABLES xiv

LIST OF FIGURES xvii

LIST OF APPENDICES xxi

CHAPTER 1: **1**

INTRODUCTION **1**

1.1. Greenhouse effects **2**

1.2. Natural climatic variability **2**

1.3. Importance of palaeoclimate research on global climate change **5**

1.4. Lakes: an important archive for palaeoclimate research **6**

1.5 Mountain lakes and their sensitivity to climate change **7**

1.5.1 Limnological sensitivity and climate change 7

1.5.2 Climate reconstruction using proxy records 8

1.6 Living and fossil Cladocera **10**

1.6.1 Life history and food habit 11

1.6.2. Cladocera fossil remains 12

1.7 Response of Cladocera to global climate change **13**

1.7.1 Temporal and spatial dynamics of contemporary communities **14**

1.7.2 Taphonomy **17**

1.7.2.1 Representativity studies 18

1.7.2.2 Taphonomic processes 21

1.7.3 Transfer functions approach to reconstruct past climate change **21**

1.7.3.1 Direct approaches 22

1.7.3.2 Indirect approaches 24

pH and alkalinity 24

Nutrients and lake trophic status 24

Water levels 24

Lake stratification 25

Ice cover 26

1.8. Aims of study **26**

1.9. Thesis outline **27**

CHAPTER 2: **29**

STUDY AREAS **29**

2.1. Introduction **29**

2.2 Loch Coire Fionnaraich (LCFR) **29**

2.2.1 Location background **29**

2.2.2 Associated research history and the selection process of LCFR **31**

2.2.3 Aims of site selection 31

2.2.3.1 Contemporary survey of Cladocera 31

2.2.3.2 Study of taphonomy of Cladocera 32

2.2.3.3 Development of a temperature transfer function and palaeoclimate reconstruction 32

2.2.4. Regional climate 33

2.2.5. Site characteristics **35**

2.2.5.1 Geomorphology, hydrology, and vegetation 35

2.2.5.2 Bathymetry 36

2.2.5.3 Physico-chemistry of lake water 36

2.2.4.4 Thermal stratification 37

2.2.4.5 Palaeolimnology 37

2.3 Training set sites **39**

2.3.1 Aims and criteria for training set sites selection **40**

2.3.1.1 Higher altitude sites 40

2.3.1.2 Common environmental variables 40

2.3.1.3 Constant alkalinity against altitudes 40

2.3.2. Selected training set sites **41**

2.3.2.1 Scottish sites 41

2.3.2.2 Norwegian sites 47

2.4 Relationship between LCFR and other selected traiuning sites **48**

CHAPTER 3: **50**

METHODOLOGY 50

3.1. Introduction 50

3.2. Field methods **50**

3.2.1. Survey of contemporary Cladocera in Loch Coire Fionnaraich **50**

3.2.1.1 Collection of cladoceran zooplankton 53

3.2.2. Taphonomy of Cladocera in Loch Coire Fionnaraich **56**

3.2.2.1 Construction of transects **56**

3.2.2.2 Collection of surface sediment samples from transects **56**

3.2.2.3 Design of sediment traps 58

3.2.2.4 Installation of the sediment trap 58

3.2.3 Training set sites **60**

3.2.3.1 Measurement of environmental variables 60

July and January air temperatures 60

Mean summer lake surface water temperature 63

Precipitation 63

Maximum depth 63

Physico-chemistry of water 64

3.2.3.2 Collection of surface sediment samples across the training set sites 64

3.2.4 Sediment cores from Loch Coire Fionnaraich **64**

3.3 Laboratory methods **65**

3.3.1 Contemporary Cladocera analysis **65**

3.3.2 Taphonomy of Cladocera **66**

3.3.2.1 Spatial surface sediment samples 66

Dry weight (DW) and loss-on-ignition (LOI) analysis 66

Fossil Cladocera analysis 66

3.3.2.2 Sediment traps 67

3.3.3 Training set sites **67**

3.3.3.1 Analysis of physico-chemical variables of water samples 67

3.3.3.2 Analysis of DW and LOI 68

3.3.3.3 Fossil Cladocera analysis 68

3.3.4 Core sequence **68**

3.4. Numerical analyses **69**

3.4.1 Ordination **69**

3.4.1.1 Principal components analysis (PCA) 70

3.4.1.2 Detrended correspondence analysis (DCA) 70

3.4.1.3 Redundancy analysis (RDA) 71

3.4.1.4 Detrended canonical correspondence analysis (DCCA) 71

3.4.1.5 Partial ordinations 72

CHAPTER 4: 73

VARIATIONS IN PATTERNS OF CLADOCERAN COMMUNITY IN LITTORAL AND OPEN WATER HABITATS OF LOCH COIRE FIONNARAICH, SCOTLAND 73

4.1 Introduction 73

4.2 Materials and methods 73

4.2.1 Field methods 73

4.2.2 Laboratory methods 73

4.2.3 Numerical analyses 74

4.3 Results 74

4.3.1 Species richness, occurrences and composition of Cladocera in LCFR 74

4.3.2 Observed patterns of the abundance of the common species of Cladocera 81

4.3.3 TWINSPAN classification and patterns of Cladocera in ordinations 81

4.4 Discussion 84

4.4.1 Diversity, abundance and composition 84

4.4.2 Autoecology of dominant Cladocera 88

4.4.3 Assemblage structure of Cladocera 89

4.5 Conclusions 90

CHAPTER 5: 91

TAPHONOMY OF CLADOCERA IN A REMOTE SCOTTISH MOUNTAIN LOCH, LOCH COIRE FIONNARAICH 91

5.1 Introduction 91

5.2 Materials and methods 91

5.2.1 Collection of fossil remains and live Cladocera 91

5.2.2 Numerical analysis 93

5.3 Results 96

5.3.1 Percentage dry weight (DW) and loss-on-ignition (LOI) 96

5.3.2 Transportation and deposition of cladoceran remains in Loch Coire Fionnaraich 98

5.3.2.1 Transect vs core sample 98

5.3.2.2 Arc-GIS approach 104

3.4.1.5 Partial ordinations 72

CHAPTER 4: 73

VARIATIONS IN PATTERNS OF CLADOCERAN COMMUNITY IN LITTORAL AND OPEN WATER HABITATS OF LOCH COIRE FIONNARAICH, SCOTLAND 73

4.1 Introduction 73

4.2 Materials and methods 73

4.2.1 Field methods 73

4.2.2 Laboratory methods 73

4.2.3 Numerical analyses 74

4.3 Results 74

4.3.1 Species richness, occurrences and composition of Cladocera in LCFR 74

4.3.2 Observed patterns of the abundance of the common species of Cladocera 81

4.3.3 TWINSPAN classification and patterns of Cladocera in ordinations 81

4.4 Discussion 84

4.4.1 Diversity, abundance and composition 84

4.4.2 Autoecology of dominant Cladocera 88

4.4.3 Assemblage structure of Cladocera 89

4.5 Conclusions 90

CHAPTER 5: 91

TAPHONOMY OF CLADOCERA IN A REMOTE SCOTTISH MOUNTAIN LOCH, LOCH COIRE FIONNARAICH 91

5.1 Introduction 91

5.2 Materials and methods 91

5.2.1 Collection of fossil remains and live Cladocera 91

5.2.2 Numerical analysis 93

5.3 Results 96

5.3.1 Percentage dry weight (DW) and loss-on-ignition (LOI) 96

5.3.2 Transportation and deposition of cladoceran remains in Loch Coire Fionnaraich 98

5.3.2.1 Transect vs core sample 98

5.3.2.2 Arc-GIS approach 104

Bosmina coregoni 104

Bosmina longispina 104

Acroperus harpae 108

Alonella nana 108

Alonella excisa 111

Monospilus dispar 111

Chydorus piger 114

5.3.2.3 The distribution of remain of Cladocera in relation to depth in LCFR 114

5.3.3 Taphonomy of Cladocra using ordination of spatial surface sediment samples **114**

5.3.3.1 Detrended correspondence analysis 117

5.3.3.2 Principal components analysis (PCA) 117

5.3.3.3 Redundancy analysis (RDA) 118

5.3.4 Sediment trap **123**

5.3.5 Sediment trap vs the composition of remains in the core sample **125**

5.3.6 Source sample vs core sample assemblages **132**

5.3.7 Integration of the surface sediment samples, the trap sample, the source sample and the core sample **136**

5.3.7.1 Ordination 136

5.3.7.2 Integration by the percentage compositions of Cladocera in the surface sediment samples, the core sample, the trap sample and the source sample 141

5.4 Discussion **141**

5.4.1 Representation of Cladocera in the sedimentary assemblages compared with the spatial surface sediment samples **143**

5.4.2 Representation of Cladocera in the trap sample **147**

5.4.3 Representation of Cladocera in the sedimentary assemblages when compared with the composition in the trap sample **149**

5.4.4 Representation of Cladocera in the sedimentary assemblages when compared with the composition in the source sample **150**

5.5. Conclusions **151**

CHAPTER 6: 152

FOSSIL CLADOCERA AS AN INDICATOR OF CLIMATE CHANGE IN MOUNTAIN LAKES: DEVELOPMENT OF A SURFACE WATER TEMPERATURE TRANSFER FUNCTION 152

6.1 Introduction 152

6.2 Materials and methods 152

6.2.1 Laboratory methods 152

6.2.2 Numerical analyses 153

6.2.2.1 Ordination 153

6.2.2.2 Weighted-averaging (WA) regression 155

6.2.2.3 HOF models 155

6.2.2.4 Development of a summer LSWT transfer function, and reconstruction of past summer LSWT of Loch Coire Fionnaraich 156

6.3. Results 159

6.3.1 Exploratory data analysis 159

6.3.1.1 Explanatory variables 159

Principal components analysis (PCA) 159

6.3.1.2 Species data 164

Detrended correspondence analysis (DCA) 164

Principal components analysis (PCA) 167

6.3.1.3 Species-environment relationships 171

Redundancy analysis (RDA) 171

Variance partitioning 180

Detrended canonical correspondence analysis (DCCA) 187

6.3.2 Niche species response (maximum likelihood) analysis 187

6.3.2.1 HOF models 188

6.3.2.2 Weighted averaging optima and tolerances for Cladocera and their response curves in HOF models 191

Daphnia 191

Bosmina longispina 194

Bosmina coregoni 194

Graptoleberis testudinaria 200

Eurycercus lamellatus 202

Camptocercus rectirostris 202

Acroperus harpae 207

Acroperus elongatus 209
Alona rectangula 212
Alona guttata 212
Alona costata 214
Alona rustica 214
Alona intermedia 214
Alona affinis 216
Alona quadrangularis 216
Alonella nana 219
Alonella excisa 219
Monospilus dispar 222
Chydorus sphaericus 222
Chydorus piger 225
Pleuroxus aduncus 227
Sida crystallina 227
6.3.3 Development of summer LSWT transfer function models **232**
6.3.3.1 WA method 232
6.3.3.2 PLS method 233
6.3.3.3 WA-PLS method 234
6.4 Discussion **236**
6.4.1 Training set **236**
6.4.2 Factors affecting composition and abundance of Cladocera in the calibration data-set **237**
6.4.3 Transfer function model for summer LSWT **240**
6.5. Conclusions **241**
CHAPTER 7: **243**
RECENT CLIMATE CHANGE IN NORTHWEST SCOTLAND: INFERRED FROM SUBFOSSIL ASSEMBLAGES OF CLADOCERA **243**
7.1. Introduction **243**
7.2. Materials and methods **243**
7.2.1 Field and laboratory methods **243**
7.2.2 Numerical analyses **244**
7.2.2.1 Zonation 244
7.2.2.2 Ordination 244
7.2.2.3 Shannon-Wiener Diversity Index 245

7.3. Results **246**
7.3.1 Dry weight and loss on ignition **246**
7.3.2 Chronology of LCFR1 **248**
7.3.2.1 Lead-210 activity 249
7.3.2.2 Artificial fallout radionuclides 249
7.3.2.3 Core chronology 249
7.3.3 Core correlation between LCFR1 and LCFR2 **249**
7.3.4 Chronology of LCFR2 **253**
7.3.5 Suitability of the core LCFR2 for Cladocera-inferred climate reconstruction in LCFR **256**
7.3.6 Succession of Cladocera in LCFR2 **258**
7.3.6.1 Zone Lcf-1 (ca. 1281 AD – ca. 1327 AD; 27.25-25.75 cm) 258
7.3.6.2 Zone Lcf-2 (ca. 1327 AD – ca. 1439 AD; 25.75-22.25 cm) 261
7.3.6.3 Zone Lcf-3 (ca. 1439 AD – ca. 1919 AD; 22.25-6.25 cm) 261
7.3.6.4 Zone Lcf-4 (ca. 1919 AD – ca. 1998 AD; 6.25 –0.25 cm) 261
7.3.7 Cladocera analysis through ordinations 261
7.3.7.1 Detrended correspondence analysis (DCA) 261
7.3.7.2 Principal components analysis (PCA) 262
7.3.7.3 Succession of Cladocera as shown by PCA axes 262
7.3.7.4 Succession of Cladocera as shown by PCA time-track 263
7.3.8 Cladocera-inferred summer lake water temperature reconstruction **263**
7.3.9 Comparison between Cladocera-inferred reconstructed summer LSWT using in LCFR2 and the instrumental temperature records **266**
7.3.10 PCA sample scores vs instrumental climatic parameters **270**
7.3.11 PCA sample scores vs reconstructed summer LSWT **273**
7.3.12 Major response variables potentially associated with recent climate change in Loch Coire Fionnaraich **273**
7.4 Discussion **275**
7.4.1.1 Direct effects 280
7.4.1.2 Indirect effects 282
Changes in trophic state 283
Habitat changes 284
7.5 Conclusions **285**

CHAPTER 8: 286
8.1 Introduction 286
8.1.1 Ecological complexity 286
8.1.2 Transfer function 287
8.1.3 Taxonomy 289
8.1.4 Taphonomy 289
8.1.5 Climate reconstruction 291
8.2 Recommendations 293
REFERENCES 296
APPENDICES 324
Appendix 1 324
Appendix 2 329
Appendix 3 336
Appendix 4 346
Appendix 5 347
Appendix 6 362
Appendix 7 378

LIST OF TABLES

TABLES	ABBREVIATED TITLE	PAGE
Table 2.1	Physico-chemistry of water in Loch Coire Fionnaraich (LCFR)	31
Table 2.2	Overview of selected training set sites in Scotland and Norway	43-45
Table 3.1	Sampling replicates of live Cladocera in Loch Coire Fionnaraich	54
Table 3.2	Exposure dates for sediment traps in Loch Coire Fionnaraich	60
Table 3.3	July, January and summer water temperatures of Scottish lochs	62
Table 4.1	Seasonal count of Cladocera among micro-habitat types in Loch Coire Fionnaraich	77-78
Table 4.2	Total count of Cladocera in micro-habitat types in LCFR	79
Table 4.3	Summary of DCA of living cladoceran samples in LCFR	83
Table 5.1	Environmental variables used in taphonomy of Cladocera in Loch Coire Fionnaraich	95
Table 5.2	Cladoceran remains in surface sediment samples of LCFR	99-102
Table 5.3	Summary of DCA of 33 surface sediment samples of Cladocera	117
Table 5.4	Summary of PCA of 33 surface sediment samples of Cladocera	118
Table 5.5	Summary of RDA of Cladocera in 33 surface sediment samples	118
Table 5.6	Variance explained by each variable when constrained with RDA	120
Table 5.7	Variance explained by each variable before forward selection	121
Table 5.8	Summary of RDA of Cladocera after forward selection	121
Table 5.9	Taphonomic loss and representation rates of Cladocera in LCFR	130
Table 5.10	Taxon rates (%) of living Cladocera in a source sample in LCFR	134
Table 5.11	Differences in taxon rates between source and core sample in Loch Coire Fionnaraich	135
Table 5.12	Summary of PCA of surface, trap, source and core samples in LCFR	138-139
Table 6.1	Summary of PCA of a total of 21 environmental variables in 14 sites of Scotland	160
Table 6.2	Summary of PCA of a total of 21 environmental variables in 58 sites of Norway	160
Table 6.3	Summary of PCA of a total of 21 environmental variables in 72 sites of combined Scottish and Norwegian training set	163
Table 6.4	Summary of PCA scores of 21 environmental variables in 72 sites of Scotland and Norway.	163
Table 6.5	Summary of a DCA of the 26 species of Cladocera in 14 sites in Scotland	164
Table 6.6	Summary of a DCA of the 24 species of Cladocera in 54 sites in Norway	167

Table 6.7	Summary of a DCA of the 28 species of Cladocera of 68 training set sites from Scotland and Norway	167
Table 6.8	Summary of a PCA of the 26 species of Cladocera of 14 Scottish sites	168
Table 6.9	Summary of a PCA of the 24 species of Cladocera of 54 Norwegian sites	168
Table 6.10	Summary of a PCA of the 28 species data of 68 training set sites from training set (a) all taxa and (b) littoral taxa	171
Table 6.11	Summary of a RDA of species-environment relationships in of 68 training set sites	171
Table 6.12	Variance inflation factors of 21 environmental variables	173
Table 6.13	Summary of a RDA of species-environment relationships in 68 training set sites from Scotland and Norway	175
Table 6.14	Potential variance explained by each environmental variable (VIF<20) before forward selection	176
Table 6.15	Summary of RDA ordination of species-environment relationship in 68 sites with 3 selected environmental variables after forward selection	177
Table 6.16	Regression/canonical coefficients, t-values of regression coefficients and inter-set correlations of three selected environmental variables	178
Table 6.17	Percentage variance explained by each environmental variable when RDA is constrained with a single explanatory variable	181
Table 6.18	Variance partitioning by Partial-RDA of Cladocera.	182
Table 6.19	Taxon-specific response to individual environmental parameters for the 22 cladoceran zooplankton taxa in Huisman-Olff-Fresco-HOF models	190
Table 6.20	Estimated WA mean summer LSWT optima and tolerances of the dominant Cladocera in the training set (N=68)	192
Table 6.21	Estimated WA mean July air temperature optima and tolerances of the dominant Cladocera in the training set (N=68)	196
Table 6.22	Estimated WA SO_4 optima and tolerances of the dominant Cladocera in the training set (N=68)	197
Table 6.23	Estimated WA sampling depth optima and tolerances of the dominant Cladocera in the training set (N=68)	198
Table 6.24	Estimated WA mean LOI optima and tolerances of the dominant Cladocera in the training set (N=68)	203
Table 6.25	Estimated WA TOC optima and tolerances of the dominant Cladocera in the training set (N=68)	204
Table 6.26	Estimated WA pH optima and tolerances of the dominant Cladocera in the training set (N=68)	210
Table 6.27	Summary status for the Cladocera summer LSWT calibration data-set	231

Table 6.28	Mean lake surface water temperature WA and tolerance down-weighted WA with cross-validation by jack-knifing in the training set (N=68)	233
Table 6.29	Summer lake surface water temperature PLS models in the training set (N=68)	233
Table 6.30	Summer lake surface water temperature WA-PLS models in the training set (N=68)	234
Table 6.31	Summer lake surface water temperature PLS models in the training set (N=64)	234
Table 7.1	Fallout radionuclide concentrations in LCFR of core LCFR1	248
Table 7.2	^{210}Pb chronology of LCFR in core LCFR1	252
Table 7.3	^{210}Pb chronology of core LCFR2 after comparison with LCFR1	256
Table 7.4	Summary of DCA of Cladocera in 55 core samples in LCFR	262
Table 7.5	Summary of PCA of 55 core samples Cladocera in LCFR	262
Table 7.6	Fraction of variation explained for regression between various climatic parameters and principal component axes of Cladocera	272
Table 7.7	PCA eigenvalues of all, littoral and planktonic Cladocera in LCFR2	273

LIST OF FIGURES

FIGURES	ABBREVIATED TITLE	PAGE
Figure 1.1	Cladocera life cycle	12
Figure 2.1	Map of Loch Coire Fionnaraich (LCFR)	30
Figure 2.2	Central England Temperature (CET) series and local temperature record of Plockton, Scotland	34
Figure 2.3	Thermal stratification in Loch Coire Fionnaraich	38
Figure 2.4	Relationship between altitude and alkalinity in training set sites	42
Figure 2.5	Selected training set sites in Scotland and Norway	46
Figure 2.6	PCA ordination of joint Scottish and Norwegian sites	49
Figure 3.1	Micro-habitat types of contemporary Cladocera in LCFR	52
Figure 3.2	Sampling methods for contemporary Cladocera	55
Figure 3.3	Locations of spatial surface sediment samples in LCFR	57
Figure 3.4	Sediment trap installed for taphonomy of Cladocera in LCFR	59
Figure 4.1	Species richness of Cladocera along seasons and habitats in Loch Coire Fionnaraich	75
Figure 4.2	Composition of planktonic and littoral Cladocera in LCFR	80
Figure 4.3	Relative abundances of common Cladocera in LCFR	82
Figure 4.4	TWINSPAN classification of 24 cladoceran samples in LCFR	84
Figure 4.5	DCA ordination of 24 cladoceran samples in LCFR	86
Figure 4.6	Classification of 24 cladoceran samples in ordination in LCFR	87
Figure 5.1	Spatial surface sediment samples along various transects in Loch Coire Fionnaraich	92
Figure 5.2	Percentage DW and LOI in surface sediment samples in LCFR	97
Figure 5.3	Bathymetric measurements of LCFR based on Arc-GIS	105
Figure 5.4	Concentration of *Bosmina coregoni* (no.gdm^{-1}) in Loch Coire Fionnaraich using the Arc-GIS	106
Figure 5.5	Interpolation of *B. longispina* (no.gdm^{-1}) in Loch Coire Fionnaraich using the Arc-GIS	107
Figure 5.6	Interpolation of *Acroperus harpae* (no.gdm^{-1}) in Loch Coire Fionnaraich using the Arc-GIS	109
Figure 5.7	Interpolation of *Alonella nana* (no.gdm^{-1}) in Loch Coire Fionnaraich using the Arc-GIS	110
Figure 5.8	Interpolation of *A. excisa* (no.gdm^{-1}) in Loch Coire Fionnaraich using the Arc-GIS	112
Figure 5.9	Interpolation of *Monospilus dispar* (no.gdm^{-1}) in Loch Coire Fionnaraich using the Arc-GIS	113

Figure 5.10	Interpolation of *Chydorus piger* (no.gdm^{-1}) in Loch Coire Fionnaraich using the Arc-GIS	115
Figure 5.11	Extent of the deposition of remains of Cladocera in subsequent depth points of LCFR	116
Figure 5.12	PCA ordination of 33 spatial surface sediment samples in Loch Coire Fionnaraich	119
Figure 5.13	Cladocera species-environment relationships in RDA in LCFR	122
Figure 5.14	Composition of Cladocera (no.dm^{-1}) in sediment traps in LCFR	124
Figure 5.15	Cladoceran remains (>5%) present in sediment traps in LCFR	126
Figure 5.16	PCA time-series analysis of cladoceran remains in traps in Loch Coire Fionnaraich	127
Figure 5.17	Taphonomic loss and representative rates of Cladocera in LCFR	131
Figure 5.18	Representation of Cladocera in LCFR with respect to taxon rates	137
Figure 5.19	PCA of surface sediment, trap, source and core samples in Loch Coire Fionnaraich	140
Figure 5.20	Representation of Cladocera in the sedimentary assemblages in LCFR using the integration of the percentage composition	142
Figure 6.1	PCA biplot ordinations of a total of 21 environmental variables for sites in (a) Scotland and (b) Norway	161
Figure 6.2	PCA biplot ordinations of a total of 21 spatial and environmental variables in 72 sites for Scotland and Norway	165
Figure 6.3	PCA bipolot ordination of 21 environmental variables in 72 sites of Scotland and Norway	166
Figure 6.4	PCA biplot ordination of (a) 26 species present in 14 samples from Scotland and (b) 24 species present in 54 samples from Norway	169
Figure 6.5	PCA biplot ordination of 28 cladoceran remains present in 68 surface sediment samples from Scotland and Norway	170
Figure 6.6	RDA biplot after the deletion of environmental variables with high VIF values. (a) samples v environment, (b) species v environment	174
Figure 6.7	RDA biplot after forward selection (a) samples v environment (b) species v environment	179
Figure 6.8	Variance partitioning of species data in RDA	184
Figure 6.9	The sources of variation for the Cladocera	185
Figure 6.10	Composition (%) of Cladocera along summer LSWT gradients	186
Figure 6.11	Relative abundances of *Daphnia* plotted against environmental gradients for the training set (N=68)	193
Figure 6.12	Relative abundances of *Bosmina longispina* plotted against environmental gradients for the training set (N=68)	195

Figure 6.13	Relative abundances of *Bosmina coregoni* plotted against environmental gradients for the training set (N=68)	199
Figure 6.14	Relative abundances of *Graptoleberis testudinaria* plotted against environmental gradients for the training set (N=68)	201
Figure 6.15	Relative abundances of *Eurycercus lamellatus* plotted against environmental gradients for the training set (N=68)	205
Figure 6.16	Relative abundances of *Camptocercus rectirostris* plotted against environmental gradients for the training set (N=68)	206
Figure 6.17	Relative abundances of *Acroperus harpae* plotted against environmental gradients for the training set (N=68)	208
Figure 6.18	Relative abundances of *Acroperus elongatus* plotted against environmental gradients for the training set (N=68)	211
Figure 6.19	Relative abundances of *Alona guttata* plotted against environmental gradients for the training set (N=68)	213
Figure 6.20	Relative abundances of *Alona costata* plotted against environmental gradients for the training set (N=68)	215
Figure 6.21	Relative abundances of *Alona rustica* plotted against environmental gradients for the training set (N=68)	215
Figure 6.22	Relative abundances of *Alona intermedia* plotted against environmental gradients for the training set (N=68)	217
Figure 6.23	Relative abundances of *Alona affinis* plotted against environmental gradients for the training set (N=68)	218
Figure 6.24	Relative abundances of *Alona quadrangularis* plotted against environmental gradients for the training set (N=68)	220
Figure 6.25	Relative abundances of *Alonella excisa* plotted against environmental gradients for the training set (N=68)	221
Figure 6.26	Relative abundances of *Monospilus dispar* plotted against environmental gradients for the training set (N=68)	223
Figure 6.27	Relative abundances of *Chydorus sphaericus* plotted against environmental gradients for the training set (N=68)	224
Figure 6.28	Relative abundances of *Chydorus piger* plotted against environmental gradients for the training set (N=68)	226
Figure 6.29	Relative abundances of *Pleuroxus aduncus* plotted against environmental gradients for the training set (N=68)	228
Figure 6.30	Relative abundances of *Sida crystallina* plotted against environmental gradients for the training set (N=68)	229
Figure 6.31	Estimated weighted averaging (WA) summer lake surface water temperature optima (^{0}C) and tolerances (^{0}C) of the Cladocera	230

Figure 6.32	PLS models of Cladocera-inferred mean summer lake surface water temperatures in the training set (N= 64)	235
Figure 7.1	Percentage dry weight and loss on ignition (LOI) profiles of LCFR1 and LCFR2 in Loch Coire Fionnaraich	247
Figure 7.2	Fallout radionuclides in the LCFR sediment core LCFR1	250
Figure 7.3	Radiometric chronology of LCFR sediment core LCFR1 showing the raw CRS and CIC model ^{210}Pb dates	251
Figure 7.4	Core cross-correlation between LCFR1 and LCFR2	254
Figure 7.5	Cross correlation between ^{210}Pb and SCP dating of sediment core of LCFR1	255
Figure 7.6	Age-depth model of LCFR2 based on ^{210}Pb chronology of LCFR1	257
Figure 7.7	Stratigraphic representation of subfossil assemblages of all Cladocera in LCFR2	259
Figure 7.8	Stratigraphic representation of subfossil assemblages of principal Cladocera, the PCA axis 1 and 2 scores of taxa, LOI and species diversity index of Cladocera in LCFR	260
Figure 7.9	PCA time-track analysis of subfossil Cladocera samples in LCFR2	264
Figure 7.10	PCA of training set samples and the subfossil samples in LCFR	265
Figure 7.11	Stratigraphic representation of subfossil assemblages of principal Cladocera and their inferred temperature reconstruction in LCFR2	267
Figure 7.12	The reconstructed summer LSWT of LCFR for the last 800 years	268
Figure 7.13	Comparison between CET (www.met-office.gov.uk) and Cladocera-inferred reconstructed summer LSWT in LCFR	269
Figure 7.14	Comparison between Cladocera-inferred reconstructed summer LSWT in LCFR and local instrumental temperature records at Plockton, Scotland	271
Figure 7.15	Most potential indicators of Cladocera and other proxy indicators to climate change in LCFR	274

LIST OF APPENDICES

APPENDICES	ABBREVIATED TITLE	PAGE
Appendix 1.1	Taxonomy and systematic of Cladocera (http://www.cladocera.uoguelph.ca)	324
Appendix 2.1	Total number of lakes and their codes available for calibration set	329
Appendix 2.2	Measurement of environmental variables in the training set sites	334
Appendix 3.1	Taxonomic notes of fossil Cladocera recovered in study sites	336
Appendix 4.1	Abbreviations for contemporary cladocera samples in LCFR	346
Appendix 5.1	Abbreviations for surface sediment samples from transects	347
Appendix 5.2	Abbreviation of Cladocera species used for ordination in Loch Coire Fionnaraich	348
Appendix 5.3	Samples taken with GPS co-ordinates and depths along transects	349
Appendix 5.4	Example of tabulated cladoceran data for Arc-GIS interpolation	350
Appendix 5.5	Distribution of *Daphnia* sp. in LCFR in Arc-GIS	351
Appendix 5.6	Distribution of *Acroperus elongatus* in LCFR in Arc-GIS	352
Appendix 5.7	Distribution of *Alona affinis* in LCFR in Arc-GIS	353
Appendix 5.8	Distribution of *Alona quadrangularis* in LCFR in Arc-GIS	354
Appendix 5.9	Distribution of *Alona guttata* in LCFR in Arc-GIS	355
Appendix 5.10	Distribution of *Alona rustica* in LCFR in Arc-GIS	356
Appendix 5.11	Distribution of *Alona intermedia* in LCFR in Arc-GIS	357
Appendix 5.12	Distribution of *Graptoleberis testudinaria* in LCFR in Arc-GIS	358
Appendix 5.13	Distribution of *Chydorus sphaericus* in LCFR in Arc-GIS	359
Appendix 5.14	Distribution of *Rhynchotalona falcata* in LCFR in Arc-GIS	360
Appendix 5.15	Distribution of *Camptocercus rectirostris* in LCFR in Arc-GIS	361
Appendix 6.1	Cladocera assemblages in selected training set sites	362
Appendix 6.2	Abbreviation of cladoceran species used in the training set sites	365
Appendix 6.3	Estimated WA of January air temperature optima of Cladocera in the training set	366
Appendix 6.4	Estimated WA of precipitation optima of Cladocera in the training set	367
Appendix 6.5	Estimated WA of Ca optima of Cladocera in the training set	368
Appendix 6.6	Estimated WA of conductivity optima of Cladocera in the training set	369
Appendix 6.7	Estimated WA of Mg optima of Cladocera in the training set	370
Appendix 6.8	Estimated WA of Na optima of Cladocera in the training set	371
Appendix 6.9	Estimated WA of Cl optima of Cladocera in the training set	372
Appendix 6.10	Estimated WA of K optima of Cladocera in the training set	373

Appendix 6.11	Estimated WA of Abs-250 optima of Cladocera in the training set	374
Appendix 6.12	Estimated WA of Al-NL optima of Cladocera in the training set	375
Appendix 6.13	Estimated WA of Al-L optima of Cladocera in the training set	376
Appendix 6.14	Estimated WA of alkalinity optima of Cladocera in the training set	377
Appendix 7.1	Cladocera recovered in the sub-fossil assemblage of LCFR	378
Appendix 7.2	Hadley Centre instrumental temperature data for North Scotland	379
Appendix 7.3	Data on North Atlantic Oscillation Index (NAOI) (www.cri.uea.ac.uk).	386

Chapter 1

Introduction

Over the last twenty years global warming has become one of the major societal concerns worldwide. Recent warming, an average rise of 0.6 ^{0}C temperature during the last 100 years, is considered to have caused polar ice melting, sea level rise, changes in patterns of thermohaline circulation, increased incidence of droughts and floods, and extensive damage to natural ecosystems (IPCC, 1995). As a result, many parts of the world have faced severe food scarcity, poverty and health problems (IPCC, 2001). Today, one of the most challenging missions for scientists is to mitigate these impacts in future, which require not only an understanding of the root causes of global climate change, but also to persuade political bodies to make decisions to avoid their consequences.

For scientists, a central question is how to differentiate between natural climate change and climate change caused by human activity. Palaeoclimatologists have initiated research on various facets of climate change along millennial to decadal time scales (Crowley, 1993). Particularly, they are concerned with rapid natural climatic variability with respect to human-induced greenhouse-gas warming in recent years (Delworth & Knutson, 2000). Palaeolimnologists are making efforts to understand this using a range of lakes located around the globe (Battarbee, 2000). Mountain lakes, in particular, are important sensors of climate variability due to their location in remote sites and their natural archive of high-resolution physical, chemical and biological proxies for climate change, such as stable isotopes, diatoms, chrysophytes, ostracods, chironomids, and Cladocera (e.g. Battarbee et al., 2001a). Most of these proxies are sensitive as lakes and lake sediments often amplify the climate change signal (Smol et al., 1991; Walker et al., 1991; Brooks & Birks, 2000; Dalton et al., 2001; Battarbee et al., 2001a; Pla, 2001). The potential of Cladocera as a climate indicator has recently been demonstrated successfully by Lotter et al. (1997) and Korhola (1999) in European mountain lakes. This study is aimed to explore this potential further in Scottish and Norwegian mountain lakes.

1.1 Greenhouse effects

The earth's atmosphere contains natural greenhouse gases, including water vapour (H_2O), carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O) and ozone (O_3). H_2O and CO_2 are the two most important greenhouse gases. Incoming short-wave solar radiation is radiated from the earth's surface back to space as infrared radiation and partially absorbed by greenhouse gases resulting in natural greenhouse warming of about 35 ^{0}C (Sinha, 1995). However, the emission of anthropogenic greenhouse gases and aerosols into the atmosphere during the industrial era has become remarkably high. IPCC (1995) reported that the measurement of CO_2 concentration in the earth's troposphere was 280 ppmv in 1800 A.D., which rose to 358 ppmv in 1994 A.D. As a result, the atmosphere has become more opaque to outgoing infrared radiation resulting in increased radiative forcing or net energy flux (Houghton, 1994). The total radiative forcing is currently estimated at about 2.5Wm^{-2}, of which CO_2 causes 1.6W m^{-2} (IPCC, 1995). This suggests that increasing CO_2 levels in the atmosphere are one of the greatest causes of rapid climatic change (Houghton, 1994; Broecker, 1999).

1.2 Natural climatic variability

Studies on the Vostok ice cores from the Greenland ice caps and other ocean cores show that the natural climatic variability of the earth in the past million years had a series of cold (glacial) and warm (interglacial) episodes (Hays et al., 1976; Crowley, 1993; Petit et al., 1997). Such episodes were the result of changes in the earth's orbital cycles around the sun thereby changing patterns of solar insolation (Horel and Geisler, 1997). For example, the last glacial cycle was terminated around 11,500 years BP and was followed by the post-glacial Holocene period (Berger and Loutre, 1991; Broecker, 1997; Broecker, 1998; Broecker, 1999). However, within the Holocene, there have been several minor oscillations (Broecker, 1999) such as the Medieval Warm Period and the Little Ice Age (Broecker, 2000) suggesting that climate changes naturally on different time-scales (Schneider, 1994). There has been increasing evidence that the factors thought to be responsible for the shorter decadal to centennial time-scale climate change include changing solar output and volcanic dust.

Changes in solar output appear to be a significant external forcing for recent climate change in the Northern Hemisphere, where solar irradiance in the 'Maunder Minimum'

during the mid-seventeenth and early eighteenth century corresponded with a cold climatic event (Mann et al., 1998). Following this, the gradual increase of solar irradiance from the early nineteenth century through to the mid-twentieth century coincided with a warming episode (Mann et al., 1998). Shindell et al., (1999) proposed a recent solar cycle variability model, in which the model reproduced 11-year climatic oscillations as well as some longer-scale variations associated with solar irradiance, which they thought were linked to the Little Ice Age.

Large volcanic eruptions are also one of the causes of external forcing for natural climate change, where discharge of high amounts of dust in the atmosphere caused cooling for short time periods (Schneider, 1994; Horel and Geisler, 1997). Climate scientists have attempted to model recent volcanic eruptions and their effects on climate change (Robock, 1981; Soden et al., 2002). However, the prediction associated with this forcing is difficult due to poor and imperfectly measured historical data (Mann et al., 1998).

In addition to these external forcings, internal forcing is also important. This is associated especially with ocean-atmosphere interactions, such as the thermohaline circulation (THC) (Houghton, 1994; Schneider, 1994). In the THC, a significant amount of heat is transported from the tropics to the North Atlantic and southern oceans (Maslin et al., 2003), where a deep convection is induced by surface cooling, sinking to depth, and upwelling at lower latitudes, with horizontal shallow and deep currents feeding these vertical flows (Marotzke, 2000; Clark et al., 2002). However, climate scientists argue that the THC has large fluctuations between oceans and several quasi-stable patterns of circulation occur at decadal to centennial time-scales (Broecker, 1997). Broecker et al. (1999) argued that in the Little Ice Age, the deepwater formation in the Southern Ocean was considerably stronger than now, but the deepwater formation in the northern Atlantic was considerably weaker. About 120 years ago, the deepwater circulation reorganised in such a way that deep-water circulation in the southern ocean collapsed and northern Atlantic circulation strengthened bringing an end to the Little Ice Age (Broecker et al., 1999; Broecker, 2000).

The North Atlantic in particular has attracted palaeoclimatologists since the deep water convection and sinking are vigorous in the Labrador and Greenland Seas due to high surface salinity compared to the North Pacific (Marotzke, 2000; Clark et al., 2002). As a

result, northward heat transport to the North Atlantic is much stronger than to the North Pacific (Wood et al., 1999). Reduction of North Atlantic heat transport may lead to a cooling of western European climate particularly during winter in the future (Broecker, 1998; Marotzke, 2000), although the recent increase in the concentration of human-induced CO_2 in the atmosphere and its effects on global warming may affect such cooling (Broecker, 1998). Indeed there is even concern that recent anthropogenic greenhouse-gas increases may lead to a collapse of the North Atlantic THC (Wood et al., 1999; Marotzke, 2000). Increased atmospheric temperature or greenhouse-gas warming causes increased production of atmospheric moisture (Broecker, 2000). The atmospheric moisture is then transported towards higher latitudes, where increased precipitation occurs (Broecker, 1998). Increased rainfall reduces the concentration of surface salinity interrupting deep convection and sinking of water, weakening the North Atlantic THC or bringing it to a halt (Broecker, 1998; Clark et al., 2002). Thus extensive research on the organisation and patterns of the North Atlantic THC is essential for understanding the natural climatic variability in the region. Assessing climatic variability of sites along the margin of the North Atlantic, as in this study, forms a key component of this research. Scotland, in particular, is an ideal location for this research since it lies close to the polar front. Latitudinal shifts of the polar front determine the climate across Scotland, whether it has Arctic or maritime influenced weather patterns. However, the warm westerlies or the North Atlantic Drift (NAD) usually dominate the Scottish weather.

The climate of Scotland has changed considerably during the Holocene. In the mid Holocene, about 5000 years BP, the annual temperature of Scotland was possibly 1-1.5 ^{0}C higher than the mid-20th century (Price, 1983). In the last 5000 years, variations in Scottish climate have occurred (Price, 1983). Between 1150 and 1300 AD, Scottish summer temperatures increased by 0.5-0.9 ^{0}C and winters were mild, but still cooler than the late 20th century (Folland et al., 2001). Price (1983) and Harrison (1997) argued that between 1900-1950 AD Scotland's average annual temperatures were 0.4 ^{0}C warmer than any time since the 15th century and increased by another 0.4 ^{0}C to the present day. Consequently, the increased growing season appears to have had a significant effects on Scottish lake ecosystems (e.g. George and Harris, 1985). Increasing precipitation across Scotland has also caused a rapid increase in river discharge resulting in an alteration of the physical structures of shoreline habitats for fish, zooplankton and invertebrates in lochs (e.g. Werritty and Acreman, 1985). Most

recently, wetter winters and drier summers in Scotland are believed to have caused more peatland erosion and such erosion could have an influence on the ecology of lake waters (Rose and Yang pers. comm.). Thus the natural climatic variability in Scotland during the late Holocene has become an important topic for palaeoclimate research.

1.3 Importance of palaeoclimate research on global climate change

General Circulation Models (GCMs) are computer-simulated atmospheric and coupled ocean-atmospheric models for predicting the earth's climate systems (e.g. Delworth and Knutson, 2000). They focus in particular on modelling climate change for a relatively short time-scale on the basis of available temperature data for the last 100 years or so (Maslin and Berger, 1997; Mann et al., 1998; Wood et al., 1999; Delworth and Knutson, 2000). However, their validity for longer time-scale reconstruction depends largely on comparisons with high-resolution palaeodata sets (Schneider, 1994; Moritz et al., 2002). Particularly, high-resolution palaeodata are needed for the last few centuries that include the Little Ice Age and the period recent anthropogenic warming.

Raynaud et al. (1993) argue that ice cores are one of the important records for providing high-resolution palaeodata since they can integrate data from terrestrial, ocean and atmospheric systems for longer time-scales. Palaeodata such as annual growth rate of trees and coral reefs are also significant for inferring past climatic variability (Horel and Geisler, 1997; Kirchhefer, 2001); and the composition of biological and chemical proxies in stratigraphic sequences of lake sediments has now become increasingly useful for palaeoclimate research. Particularly, methods used in lacustrine proxy records such as site selection and sampling techniques for palaeoclimate research have been improved significantly (Lotter and Lemcke, 1999). Proxy records from annually laminated sediments of lakes are especially useful as they provide a more reliable chronology for climatic events in the past (Brauer et al., 1999, Brauer and Nagendank, 2002). However, annually laminated sediments are rare in mountain lakes. In recent years the proxy records from non-laminated sediments of lakes have also been used for high-resolution palaeoclimate research (Birks, 1998). Due to the development of powerful multivariate techniques such as transfer function (Birks, 1995; Battarbee, 2000), non-laminated sediment cores can also be used for palaeoclimate reconstructions.

Transfer function requires the development of a calibration training set, which describes the relationships between species and their environment (e.g. climate). Such relationships are usually shown by unimodal or Gaussian response models (ter Braak and Juggins, 1993) and tested with powerful statistical techniques such as Monte Carlo permutations tests (Manly, 2000). The species optima or tolerances with respect to temperature are estimated with a variety of regression techniques (ter Braak, 1987). These also include other robust statistical procedures for cross validation and error estimations and are now successfully used for palaeoclimate research (Birks, 1995) such as reconstruction of the past air temperature (Lotter et al. 1997) and surface water temperature (Walker et al., 1991).

1.4 Lakes: an important archive for paleoclimate research

In recent years, lakes have been found to be excellent sources for palaeoclimatic studies on a large range of time-scales (Lotter et al., 1992; Peck et al., 2002) since they are able to archive a high-resolution record of trace materials deposited from the atmosphere, and inorganic and organic components originating within the lake itself and from their catchments (Battarbee, 1991). In many lakes, the sediment accumulation rate is rapid (>1mm per year) and sediment cores collected from such lakes can be sub-sampled for high-resolution palaeodata (Battarbee, 2000; Peck et al., 2002). Zolitschka & Negendank (1999) argue that lacustrine records are often found to provide annual resolution (varves), which are rarely obtained in marine sediments. Varved sediments in the marine environment can form mostly in oxygen minimum zones with high sedimentation rates (Zolitschka, 2003).

Many types of lakes can be used for studying climate change (Battarbee, 2000). Most closed basin or salt lakes, with relatively high evaporative rates and water-level fluctuations, have sediments suitable for reconstruction of climate change through changes in salinity, water-level and variations in stable isotopes (Battarbee, 2000). For open basins or freshwater lakes, climate reconstruction from sediment records, are more indirect based on changes in acidity and productivity from the large range of microfossils and macrofossils that are preserved in lake sediments. High mountain lakes, which especially contain a wide range of chemical and biological proxies (Guilizzoni et al., 1996), have become excellent sensors for climate change research (Lotter et al., 1997; Marchetto, 1998; Battarbee et al., 2002b).

1.5 Mountain lakes and their sensitivity to climate change

Mountain lakes are appropriate for climate change studies as they are often remote and relatively undisturbed by human impacts (Battarbee, 2000). Moreover, recent limnological and palaeolimnological investigations in these lakes have shown their strong sensitivity to climate change through patterns of ice cover, seasonality, stratification, hydrology, biogeochemistry and biological communities (Flower et al., 1990; Hauer et al., 1997; Lotter et al., 1997; Amman et al., 2000; Hofmann, 2000; Ventura et al., 2000; Catalan et al., 2002b; Stefanova et al., 2003).

1.5.1 Limnological sensitivity and climate change

In comparison to other mountain lakes, European mountain lakes have been studied more intensively to understand their response to climate change (Battarbee et al. 2001a; Agusti-Panareda and Thompson, 2002; Battarbee et al., 2002a & b; Korhola et al., 2002a). Mountain lakes freeze over during winter and British and Scandinavian lakes, in particular, receive increased amount of solar radiation during summer due to longer light hours, which have a subsequent influence on growing seasons (Sommaruga and Psenner, 1997; Sommaruga et al., 1997). Global warming can decrease the patterns of ice-cover in these lakes (e.g. Schindler, 1997), and increased temperature during summer also influences the patterns of stratification and in particular causes thermoclines to deepen, particularly in small lakes (Schindler, 1997). As a result, an enlargement of metalimnetic and shrinkage of hypolimnetic habitats of aquatic communities occurs (Pompilio et al., 1996; Schindler, 1998). The thickness of the epilimnetic layer is also ecologically significant because it determines, in part, the photosynthetically available irradiance and dissolved oxygen conditions in the mixed layer (Fee et al., 1996; Pompilio et al., 1996). However, most coastal mountain lakes in northwest Scotland and Norway experience mild winters and strong winds. As a result, stratification becomes less strong due to mixing. Ice-cover also decreases significantly due to mild winter weather conditions and further results in an increase in the length of the growing seasons. The major consequences of these impacts are considered to be on the loss of habitats to vertically migrating flora and fauna (e.g. Catalan et al., 2002b). Variation in patterns of ice cover also has impacts on the hydrology of these lakes (e.g. Hauer et al., 1997). Webster et al. (1996) reported that climate change could result in changes to either wetter or drier conditions and in hydraulic properties and hydrologic

flow paths of lakes. Increased evaporation during warm seasons can reduce the flow of streams in lake catchments and thereby influence the residence time of the water and the flux of allochthonous inputs to the lake (Carpenter et al., 1992; Schindler, 1998). However, low altitude lakes of Northwest Europe do not receive snow thereby differences in temperature between summer and winter is low. During colder seasons, mountain lakes can be influenced by increased precipitation (Busuioc et al., 2001), and the patterns of changes in the ecology of the most Northwest lowland mountain lakes could occur via changes in hydrology, water level fluctuations and the catchment dynamics (e.g. George et al., 2004).

Changes in climate can also influence mountain lakes indirectly by changing nutrient and acidity balances. Nutrient concentrations in mountain lakes vary with respect to the nature of the catchments (Kopáček et al., 1996 a&b; Kopáček et al., 2000; Korhola et al., 2000) and climate forcing (Catalan et al., 2002a). For example, in many European mountain lakes, important indicators of lake productivity such as elementary nitrogen and total caretonoids have been found to vary significantly with recent climate change (Catalan et al., 2002a). Similarly, the high values of sulphur in late 20^{th} century have also been been reported due to the effects of climate warming and the biogeochemical cycle of the lake (Catalan 2002a). During dry periods, particularly in droughts, sulphur stored in the upper areas of the littoral zone can be re-oxidised, causing lakes to re-acidify (Psenner and Schmidt, 1992; Yan et al., 1996; Dillion & Lazerte, 1992). Smaller streams may also dry out and chemical inputs from the catchments are reduced resulting in fluctuation of the water chemistry in the lake (Schindler, 1997; Schindler, 1998). However, elevated water temperature increases the decomposition rate of organic compounds resulting in an increased CO_2 in the water column and decreased alkalinity, which in turn results in a greater seasonal fluctuation of pH (Psenner & Schmidt, 1992). These processes may not operate in the same way in Scottish and Norwegian mountain lakes where increased precipitation may be important by causing a decrease in alkalinity through dilution of base flow (Monteith et al., 2000).

1.5.2 Climate reconstruction using proxy records

Many limnological parameters of mountain lakes are sensitive to climate change. However, good quality monitoring records of both limnological and climatic variables are generally short in time-scale. Therefore to reconstruct these variables over a longer

timescale requires the analysis of proxy records in the sedimentary archives (e.g. Smol et al., 1991; Battarbee, 2000).

Sediment proxies in mountain lakes are important for reconstructing climate change since they can provide insight into the response of ecosystems to natural and anthropogenic disturbances (Zolitschka & Negendank, 1999). For this, a range of different techniques can be used.

Stable isotopes (e.g. $\delta^{18}O$ and $\delta^{13}C$) and geochemistry (e.g. Mg and Sr) have been increasingly used for climate reconstruction in recent years (Schwalb & Dean, 2002; Dean, 2002; Baier et al., 2004). Composition of stable isotopes derived from freshwater ostracods and diatoms, in particular, has been popular in palaeoclimate research. Schwalb and Dean (2002) reported that ratios of the stable isotopes of oxygen and carbon in benthic ostracods of lakes in north-central Minnesota are able to reflect the Holocene hydrological and vegetation changes. Oxygen isotopes were important for indicating the past hydrological regimes of the lakes, while the carbon isotopes were crucial for showing past vegetation changes in lake catchments (Schwalb and Dean, 2002). Rioual et al. (2001) used the oxygen isotopic composition in freshwater-diatom biogenic silica ($\delta^{18}O_{si}$) to reconstruct temperature variability of the last interglacial period of a south-western European lake, and found that the diatom silica was a significant indicator of interglacial climatic variability. Hu and Shemesh (2003) reported that the oxygen-isotopic composition in diatom silica increased from 19-25% between 12,340 and 11,000 ^{14}C cal yr BP showing marked climatic warming at the end of the last glaciation in a lake in south-western Alaska, USA. Apart from using stable isotopes from diatoms, Wolfe et al. (2001) reconstructed summer relative humidity in the Holocene using cellulose-inferred $\delta^{18}O$ in a high mountain lake (4300 masl) in Bolivia, and found a 10-20% greater relative humidity at 2000 cal yr BP than at present. A recent investigation of the sedimentary and geochemistry data from a lake in the Andes, Bolivia suggests that the stable isotopes have significant potential to reflect the Holocene palaeohydrology and glacial history in the region (Abbott et al., 2003).

A variety of biological proxies in mountain lakes have also been used for inferring climate change. These mainly include diatoms, chrysophytes, chironomids and Cladocera (Lotter et al., 1997; Korhola, 1999; Brooks & Birks, 2000; Pla et al., 2003; Stefanova et al., 2003). Most of these proxies are widely distributed, well preserved,

and most have well defined taxonomy (Battarbee et al., 2001b, Korhola et al., 2000, Walker, 2001; Zeeb & Smol, 2001). Recently, Bigler & Hall (2002) have developed a diatom-based mean July air temperature transfer function (RMSEP = 0.96 ^{0}C) from a training set of 100 lakes located across a wide range of altitudes in north Sweden. Chironomid-based temperature transfer functions have become increasingly robust since they are found to respond to climate change (Walker et al., 1991). For example, by using chironomid fossil remains Porinchu & Cwynar (2002) discovered the late-glacial warming in Siberia disrupted by a marked cooling event. Pla (2001) reported the value of chrysophyte cysts as an important indicator of climate change in European mountain lakes. Recently, cladoceran microfossils have also become an important proxy indicator for reconstructing past climate change (Lami et al., 1996, 1997). Cladoceran zooplankton are distributed across lakes with wide climatic gradients and with variable microhabitat structures. They also have a short generation time and thus are able to react faster to environmental change than terrestrial vegetation such as trees and shrubs (Lotter et al., 2000a). Modern surface sediments provide material for the construction of quantitative cladoceran training sets, and these show that these animals have considerable potential as quantitative climate indicators (Lotter et al., 1997; Korhola, 1999; Ammann et al., 2000; Duigan and Birks, 2000; Korhola and Rautio, 2001).

1.6 Living and fossil Cladocera

Cladocera are one of the important groups of the branchiopod Crustaceans consisting of 11 families, 80 genera and 400 species worldwide (e.g. Hanner, 1997; Appendix 1.1). Cladocerans, commonly called water fleas due to their small size and jerky swimming motion, thrive in most freshwater habitats including the open water, profundal or littoral zone. The body of a Cladocera is a completely enclosed by an uncalcified shell (or carapace) and has 9 or 10 pairs of appendages (antennules, antennae, maxillae and mandibles attached to the head), and five or six trunk limbs, which are using for feeding and respiration. The body (abdomen) ends with the postabdomen, which has a series of denticles along the dorsal margin, lateral setae and a terminal pair of postabdominal claws. The unhinged shell is attached to the headshield. The headshield-shell junction constitutes the ecdysial line, which spreads apart at molting. They can range in size from 0.3mm to 6mm. All the species mature through a series of juvenile stages (or instars), gradually becomes larger at each molt.

They have global significance for environmental change research due to their well-defined taxonomy, life history behaviour and wide ecological preferences as well as preservation of their fossil remains in lake sediments (Korhola & Rautio, 2001; Sacherova and Hebert, 2003). Remains of some cladoceran species are composed of chitin, a resistant compound that enables preservation in sediments. Mainly ephippia, mandibles, headshields, shells and postabdomens and their claws are commonly preserved quantitatively in lake sediments. Ephippia are commonly preserved as fossils as far back as the Oligocene and probably from the Cretaceous.

1.6.1 Life history and food habit

Temperature plays a profound role on the life history behaviour of Cladocera. Adult Cladocera females produce a large number of parthenogenetic females during spring (Allan, 1976; Frey, 1982). However, under adverse climatic conditions, such as threatened drying up of ponds, limited food and oxygen resources, diploid males are produced parthenogenetically. Then females change their reproductive state and produce haploid resting eggs. The haploid eggs are fertilized with haploid sperm a process called gamogenesis (Allan, 1976; Frey, 1982; Korhola & Rautio, 2001; Duigan 2001; Figure 1.1). Gamogenesis is essential for Cladocera particularly in high mountain lakes of temperate regions (e.g. Sarmaja-Korjonen, 2003). Because of the short summer in these lakes, Cladocera adopt a reproductive strategy for producing ephippia, usually in July that continues through ice-free seasons (Frey, 1982). Resting eggs also have the inherent capacity for dispersal and are protected from physical, chemical, and biological pressures (Carter et al., 1980). Cladoceran ephippia are small (50-500 μm) in size, depending on species. By virtue of being resting stages, they can easily be transported through river connections, lake systems and other passive transport mechanisms such as by birds, mammals and insects and by wind (Maguire, 1963; Figuerola & Green, 2002). As a result, they are distributed widely and occur in many microhabitats (Allan, 1976).

Cladoceran communities are patchily distributed in space between lakes. Species-specific preferences for physical, chemical and structural variables are the main reasons of patchiness (Williams, 1982). Some species of Cladocera are predominantly limnetic filter feeders consisting of the genera *Bosmina, Daphnia, Ceriodaphnia* and *Diaphanosoma*, primarily feeding on small phytoplankton, bacteria and detritus. Limnetic predators such as *Leptodora* and *Bythotrephes* feed mostly on smaller

zooplankton (Frey, 1986). The other group of littoral specialists, mostly chydorids, are chiefly associated with shoreline and bottom macrophytes, sands, mud and gravels, feeding mainly at the substrate-water interface where they obtain food by scraping algae and detritus from surfaces over which they crawl or from sediments in which they burrow (Fryer, 1974; Frey, 1976; Frey, 1986; Whiteside and Swindoll, 1988). Some littoral specialists such as, *Sida*, *Simocephalus*, *Scapholoberis* and *Ceriodaphnia* are filter feeders and others, such as *Polyphemus* are predators (Frey, 1986).

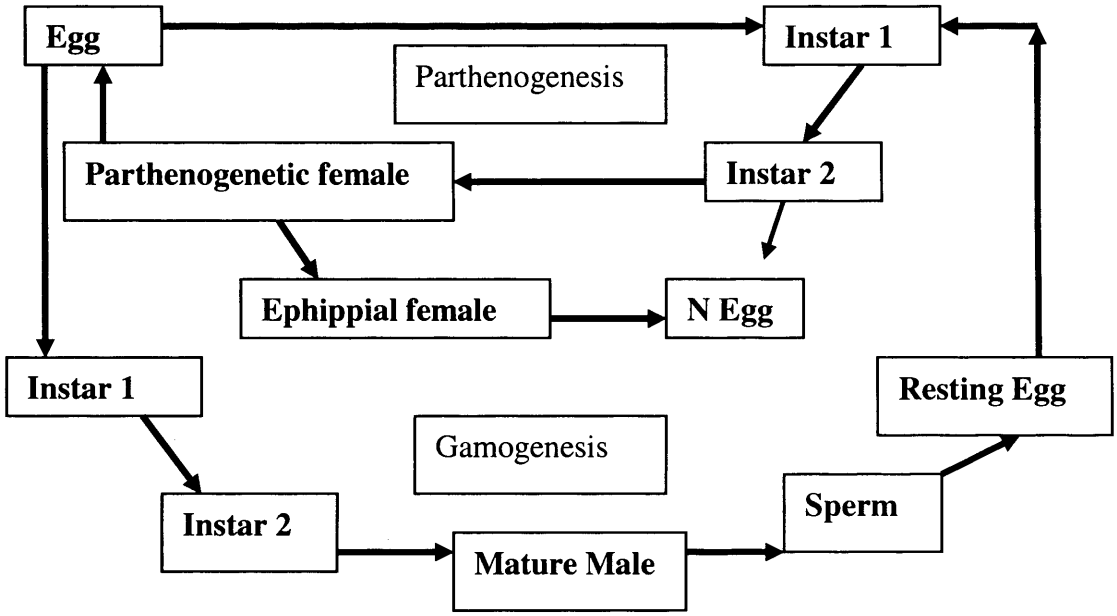


Figure 1.1: The lifecycle of Cladocera (www.cladocera.fsnet.co.uk/lifecycle.htm)

1.6.2 Cladocera fossil remains

The significance of Cladocera on global climate change studies has increased noticeably once Frey discovered the preservation of their remains in the sediment after moulting and death (Frey, 1958). Frequently, many species of planktonic and littoral Cladocera, at death and moulting are disarticulated into component pieces such as headshield, shell, post-abdomen, post abdominal claws, antennules, antennel segments, mandibles, and portions of trunk limbs (Frey, 1976; Frey, 1986; Korhola and Rautio, 2001). Particularly, the remains or exuviae of families Chydoridae and Bosminidae are well preserved quantitatively except for a few instars (Harmsworth, 1968; Frey, 1976; Frey, 1986; Korhola and Rautio, 2001). However, for the family Daphnidae, only the mandibles, post-abdominal claws and ephippia are preserved although sometimes also the distal part of the post abdomen and the filter combs of trunk limbs III-V are preserved (Frey, 1976). Those individuals that produce gametes also contribute

ephippia, copulatory hooks and specialized headshields and post-abdomens (Frey, 1986). After a significant amount of effort by Frey and many other scientists in Europe and North America, important keys for collecting and analysing sediment and identifying fossil Cladocera up to species levels are now available (Frey, 1958; Whiteside et al., 1978; Frey, 1986; Korhola & Rautio, 2001; see also Appendix 3.1). As a result, the assemblage structure of these microfossils has become an important indicator for inferring past climate change.

1.7 Response of Cladocera to global climate change

The potential of Cladocera in reconstructing global climate change can be assessed from how sensitively they respond to major climatic oscillations in the past such as the late-glacial or the Holocene periods (Hofmann, 1993) and more recently the twentieth century human-induced warming. Chydorids and Bosminids, in particular, are reported to be the best indicators among cladoceran fauna for global climate change (Whiteside, 1970; Frey, 1986; Lotter et al., 1997; Korhola, 1999) since these animals are sensitive to a variety of environmental stresses in lakes located along wide altitudinal gradients (Fott et al, 1992; Fott et al., 1994). High mountain lakes preserve remains of these animals in the sediment for long periods (De Costa, 1968; Manca & Comoli, 1995).

However, precautions are needed while studying Cladocera fossil remains in mountain lakes. Sometimes, Cladocera can have a lagged response to environmental change, and other independent climate proxies may be required to support interpretation of climate reconstruction (Lotter et al., 2000b). In addition, sedimentation processes such as mixing, transportation, resuspension, bioturbation and diagenesis can have significant effects on death assemblages of Cladocera (Korhola, 1999) thereby resulting in variation in distribution and homogenisation of fossil remains, and such processes need to be taken into account while interpreting the results (Anderson & Battarbee, 1992).

Thus understanding the response of Cladocera to climate change can be assisted by various studies such as seasonal surveys of Cladocera populations, their taphonomy and using the transfer function approach. Contemporary surveys of Cladocera provide information on community structure and autoecology, while taphonomic studies provide data on their representation in the sediment and the subsequent use of these data in biasing climate reconstructions. The use of transfer functions is one of the best

approaches to interpret the response of fossil Cladocera to global warming. This approach has a number of advantages: it can be used to reconstruct climate change over long time-scales (Lotter et al., 1997); it is statistically robust (Birks, 1995) and can also be compared with instrumental records if the reconstruction has been made over the last 200 years (Battarbee et al., 2001a). Comparative analyses of other biotic groups including diatoms, macrophytes, ostracods and chironomids and their relation to climate change are also equally useful while interpreting the results (Fritz, 1996; Duigan & Birks, 2000; Korhola & Rautio, 2001; Battarbee et al., 2001b).

1.7.1 Temporal and spatial dynamics of contemporary communities

The seasonal dynamics of the contemporary community structure of Cladocera have been reported to be one of the significant indicators of recent climate change in Arctic and alpine lakes (Hauer et al., 1997; Stemberger et al., 1996; Rouse et al., 1997). However, in order to obtain a strong response to climate change, the research lake should be located in such an area where climate is the major forcing factor for ecosystem processes (Rouse et al., 1997) and at least inter-annual or decadal scale seasonal data for Cladoera are essential (Gerten and Adrian, 2000; Ventura et al., 2000).

Mountain lakes, close to the ocean tend to respond to climate through seasonal changes in thermal regimes in a way that influences the community structure of Cladocera. For example, the NAO and El Niño have been shown to cause significant seasonal variations on a range of time-scales among zooplankton populations in northern Europe and America (Stemberger et al., 1996; Gerten and Adrian, 2000). A direct response of NAO-induced climatic variability on seasonality of northwest European mountain lakes has been observed through significant changes in air temperature gradients (George & Winfield, 2000). The surface water temperature of a lake is the main parameter, which has major direct impact on lake ecosystems (Battarbee et al., 2002b), since the surface water temperature is significantly associated with atmospheric air temperature (Livingstone & Lotter, 1998), particularly in lakes that do not freeze during winter (George et al., 2000). The indirect response of NAO-associated climate change on seasonality, however, occurs via changes in precipitation, riverine runoff, snowfall and snow-pack accumulation and evapo-transpiration of lake-water (Clair & Ehrman, 1996; George et al., 2000). The NAO has a significant impact on the patterns of zonal and meridional heat and moisture transport. As a result, changes in temperature and

precipitation patterns occur across northern Europe. The prolonged positive index of NAO over recent decades is associated with above normal temperature and precipitation enhancing the riverine runoff and ice-melting. Changes in wind speed and direction are also associated with climate change in northwest Europe and can play an important role in lake ecosystems (Battarbee et al., 2002b). Recent investigations show that the mean precipitation is significantly higher (upward shift) for spring and autumn compared to summer (August) in many part of northwest Europe for the last decade or so (e.g. Busuioc et al., 2001; Fowler & Kilsby, 2002). Because of exposure to rapid seasonal and interannual variations in weather patterns, most northwest European mountain lakes experience changes in the timing and intensity of thermal stratification, ice-cover, turbidity and light penetration (Catalan et al., 2002b). If such changes in weather patterns are sustained over longer time-scales, changes in microhabitat types will occur and cause shifts in aquatic biota.

The structural variables, or microhabitat types, in particular, are severely influenced by climatic events, such as high precipitation and floods. As a result, most northwest European mountain lakes experience variations in habitat structure, especially the balance between stony, sandy, macrophyte and open-water habitats. For example, sand, silts and clay washed into lakes by rivers can form deltas, which can become a preferred microhabitat type for certain groups of Cladocera (Tremel et al., 2000). Such littoral substrata may soon become colonised by submerged macrophyptes and may be favoured by other groups of Cladocera (Whiteside et al., 1978). Increased precipitation in catchments can also cause changes in biological, chemical and hydrodynamic conditions in lakes, which in particular have significant effects on planktonic Cladocera through lake-level changes or variations in depth.

Lake depth determines biological activities along vertical gradients of the open-water habitat (Fee et al., 1996). Most clear-water lakes absorb higher amounts of sunlight and temperature for photosynthesis causing increased growth and reproductive activity of phytoplankton and zooplankton (Leibold, 1990). Climate change in northwest Europe has noticeable effects on the mixing depths in the planktonic habitat during summer (George et al., 2000). The mixing layer is very dependent upon NAO-induced weather patterns such as variations in rainfall and wind, which usually induce variations in plankton biomass. Shallow littoral marginal habitats of mountain lakes may, however, have lower biological activity than open-water habitats since the dynamics of

macrophytes along shorelines of these lakes are minimal. Shoreline habitats composed by rocks and boulders, often slope steeply (Rasmussen, 1988), and are not as suitable as macrophytes and sand for colonisation by littoral biota.

Some species of Cladocera predominate in open water conditions (Frey, 1986) while others live in weed, sand or gravel along littoral or sub-littoral margins (Goulden, 1971; Fryer, 1974). As temperature has a large influence on reproduction (Whiteside, 1974), temperature changes on a longer time-scale will cause changes in life history behaviour and zoogeographic patterns of these fauna. Chen and Folt (1996) found that autumn warming altered the life history behaviour of *Daphnia catawba* in a temperate lake. The *Daphnia* populations produced from sexual reproduction switch to asexual reproduction. As a result, the production of resting eggs is delayed, and the number of resting eggs reduced dramatically, disrupting the life-history stages of *Daphnia* (Chen and Folt, 1996). Similarly, Keen (1973) studied seasonal variations in the population dynamics of Chydorid Cladocera in a North American lake, Lake Lawrence, Michigan, and showed that the population size of the various species of Chydorids was lowest during summer, which was thought to be related to variations in species-specific response to summer temperature for hatching (Keen, 1973). Loss or modification of microhabitats due to seasonal variations in climate warming or cooling would also influence reproductive cycles and food habitats thereby changing the patterns of assemblage structure of Cladocera between seasons (Rouse et al., 1997).

Two groups of planktonic Cladocera (Bosminidae and Daphnidae) predominate in planktonic habitats of many Scottish lochs (Maitland et al., 1981). They can have trade-offs along vertical and horizontal gradients for food resources, predator avoidance and reproduction (Smiley and Tessier, 1998; White, 1998). The littoral Cladocera, mainly Chydoridae are found to use substrate-water interfaces such as muddy, vegetated zones or sandy and boulder substrata (Rasmussen, 1988; Tremel et al., 2000). Some species of littoral chydorids are also reported to occur in the plankton for predator avoidance and food resources. Many taxa within littoral families may differ greatly with seasons and habitat types (Whiteside, 1974; Whiteside et al., 1978). In the family Chydoridae, taxa such as *Alona rustica* and *Eurycercus lamellatus* prefer macrophyte and weedy substrata, while other taxa such as *Rhynchotalona falcata*, *Monospilus dispar* prefer sandy substrata and taxa such as *Alona rectangula* and *A. elongatus* prefer habitats with firm bouldery substrata (Frey, 1986; Dole-Oliver et al., 2000). Some taxa such as

Acroperus harpae and *Alona quadrangularis* prefer diverse habitat types (Fryer, 1993; Dole-Oliver et al., 2000).

1.7.2 Taphonomy

Over recent decades interest in taphonomy has increased since both neoecologists and palaeoecologists are interested in working together to reconstruct rapid climate change (Behrensmeyer and Kidwell, 1985). In palaeoecology, the term 'Taphonomy' (Gr. *Taphos*, burial; *nomos*, law) is the transit of organic remains from the biosphere to lithosphere and involves an understanding of the manner and cause of death of organisms, the process of decay and decomposition, transportation and burial of fossils, and the diagenesis of remains.

Since Efremov (1940) highlighted the importance of taphonomy, several authors have studied the implications of taphonomy on palaeoecological research on various organisms in aquatic and terrestrial environments (e.g. Behrensmeyer and Kidwell, 1985). A number of studies have been carried out on taphonomy of diatoms and its relevance to understand lake acidification in the past (Jones and Flower, 1986; Flower, 1993; Cameron, 1995), but the taphonomy of Cladocera and its significance on past climate change in mountain lakes is virtually unknown.

The exuviae generated by each species of Cladocera are well preserved in lake sediments (Frey, 1976; Frey, 1986; Whiteside and Swindoll, 1988; Hofmann, 2000; Korhola & Rautio, 2001). The preservation of fossil remains in the sediment is considered to be dependent on the content and type of chitin present in the cladoceran exuviae. Chitin is very inert chemically, though all Cladocera may not be equally resistant to biodegradation (Korhola and Rautio, 2001). Deevey (1964) argued that if the crystalline structure in the chitin polymers in the cladoceran exuviae is hydrated, such exuviae should be relatively well preserved in the sediment. Particularly, the exuviae of families Chydoridae and Bosminidae, which are well preserved quantitatively (Harmsworth, 1968; Frey, 1976; Frey, 1986; Korhola & Rautio, 2001). However, for the family Daphnidae, only the mandibles, post-abdominal claws and ephippia are well preserved (Frey, 1976). Frey (1964) reported that the ephippia of *Ctenodaphnia* have been found as far back as the Tertiary and perhaps Triassic period.

1.7.2.1 Representativity studies

One of the most important aspects of cladoceran taphonomy is 'representativity', in which the taphonomy of Cladocera is addressed through a variety of statements associated with their representation in lake sediments.

Representation of Cladocera preserved in the fossil assemblages in lake sediments

This statement addresses how well the past abundance and composition of Cladocera are reflected by the fossil assemblages. One approach of estimating the representation of abundance and composition of fossil Cladocera in the past can be by radiometric dating (e.g. ^{210}Pb) of the sediment core and calculating the sediment and Cladocera accumulation rates (Appleby et al., 1990). The accumulation rate of the Cladocera fossil remains is calculated as the amount (gm) or numbers of remains accumulated in the sediment each year. For example, the accumulation rates of cladoceran remains (number $cm^{-2}yr^{-1}$) can be calculated from the number of shells per gram dry weight, the ratio of dry weight/sediment volume, and the sediment accumulation rate (Hofmann, 1986). However, it is difficult to relate the accumulation rates of cladoceran remains to past animal abundance. Kerfoot (1974) argued that accumulation rates are only indirectly related to animal abundance because of the problems of shedding of exuviae, differential transportation, and temperature-related turnover rates. The number of exoskeletons shedding from an individual Cladocera is usually uncertain. Some individuals may have increased numbers of moulting, and some may die before all moultings are completed (Frey, 1986).

A second issue is the extent to which the fossil Cladocera are assumed to have been preserved and distributed along the core sequence evenly. The composition, abundance and distribution of Chydorid Cladocera are high in lake-inshore environments since these animals commonly inhabit the shallow littoral and macrophyte dominant habitats. Bosminids and Daphnids, however, predominantly live in the offshore pelagic zone. Even though they have contrasting habitat preferences, the exoskeletal remains of both littoral and pelagic fauna are eventually transported, accumulated and preserved in the deeper sediments (Frey, 1988). The amount of transport varies with the individual characteristics of the lakes (Frey, 1986; 1988). Korhola and Rautio (2001) argued that the distribution and abundance of cladoceran remains is influenced by several *in situ* factors of the lake, including movement and mixing of sediments by burrowing organisms (e.g. bioturbation mainly from fish), lake morphology, water depth and

associated water movements. Thus caution should always be taken while interpreting the results.

Representation of Cladocera in the source communities by lake sediment assemblages
This statement relies on comparative studies between surveys of the composition of Cladocera in contemporary communities and the fossil Cladocera assemblages in surficial sediments. De Nicola (1986), Jones & Flower (1986) and Ryves et al. (2003) have successfully used this approach with diatom taxa. However, it has been rarely used in cladoceran studies. Rautio et al. (2000) attempted to compare faunistic assemblages of Cladocera between contemporary and surficial sediments in Lake Saanjärvi, Finland and found a rare representation of fossil littoral assemblages of Cladocera in lake sediments. The data were derived from only two sediment sub-samples, which may have been the reason for the rarity (<3%) of littoral fauna in the community rather than the lack of littoral macrophytes (Rautio et al., 2000). An increased number of spatial samples associated with the littoral micro-habitat types of a lake would answer the question of how littoral Chydorids are represented in the fossil community. Studies have shown that samples of surficial offshore sediments yielded the same percentage composition of individual chydorid species suggesting that littoral chydorid Cladocera become integrated by species before they are incorporated in the sediments (Frey, 1986; Frey, 1988).

Representation of Cladocera with respect to spatial variability in surficial sediments
This statement addresses the effectiveness of fossil representation due to the position of the core. Frey (1986) argued that a single offshore core taken from the deepest point of the lake could be adequate to reconstruct environmental change over time from the proportional representation of chydorid species. However, it cannot be assumed that the composition of fossil Cladocera assemblages is uniform across the basin. Bradbury and Winter (1976) examined variations in the diatom composition of the surface sediment along transects in Lake Sallie, Minnesota and showed that diatom valves were preferentially deposited in the area of their living habitats. As for diatoms, the Cladocera, particularly Chydorids, have diverse preferences for microhabitat types such as macrophytes, sandy and stony shoreline habitats. Thus the compositions of the surface sediment assemblages are likely to reflect the micro-habitat types where littoral Cladocera are living. Little research has been conducted to assess the relationship between the composition of Caldocera in sediment cores and their sources though it is

generally assumed that littoral taxa are transported efficiently to the central parts of lakes from which sediment cores are usually taken and they are treated as representatives of the living community of those lakes (e.g. Frey, 1960; Goulden, 1964; Goulden, 1969; Frey, 1986).

In order to test the 'representativity' hypothesis various authors used a number of different approaches on a variety of lake biota. Mueller (1964) studied the variability in population size of fossil Cladocera in surface sediments along transects of three lakes in northern Indiana. He found that microfossil populations were randomly distributed in the sediments. Battarbee (1979) presented an approach in which the species representativity of diatoms was assessed by comparing a sediment core with data from old algal samples. However, this approach was found to be limited due to taxonomic inconsistencies between sediment samples and algal collections. DeNicola (1986) described a new method to assess diatom representativity of fossil assemblages in two North American lakes using seasonal and spatial data for living diatom communities. The approach was found to be realistic in only one of the lakes studied in which the sediment assemblage was similar to the epipelic diatom community. Jones and Flower (1986) used a similar approach in an acidified Scottish loch. They suggested that the surface sediment was considered to provide a good record of the floristic composition of the non-planktonic diatom communities. Cameron (1995) compared fossil diatom assemblages in recent sediments of a Scottish loch with its contemporary diatom flora collected from source communities and sediment traps. He found that changes in the living community were similar to those in the sediment traps, but the response of sediment cores was delayed. He argued that the time-averaging process was the main cause of the apparent lag in the core response. Rautio et al. (2000) also reported that the dominant cladoceran taxa found in living communities also occurred in sediment traps, but were absent in the sediment core itself. Recently, Ryves et al. (2003) reported that fundamental taphonomic change occurs in diatom communities while transporting from water column to the surface sediments of Lake Baikal. They argue that about 99% of planktonic diatoms do not preserve into the sedimentary assemblages of Lake Baikal. Similarly, Kato et al. (2003) estimated the annual fluxes of marine planktonic diatoms, in which fluxes from the surface sediments were much smaller than the annual sinking flux calculated from the trap samples. They argued that the major loss of diatom frustules occurred at the sediment-water interface. It can therefore be argued that the abundance and composition of microfossils are a biased reflection of the living

communities from which they were derived and the taphonomic processes should be taken into account when quantifying palaeoecological reconstructions.

1.7.2.2 Taphonomic processes

The understanding and use of fossil assemblages in lacustrine environments require a thorough knowledge of the effects of taphonomic processes such as the transfer of materials from the source communities, the transportation mechanisms in the water column, and deposition processes in the receiving basin (Chumra et al., 1999). The spatial distribution and preservation of these 'taphofacies' is related to a variety of environmental factors such as the micro-habitat types of the source community, water depth, sediment types, degree of exposure of fossils and geochemical processes of lake sediments (Powell et al., 2002). In particular, the lake water depth and types of organic matter present in lake sediments influences variations in fossil assemblages due to changes in lake morphometry and sediment focusing (Blais & Kalff, 1995) while micro-habitats of the living communities influence the composition of fossil assemblages before being reworked by water currents. For example, Sherrod (1999) reported that epipsammic diatoms are often scoured off the substratum by currents and transported into adjacent environments. Consequently high-energy systems can physically activate the remains before incorporation into the sediment records. Charles (1985) also highlighted the role of lake morphometry on the type and relative size of specific diatom habitats. As for diatoms, taphonomic processes can also alter cladoceran fossil representation in lake sediments and bias the current relationship between species and environmental variables. In such processes, species can be selectively removed due to breakage or dissolution by various abiotic and biotic means or transported by water currents, and eventually this provides insights on the reliability of climate reconstructions when using transfer functions approach.

1.7.3 Transfer functions approach to reconstruct past climate change

Sediment cores taken from the deepest point of the lake contain diverse remains of littoral and planktonic Cladocera (Frey, 1986; Korhola and Rautio, 2001). The fossil remains of these Cladocera are potentially important for reconstructing surface water temperature since it is significantly correlated with atmospheric temperature in mountain lakes (Livingstone & Lotter, 1998). Such reconstructions can be either direct (e.g. temperature), where the temperature optima for Cladocera are known or indirect,

where the variables such as pH, water levels, trophic structure and lake stratification are greatly dependent on climate (Battarbee, 2000). In recent years, palaeolimnologists have been successful in developing both direct and indirect approaches of climate change reconstruction using fossil Cladocera as an indicator.

1.7.3.1 Direct approaches

The direct reconstruction of climate change using a variety of microfossils in mountain lakes has been pioneered by the latest developments of statistical inference models such as weighted averaging-partial least squares regression (WA-PLS) (ter Braak, 1987; Walker et al., 1991; Birks, 1995; Lotter et al., 1997; Bigler & Hall, 2002); and has been successfully used to show the response of fossil Cladocera to global warming (Lotter et al., 1997, Korhola, 1999; Ammann et al., 2000).

The use of cladoceran microfossils to reconstruct temperature began in the 1950s. Using Poisson distributions, Megard (1967) reconstructed the climate of a montane lake, Lake Zeribar (1300m a.s.l.), Iran, using both planktonic and littoral cladoceran fossil remains. He argued that the fauna prior to 12,000 years ago was similar in several ways to the fauna in Alleröd lake sediments in Germany and England, thus implying cool temperate climate in the vicinity of Lake Zeribar during the late Pleistocene. The replacement of northern species by southern species between 12,000 and 5,000 years ago indicated a gradual warming but, the temperature probably never became higher than today (Megard, 1967).

Different species of Cladocera are reported to have different temperature optima and tolerance ranges (Hofmann, 2000). Chydorids, in particular, showed a clear response to climate change occurring at the end of the Younger Dryas through characteristic shifts in species composition and diversity (Hofmann, 1993). In the Younger Dryas the fauna was composed of cold tolerant species that at the present time are predominant in Arctic and sub-Arctic conditions, while in the Holocene this assemblage was replaced by less cold-tolerant species that at present predominantly occur in the temperate zone (Hofmann, 1993).

Cladocera often show species-specific response to climate change with respect to their microhabitat preferences (Mezquita and Miracle, 1997). For example, Lotter et al. (1997) studied 68 small lakes between 30-2350m a.s.l. in Switzerland. They included

43 environmental predictors such as physical limnology, geography, catchments characteristics, and climate and water chemistry of these lakes using various microfossil indicators including cladocerans. Using the unimodal multivariate analysis, canonical correspondence analysis (CCA) and Monte Carlo permutation tests, they showed that mean annual temperature is the best predictor for benthic cladocerans while spring temperature is the best predictor for planktonic cladocerans. Further, their temperature inference model suggests that compositional assemblages of planktonic cladocerans were significantly related to climate change. However, they argued that there are no true stenotherms among the chydorids, which could be used as indicators. Further they recommended that both quantitative and qualitative palaeoecological interpretations should not be based on single taxa but on the overall structure and composition of the assemblage, e.g. species diversity and presence/absence of temperate species.

Korhola (1999) studied cladoceran-inferred temperature reconstruction using the surface sediments of 53 small subarctic lakes in Finland. A constrained redundancy analysis (RDA) and associated Monte Carlo permutation tests indicated that maximum lake depth, sediment organic content, epilimnetic summer temperature, lake perimeter and lake catchment area made significant contributions to the variation in cladoceran assemblages. Quantitative inference models were developed for mean July water and air temperature using the partial least squares regression (PLS) model. The PLS model produced a low mean square error of prediction (RMSEP), as assessed by jack-knifing, of 1.19 ^{0}C for the Cladocera water temperature dataset, but the cladoceran assemblage showed a weak relation to mean July air temperature. Overall results suggest that cladoceran communities have considerable potential as quantitative indicators of temperature changes.

Similarly, Lotter et al. (2000a) applied linear and unimodal-based inference models (PLS, WA, WA-PLS) to a high-resolution cladoceran stratigraphy from Gerzensee, Switzerland, to reconstruct mean summer temperatures. Climate change was investigated for the Alleröd, the Younger Dryas, and the Pre-Boreal periods looking at the characteristic major and minor oscillations (Gerzensee oscillation, onset and end of Younger Dryas stadial, and the Pre-Boreal oscillation). It was reported that the cladoceran-inferred reconstruction suggests generally warmer summers in the Alleröd. They found that Alleröd summer temperatures ranged between 11 and 13 ^{0}C and also

suggested a drop of 9-10 ^{0}C at the beginning of the Younger Dryas. During the Pre-Boreal, cladoceran-inferred summer temperatures were up to 14-15 ^{0}C.

Ammann et al. (2000), who used a multi-proxy approach, including Cladocera, outlined responses to rapid climatic changes around the Younger Dryas and reported that the responses of plant and animals to climate change were species specific, and were dependent on changes in individuals (e.g. productivity and phenology), populations (e.g. population dynamics), spatial distributions (e.g. migrations) and ecosystems (e.g. trophic state) respectively.

1.7.3.2 Indirect approaches

As indicated earlier, mountain lake ecosystems are complex, where climate plays an important role in catchment dynamics, ice-cover, physico-chemistry, evaporation, stratification and water-level fluctuations. Climatically-induced lake level changes in the past have been identified by lithological and biostratigraphical studies of sediment cores using macrofossils and aquatic pollen. However, in recent years, reconstruction of some important parameters such as pH, alkalinity, nutrients and water levels have been successful using a range of biological communities including fossil Cladocera (Sarmaja-Korjonen & Alhonen, 1999; Battarbee, 2000).

pH and alkalinity

Variations in temperature influence lake water pH and alkalinity, and thereby influence biological communities (Psenner, 1988). But in many regions of Europe, this influence is exceeded by the effects of acid deposition. Although there have been attempts to identify the influence of temperature separately from acid deposition on diatoms (e.g. Psenner & Schmidt, 1992), this possibility has not yet been addressed for Cladocera

Nutrients and lake trophic status

Climate change can also influence the nutrient status of lakes. Again however, this influence is usually masked by anthropogenic influences especially from sewage effluences and agricultural fertilizers (Boucherle and Züllig, 1983).

Water levels

Climate change such as increased temperature and precipitation can influence the cladoceran community structure indirectly due to changes in hydrologic regimes and

lake levels (Alhonen, 1970). Increased lake level results in an increased volume of the pelagic zone allowing an enlargement of planktonic habitats (Sarmaja-Korjonen and Alhonen, 1999), and a relative shrinkage of littoral habitats (Schindler, 1998) potentially causing distinct variations in the relative abundance of planktonic and littoral Cladocera. Thus the ratio of fossil remains of planktonic/littoral Cladocera can be used as an indicator for lake-level changes in the past (Alhonen, 1970; Frey, 1988; Hofmann, 1998a). Korhola et al. (2000) studied the depth of 53 lakes that are located near the timberline in northern Fennoscandia using the Cladocera fossil remains in surface sediments. On the basis of the series of statistical approaches including constrained RDA, Monte Carlo permutation tests, and variance partitioning, they showed that maximum lake depth was the most important factor explaining cladoceran distribution. Korhola et al. (2000) used PLS regression and calibration, weighted averaging (WA) with an 'inverse' deshrinking regression, and weighted averaging partial least squares (WA-PLS) to develop quantitative inference models for lake depth.

Schmidt et al. (2000) reconstructed the past climate and lake level change using multi-proxy approaches including Cladocera at Lake Varna, a large karstic lake on the Island of Cres (Croatia). They discovered that the abundance and species diversity of the Cladocera increased from the data-set of the Younger Dryas sediment to the older Holocene sediment and suggested that it was due to increased climatic warming over the period. They argued that the littoral chydorids such as *Graptoleberis testudinaria*, *Acroperus harpae*, *Alona guttata*, *A. guttata* var. *tuberculata* and *A. rustica* are the best indicators of temperature. It was argued that the rise of the abundance of planktonic Cladocera such as *B. longispina* and *B. longirostris* in the lake during the Holocene was caused by rainfall associated lake-level fluctuations (Schmidt et al., 2000). However, a number of other factors such as the impact of predators, lake morphometry and changes in trophic status may also influence the ratio of planktonic and littoral Cladocera (Frey, 1986, Hofmann, 1996, Sarmaja-Korjonen and Alhonen, 1999). Extreme caution should therefore be taken into account while interpreting changes in the planktonic/littoral ratio over time.

Lake stratification

Increased global warming, together with increased UV radiation, may cause stronger lake stratification and an increase in the depth of epi- and metalimnetic water temperature thereby resulting in a reduction of summer hypolimnetic habitats for cold

stenotherms (Schindler et al., 1990; Schindler, 1998). If the preference of individual Cladocera with respect to epilimnetic and hypolimnetic habitats were known, a reconstruction of lake stratification might be possible using fossil Cladocera. However, studies on Cladoceran preference for lake-water column position are rare (Matsumura-Tundisi et al., 1984) and those available are mostly confined to Daphnids (Loose & Dawidowicz, 1994), whose body parts are not as well preserved in the sediment as Bosminids and Chydorids (Frey, 1986).

Ice-cover

Global warming has greater impacts on high altitude lakes, which in turn influences ice-cover (Ventura et al., 2000). Battarbee (2000) has highlighted the importance of reconstructing ice-cover in Alpine lakes. However, there have been no attempts so far to reconstruct this variable using fossil Cladocera.

1.8 Aims of study

Most European mountain lakes are highly sensitive to climate change (Psenner & Schmidt, 1992; Battarbee, 2001a; Pla et al., 2003; Stefanova et al., 2003). Recently these lakes have become focal points for researching future warming of the earth's climate (Lotter et al., 1997) since the European mountain regions, especially in the northwest, are subject not only to increasing temperature but also to changing precipitation patterns associated, for example with the North Atlantic Oscillation (NAO) and Arctic Oscillations (Delworth & Knutson, 2000; Moritz et al., 2002). It has also been argued that the NAO is linked to changes in the patterns of the THC (Delworth and Dixon, 2000) that also has an important influence on European climate. As a result, the sediment records of these lakes potentially provide a wide range of high-resolution (decadal or sub-decadal) palaeoclimate data, which are suitable for multi-proxy climate reconstructions, particularly for late Holocene climate variability such as the cold climatic episodes in the Little Ice Age and the human-induced twentieth century warming episodes (Hurrel, 1995; Battarbee, 2000; Cooper et al., 2000; Delworth & Knutson, 2000; Battarbee, et al., 2001a).

Cladocera-inferred environmental reconstructions for variables such as pH and water levels have been carried out in the past (Nilssen & Sandoy, 1990; Korhola et al., 2000). A direct Cladocera-based temperature reconstruction has, however, rarely been

attempted, although its potential for examining climate variability is becoming increasingly recognised (Duigan, 1996; Lami et al., 1997; Lotter et al., 1997; Korhola, 1999; Hofmann, 2003; Stefanova et al., 2003). Thus the general aim of this study is to examine the role of Cladocera in reconstructing climate change of northwest European mountain lakes. The specific aims are: (i) to carry out seasonal surveys of the community structure of contemporary littoral and planktonic Cladocera along various micro-habitat types in a Scottish mountain loch; (ii) to assess the cladoceran representativity in fossil assemblages by comparing the composition and abundance of Cladocera in contemporary and surface sediment samples as well as the sediment trap assemblages in a Scottish mountain loch; (iii) to assess the response of Cladocera to a range of direct and indirect climatic signals using Cladocera fossil remains across a training set of Scottish and Norwegian mountain lakes; and (iv) to generate high quality, well-calibrated Cladoceran palaeodata in a core sequence from a Scottish mountain loch and apply a transfer function model for reconstructing the summer lake surface water temperature of the loch.

1.9 Thesis outline

In chapter two, the background limnological and palaeolimnological data on the study areas are presented. In this chapter, the criteria for training-set site selection are also described. Chapter three describes field, laboratory and numerical methods. In chapter four, seasonal variations in the community structure of contemporary Cladocera along various micro-habitat types in a remote northwest Scottish mountain loch, Loch Coire Fionnaraich will be addressed. In chapter five, a detailed comparative study of the relationship between Cladocera in the surface sediments and contemporary Cladocera as well as sediment traps in Loch Coire Fionnaraich will be addressed to understand the taphonomy of Cladocera in the loch. In chapter six, variations in the modern assemblage structure of Cladoceran remains in surface sediments of selected cladoceran taxa in the training set sites of Scotland and Norway will be addressed. In this chapter, a Cladocera-inferred summer lake surface water temperature (LSWT) transfer function model will also be developed. The fossil assemblage structure of Cladocera in a core sequence will be examined in chapter seven, in which the transfer function developed in chapter six will be applied to reconstruct recent climate change in a sediment core from Loch Coire Fionnaraich. Finally, in chapter eight, conclusions and recommendations of the overall PhD study will be addressed by assessing the strengths and weaknesses of

the Cladocera inferred climate record in comparison with other multiproxy biological and instrumental records for the region.

Chapter 2

Study Areas

2.1 Introduction

This chapter describes the study areas in Scotland and Norway. Firstly, this outlines the location of a remote Scottish mountain loch, Loch Coire Fionnraich (LCFR), where the most comprehensive studies on contemporary and sub-fossil assemblages of Cladocera were carried out. The history of limnological and palaeolimnological research associated with this site and the major limnological characteristics of the site are also presented. Secondly, this chapter describes the training set sites across Scotland and Norway. The criteria for training set site selection are highlighted and the general characteristics are described. Finally, the relationships between LCFR and the training set sites and the relevance of selecting LCFR for Cladocera-inferred climate reconstruction is discussed.

2.2 Loch Coire Fionnaraich (LCFR), Scotland

2.2.1. Location background

Loch Coire Fionnaraich (National Grid Ref. NG9498/49820) is a small (area, 9 ha), oligotrophic loch, located at 57.49 ^{0}N, -5.01 ^{0}W and 235 m altitude in Northwest Scotland (Figure 2.1). The total phosphorous (TP) concentration of the loch is very low (2.5 μgl^{-1}). The lake water is dilute (mean conductivity, 24 μScm^{-1}) and acidic (mean pH 5.9). The catchment (c. 30 ha) of the loch is dominated by bare bedrock at the highest elevations and moorland vegetation elsewhere. Because of its location close to the coast, the loch is influenced by changes in the North Atlantic weather patterns.

The loch and its catchment is relatively undisturbed by anthropogenic impacts. However, a footpath crosses the catchment, sheep farming is still practised in the catchment and wild deer are also common in the area. Detailed characteristics of the loch are presented in section 2.2.5

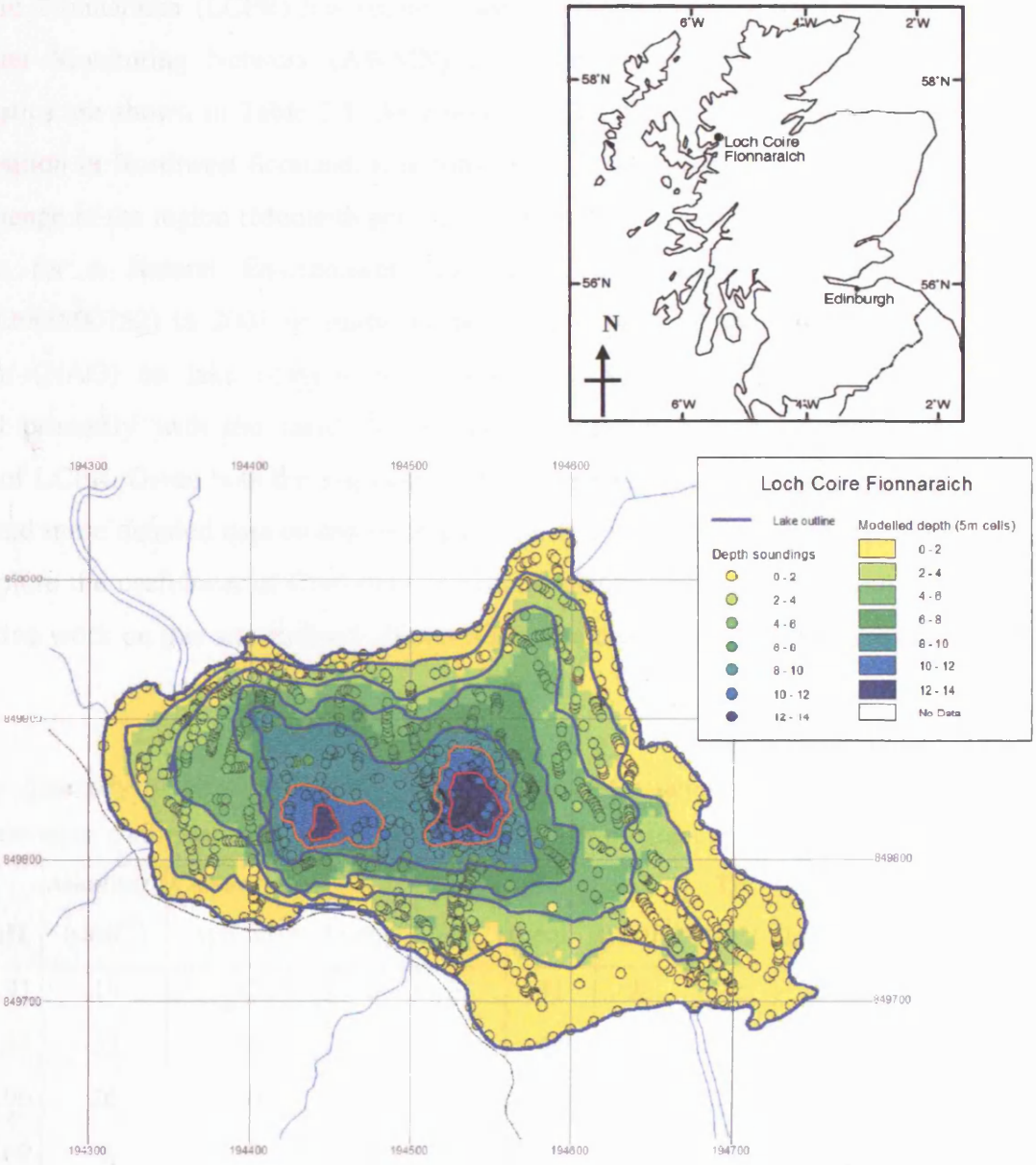


Figure 2.1: Map of Loch Coire Fionnaraich showing location, lake bathymetry and catchment. Bathymetric measurement is based on Arc-GIS. Each grid has 100 m spacing (Source: Mike Hughes).

2.2.2 Associated research history and the selection process of LCFR

Loch Coire Fionnaraich (LCFR) has recently been included in the United Kingdom Acid Water Monitoring Network (AWMN) as a control site. Its basic chemical characteristics are shown in Table 2.1. As a non-acidified site in an area of very low acid deposition in Northwest Scotland, it is considered to be an ideal site for studying climate change in the region (Monteith pers. com.). Consequently, the site also became the focus for a Natural Environment Research Council project (Award No.: NER/B/S/2000/00752) in 2001 to study the potential impacts of the North Atlantic Oscillation (NAO) on lake ecosystems in Northwest Scotland. This project was concerned primarily with the fossil diatom and chrysophyte record in the recent sediment of LCFR. Given both the availability of background data on the site from the AWMN and more detailed data on the sediment record, it was considered an excellent site to explore the usefulness of Cladocera in climate change studies. Apart from this, collaborative work on this site enabled efficiencies in fieldwork and fieldwork costs to be saved.

Table 2.1: Summary of physico-chemistry parameters of water samples of LCFR. Water samples were taken during various seasons (Source: UKAWMN programme).

Date	pH	Alkalinity (μeql^{-1})	Conductivity (μScm^{-1})	K^+ (μeql^{-1})	Mg^{2+} (μeql^{-1})	Ca^{2+} (μeql^{-1})	Cl (μeql^{-1})	TP (μgl^{-1})	TN (μgl^{-1})	TOC (mgl^{-1})
Oct'94	5.91	16	17	6	35	41	96	2.5	144	2.8
May'01	6.34	33	36	9	56	49	227	2.5	212	3.1
Aug'01	5.96	26	20	5	35	34	100	na	na	6.6
Sep'01	5.69	8	19	5	31	29	109	11	100	4.6
Nov'01	5.61	5	28	8	47	37	184	na	na	na

2.2.3 Aims of selection of LCFR for research on Cladocera

Three important aims were developed for the research of the contemporary and fossil Cladocera from Loch Coire Fionnaraich.

2.2.3.1 Contemporary survey of Cladocera

During the survey of the Northwest Scottish mountain lochs in May 2001, a number of contemporary cladoceran samples were also taken from each loch surveyed and these

were identified in the ECRC laboratory. The LCFR contained a relatively high number of cladoceran species (> 30) compared to other sites surveyed in the region (Chapter 4). Thus LCFR was considered to be a good site for studying the contemporary cladoceran community structure. The loch is also located at a relatively low altitude (235 m) in northwest Scotland suggesting that the cladoceran productivity and diversity should be greater than higher altitude sites due to its higher temperature. The Loch Coire nan Arr, one of the closest sites at a similar altitude in northwest Scotland shows the relative importance of fish and macrophyte diversity, suggesting that the Loch Coire Fionnaraich could be important for studying the contemporary cladoceran community structure (Monteith & Evans, 2000). In addition, the loch contains aquatic vegetation and sandy substrata food habitats for chydorid Cladocera along its shoreline, which was considered to be very useful for studying the species-specific preferences of contemporary Cladocera to the micro-habitat structures.

2.2.3.2 Study of taphonomy of Cladocera

Remains of Cladocera are deposited and preserved in the deeper water of lakes (Frey, 1986). However, how the fossils are transported into a central part of a lake, how they are deposited and preserved, and how representative the fossil assemblages of Cladocera are with respect to the source community structure, are still not fully understood. During the survey of LCFR in May 2001, two sediment cores were taken. A small portion from the top of one of the sediment cores was analysed in the ECRC laboratory to confirm that the cladoceran remains were well preserved and could be identified easily. Contemporary diversity and sedimentary assemblages of Cladocera in LCFR showed that the loch was also suitable for a taphonomic study of Cladocera. The detailed methodology on taphonomic study of Cladocera is described in Chapters 3 and 5.

2.2.3.3 Development of a temperature transfer function and palaeoclimate reconstruction

Many northwest Scottish mountain lochs are considered to be important for climate change studies due to physico-chemistry characteristics of water, where they are relatively less impacted by acid deposition (Monteith and Evans, 2000). These lakes are likely to be driven by rapid climatic change e.g. related to the NAO (Birks, 1996; Monteith and Evans, 2000). Hurrel (1995) reported that northern Europe and parts of Scandinavia have generally experienced wetter than normal conditions since 1980. The

cladoceran assemblage structure in these lochs has been rarely studied in the past and it was considered that it would be important to develop a Cladocera-inferred temperature transfer function to the sediment core retrieved from LCFR.

In many ways, LCFR appears to be an ideal site for ecological and palaeoecological studies. As described earlier, it contains a high diversity of contemporary Cladocera and this site also has well preserved sedimentary assemblages of Bosminids and Chydorids, which are important indicators for past climate change (e.g. Frey, 1958; 1960; 1986). The fossil assemblages of Cladocera in LCFR are also representative of assemblages in the Scottish and Norwegian training-set sites and the use of the loch in applying the temperature transfer function for palaeoclimate reconstruction was thought to be appropriate. However, on the other hand, LCFR also appears to have some weaknesses as a study site for climate change. It does not undergo strong thermal stratification, it is a relatively warm, low altitude site compared with most lakes in the training set and rarely freezes in winter.

2.2.4 Regional climate

In matching the sediment record to instrumental data later in this thesis, use has been made both of the Central England Temperature (CET) Series and data from the nearest meteorological station temperature at Plockton, Scotland. The CET is used as one of the most representative temperature data series across Europe including the UK (e.g. Jones et al., 1997a). CET spans more than 300 years and is the longest, continuous, homogenous record in the world (Bradley et al., 2003), and the lake surface water temperatures of the UKAWMN sites of the Northwest Scotland have been found to match perfectly with the CET (Monteith pers. com). The mean January, July and mean summer (average of June, July and August) air temperatures of the CET from 1659 to 2000 AD is presented in Figure 2.2.

The mean instrumental temperature data from 1980 to 1999 for the Scottish site at Plockton is also presented for the comparison with the CET data series (Figure 2.2). The Plockton meteorological station is located at 57.2^{0}N and 5.40 ^{0}S, very close to Loch Coire Fionnaraich, south of Lochcarron. The mean July temperature, as would be expected, for Plockton is different from the CET series, although the mean January

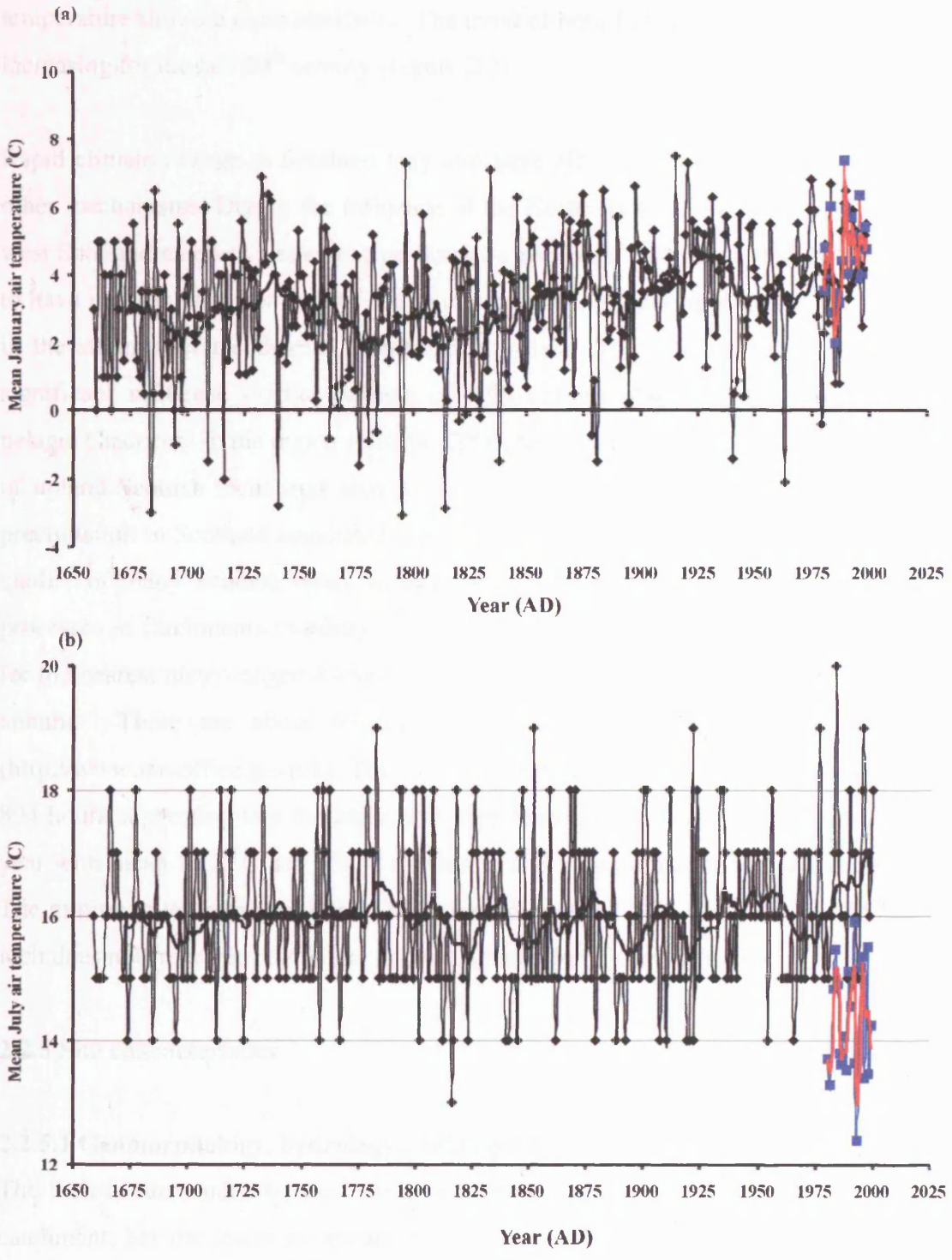


Figure 2.2: Mean July and January air temperatures from 1659 to 2000. Temperatures are derived from the Central England Data Series (www.metoffice.gov.uk). (Moving average = 15). Temperatures recorded from 1980 to 1999 of one of the closest Meteorological Station, Plockton, from Loch Coire Fionnaraich, Scotland, is also incorporated in the diagrams with moving average 2.

temperature shows a close similarity. The trend of both July and January temperature is increasing for the late 20th century (Figure 2.2).

Rapid climate change in Scotland may also have effects on lakes through a variety of other mechanisms. Due to the influence of the North Atlantic Oscillations (NAO), the west Scotland receives westerly wind flows on an almost daily basis. The NAO is likely to have impacts on water quality due to increased mixing during summer and reduction in the strength of the thermal stratification in lake. The NAO is reported to have a significant influence on the patterns of NO_3 concentration and the productivity of pelagic Cladocera in the region (George, 2000; Monteith et al., 2000). The water quality of upland Scottish lochs may also be mediated via water temperature and amount of precipitation in Scotland associated with NAO during winter (e.g. Hurrel, 1995). Water quality of many Scottish rivers is reported to have been influenced by hydrological processes in catchments (Soulsby et al., 2002). The mean precipitation (30 year mean) for the nearest meteorological station in Northwest Scotland recorded is 2277.8 mm per annum. There are about 60 days of a year with frost cover in the region (http://www.metoffice.gov.uk). The average sunshine per year in the region are about 894 hours suggesting that the lakes here experience rather cloudy days for most of the year with mean 12.2 ^{0}C and 4.9 ^{0}C maximum and minimum temperatures respectively. The minimum temperatures during the winter do not fall below zero indicating that the loch does not freeze during winter and has a rather long growing season.

2.2.5 Site characteristics

2.2.5.1 Geomorphology, hydrology, and vegetation

The loch is surrounded by the Torridonian Mountains with bare bedrock in the upper catchment, but the lower slopes are peat covered with moorland vegetation. A small patch of peat erosion is apparent on the North shore slope, otherwise the catchment is undisturbed except for an old raised shoreline some 50 cm above the current level. Since neither the outflow nor the drainage hydrology seems to have been interfered with, this raised level may reflect wetter conditions in the past.

At least six stream channels join the LCFR, of which the main stream-inflow enters the loch from the northwest (Figure 2.1). Most other inflows are relatively small. At least two of them in the northwest of the loch flow through unvegetated sandstones and

appear to carry inorganic minerals into the loch, while the other four streams flow through vegetation-dominant catchments and bring more organic material into the loch (Figure 2.1). The vegetation of the catchment is characterised by acid moorland species, notably *Calluna vulgaris*, *Molinia caerulea* and *Eriophorum* spp. Aquatic macrophytes inhabit the loch and are typical of acid oligotrophic lakes with mainly *Isoetes, Lobelia* and *Juncus bulbosus* dominating the submerged community. However, other species that are dominant in acidic water such as *Sphagnum* are also present in the loch. The growth of macrophytes especially was noticed around the western inflow during various sampling trips particularly in spring and summer 2001 and 2002.

2.2.5.2 Bathymetry

A bathymetric survey was carried out by the UKAWMN programme in 2001 (Figure 2.1). The loch covers an area of c. 9 ha. It has a catchment area of approximately 800 ha. The loch has two deep basins, with the maximum depth (14.5m) in the east basin. The mean depth of the loch is 11 m. The loch bed appears to be steepest to the south and southeast but has a rather shallow gradient in the northwest.

2.2.5.3 Physico-chemistry of the lake water

The seasonal monitoring of the lake water chemistry has recently been started more regularly as a part of the UKAWMN, although one measurement of water chemistry was taken previously in 1994. Only nine physico-chemical variables (pH, alkalinity, conductivity, K^+, Mg^{2+}, Ca^{2+}, Cl^-, TP, TN and TOC) were measured in Loch Coire Fionnaraich during this period. Other important variables such as surface water temperature and dissolved oxygen were not measured. Important variables, such as TP and TN, were irregularly measured. The results show that the average measurement of pH in year 2001 was 5.91 (Table 2.1). Values for TOC during summer were more than twice that of during autumn (Table 2.1). In many ways, the water chemistry of Loch Coire Fionnaraich can be compared with Loch Coire nan Arr, a nearby loch, for which more data are available (Monteith and Evans, 2000). Loch Coire nan Arr is potentially susceptible to acidification though it has not received high amounts of anthropogenic S and N deposition and is not yet acidified. Rose & Rippey (2002) argued that the Loch Coire nan Arr is one of the least contaminated sites in the region, suggesting that Loch Coire Fionnaraich has also received limited pollution. The proximity of this site to the coast indicates that the loch could receive a large amount of marine ion inputs especially Na^+ and Cl^-. An increasing trend of DOC and non-labile Al were observed

within the past decade in Loch Coire nan Arr (Monteith and Evans, 2000). Very low measurement of TP suggests that the loch is within oligotrophic.

2.2.5.4 Thermal stratification

Data for the thermal stratification of LCFR is not available until 2001. Measurement of the epilimnetic and hypolimnetic temperatures of the loch was carried out on seven seasonal visits between August 2001 and July 2002 by the UKAWMN programme (Figure 2.3). The results show that the thermal stratification of LCFR appears to be rather temporary during spring and summer and is not strong enough to influence the biological community structure in the loch since the differences in eplimnetic and hypolimnetic temperatures are not very high (Figure 2.3). In July 2002, the temperatures measured at 1m and 12m depths from the surface of LCFR were 21 ^{0}C and 14 ^{0}C respectively (Figure 2.3). Seasonal and inter-annual variations in climate of the region could have played an important role on the temporary stratification of LCFR during summer 2001 and 2002 (e.g George, 2000). The location of the loch close to the sea, relatively low depth and wind-induced mixing of lake water are important factors that prevent strong thermal stratification (Monteith pers. com.). It is considered that the occurrence of thermal stratification during summer can have potential impacts on the pelagic ecosystems as well as the taphonomy of Cladocera, as stratification influences the vertical migration of Cladocera such as *Daphnia* with respect to reproduction, feeding and avoiding predators (Gliwicz, 1986). Thermal stratification also reduces the mixing of epilimnetic and hypolimnetic water bodies and the depositional rate of remains (Frey, 1988). Stratification may also cause problems for the reconstruction of the water temperature since in water temperature reconstruction for Cladocera in sediments, since an assumption is made that the surface water and the atmospheric air temperatures are positively correlated (e.g. Livingstone et al., 1998). In the case of LCFR, lack of stratification is therefore advantageous.

2.2.5.5 Palaeolimnology

This study is one of the first multi-disciplinary studies on the palaeolimnology of Loch Coire Fionnaraich. Two sediment cores, LCFR1 and LCFR2 were taken from the centre of the loch for bulk sediments as well as palaeoecological analyses of subfossil assemblages of Cladocera, diatoms and chrysophytes. Details are presented in Chapter 3 (section 3.2.4) and Chapter 7.

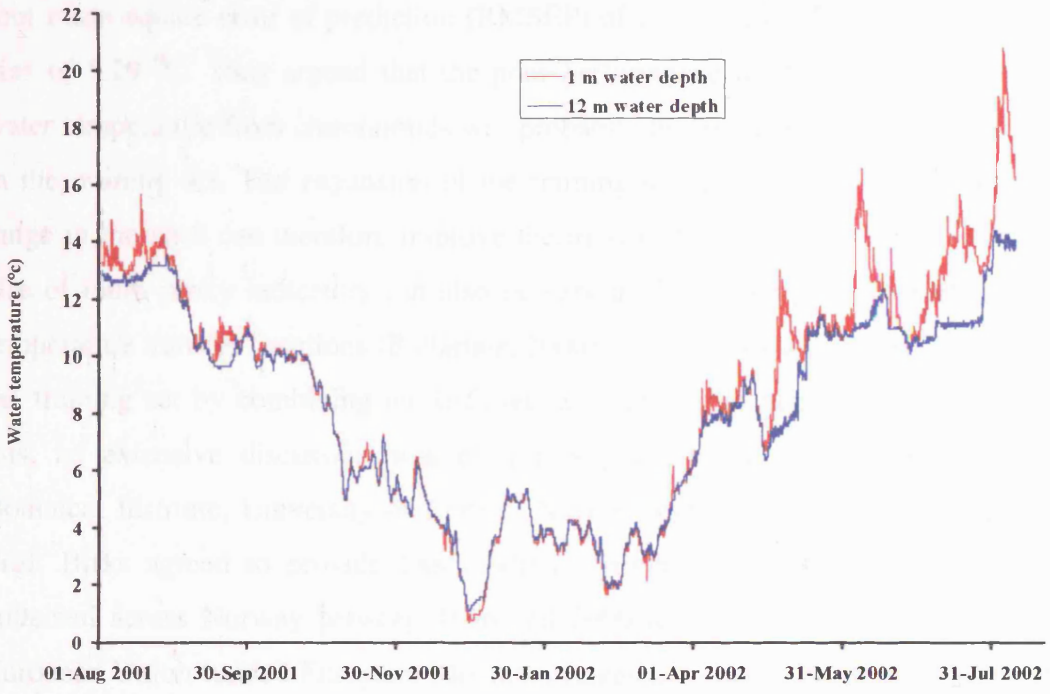


Figure 2.3: Loch Coire Fionnaraich epilimnion and hypolimnion temperature between August 2001 and July 2002. Two hourly measurements were carried out using VEMCO submersible thermistor logger (Source: Monteith unpublished data).

2.3 Training set sites

Brooks and Birks (2000) developed a chironomid-inferred summer lake surface water temperature transfer function using training set across western Norway. Based on the Weighted Averaging Partial Least Squares regression, the calibration function had a root mean square error of prediction (RMSEP) of 2.2 ^{0}C, a r^2 of 0.30 and a maximum bias of 5.29 ^{0}C. They argued that the poor performance for the summer lake surface water temperature from chironomids was probably due to the limited temperature range in the training set. The expansion of the training set sites as well as the temperature range in the sites can therefore improve the transfer function (e.g. Lotter et al. 1997). Use of multi-proxy indicators can also be very useful to compare the performance of temperature transfer functions (Battarbee, 2000). In this study it was possible to enlarge the training set by combining the data-sets available from Scotland and Norway. For this, an extensive discussion was carried out between Prof. John Birks from the Botanical Institute, University of Bergen, Norway and the colleagues in ECRC/UCL. Prof. Birks agreed to provide 188 modern surficial sediment samples, which were collected across Norway between 1996 and 2000 for this study (Appendix 2.1). The European Union funded European Mountain Lakes Ecosystem Programme (EMERGE) also provided 30 Scottish surface sediment samples and 2 samples were collected from Northwest Scotland during the visit for the UK Acid Waters Monitoring Network (UKAWMN) programme in May 2001. Altogether, 220 surface sediment samples were available for this study.

One of the main reasons to combine the three data-sets into a single training set was due to their common potential use for climate change reconstruction in the region consequently sites were selected to cover a long temperature gradient but to keep other variables as constant as possible. Most of the sites had varied characteristics with very high and low concentrations of lake water chemistry and altitudinal and latitudinal variations. Most sites in Norway ranged from lowland forests to tundra. However, EMERGE Scottish sites were distributed only above the tree-line and the UKAWMN sites were located in low altitudinal zones of Scotland. In order to avoid the effects of chemistry and anthropogenic disturbances on lake ecosystems and to maximize the temperature gradients, certain aims and criteria were developed to select the most appropriate sites from the all three data-sets for a combined Cladocera-inferred temperature calibration set in the region.

2.3.1 Aims and criteria for training set site selection

The central aim of the training set site selection was to select a group of lakes distributed along wide altitudinal and latitudinal gradients in Scottish and Norwegian mountain ranges for studying the modern Cladocera fossil assemblage structure, and to explore its role in inferring past summer lake surface water temperature (LSWT) by developing a climate inference model. The main purposes in the development of the model were to estimate the optima and tolerances of each cladoceran taxon to summer LSWT as well as other important physico-chemistry gradients of lakes such as July and January air temperatures, precipitation, lake depth, pH, alkalinity, sulphate and NO_3. A second aim was to assess the characteristics of mountain lakes with respect to their physico-chemistry gradients. A third aim was to explore the responses of modern fossil cladoceran assemblages in these lakes to summer LSWT and other physico-chemistry variables through indirect and direct gradient analyses. The inference model was then applied to the subfossil assemblage in a core sequence from Loch Coire Fionnaraich to derive estimates of past summer LSWT as described by Brooks & Birks (2000, 2001).

2.3.1.1 Higher altitude sites

All EMERGE-Scottish sites were located above 500 m altitudes. Most of these sites had bare or tundra catchments. The AWMN and Norwegian sites, however, were located between 10 m and 1500 m altitudes. In order to maximize the temperature gradient, lakes were chosen across a wide range of altitude and latitudes, although to avoid lakes with increased human impacts, very lowland sites were not selected for the training set unless located at 100 m or above.

2.3.1.2 Common environmental variables

Since three different institutional environmental data-sets were used for this study, a few environmental variables were not common to all data-sets. For example, variables such as TP were partly measured in Norwegian sites while the variable SiO_2 was measured only in Scottish sites. Thus only sites with common variables measured were selected for this study. The common physico-chemistry variables for AWMN, EMERGE Scotland and Norwegian sites selected for this study were: pH, alkalinity, conductivity, Na, NH_4, K, Mg, Ca, Cl, NO_3, SO_4, Al-NL, Abs-250, TOC, LOI, mean July air temperature, mean January air temperature, mean summer lake surface water

temperature, maximum lake depth and precipitation. The common geographical variables for the three data-sets were altitude, latitude and longitude.

2.3.1.3 Constant alkalinity against altitudes

Previous research has shown that most mountain lakes of Northwest Europe have relatively low pH and low base status (Jones et al., 1993). The zooplankton assemblage structure in these lakes is associated with the physico-chemistry of water released from their catchments (Sandøy and Nilssen, 1986). In particular, alkalinity plays a significant role on the acid-base profile of the lake and variation in abundance and distribution of zooplankton (Nilssen and Sandøy, 1990). Thus, in order to minimize the effects of alkalinity on cladoceran assemblages on training set sites, a constant alkalinity profile against altitudinal gradients was considered appropriate through regression analyses. As a first step, from the pool of total samples (N=220), sites located below 100m altitudes were excluded. Then a median value for alkalinity was calculated followed by a regression analysis between alkalinity and altitude. However, the range of alkalinity along the altitudinal gradient was not constant. Thus sites with highest and lowest alkalinity values were excluded and a second regression analysis performed. This process was repeated with the subsequent exclusion of the highest and lowest alkalinity values until the range of alkalinity was independent of altitudinal gradients (Figure 2.4). A total of 72 sites (UKAWMN = 2, EMERGE Scotland = 12, Norway = 58) with alkalinity values ranging from 17μeql^{-1} -57μeql^{-1} (Median = 32.5μeql^{-1}) met the criteria above and were selected for this study (Table 2.2).

2.3.2 Selected training set sites

2.3.2.1 Scottish sites

A total of 14 Scottish lochs were selected, in which 12 lochs were from European EMERGE (Scotland) and 2 sites were selected during the survey of the UK Acid Water Monitoring Network (UKAWMN) programme in May 2001 (Figure 2.5). Many European EMERGE Scottish sites (Table 2.2) have very similar biological and physico-chemical properties. Catchments of these sites are characterised by granites and gneisses and poorly developed soils with sparse vegetation, so that nutrient fluxes such as TP and TN, into the lakes are very low (e.g. Battarbee, 2000). These EMERGE lakes are subjected to relatively longer period of ice cover, showing a strong response to seasonality. Since they are located in remote high altitude sites, the anthropogenic

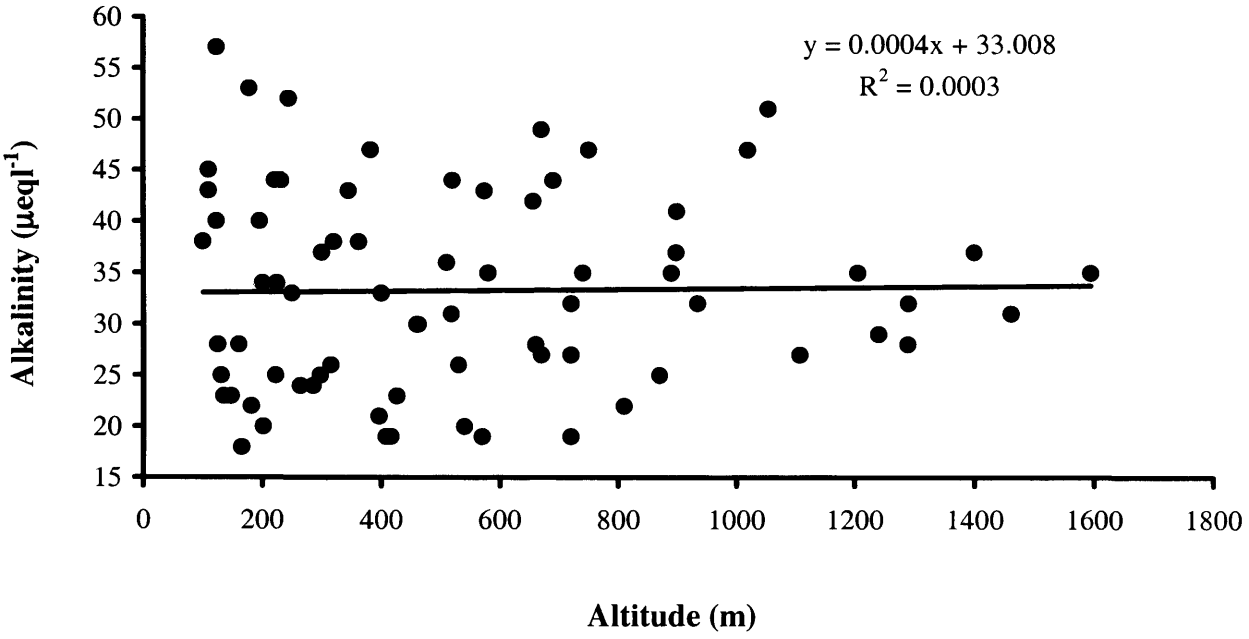


Figure 2.4: Relationship between altitude and alkalinity among 72 sites along altitudinal gradients range from 100m to 1594m in Scottish and Norwegian moutain lakes. Alkalinity Range = 17 μeql^{-1} – 57 μeql^{-1} (median = 32.5μeql^{-1}).

Table 2.2: An overview of selected Scottish and Norwegian sites for Cladocera analysis and important environmental variables are also presented. The first 12 sites are EMERGE Scottish sites located only above the tree-line. The last two sites are the Scottish UKAWMN sites located in low altitude region of north-west Scotland. All the remaining sites are Norwegian sites located in varying altitudes. Details are presented in Appendix 2.1 and Appendix 2.2 respectively.

Site Name	Modified Code	Latitude (^{0}N)	Longitude (^{0}W/E)	Altitude (M)	pH	Alkalinity (μeql^{-1})	Mean summer lake water temp. (^{0}C)	Mean July air temp. (^{0}C)	Mean January air temp. (^{0}C)	LOI %	Maximum depth (m)	SO_4 (μeql^{-1})
Un-Named	L007MED	57.52	-4.90	670	6.58	49	11.20	10.51	-0.70	50.29	8.20	23.00
Loch Coire Choille Rais	L008AIS	57.25	-4.58	750	6.66	47	10.99	10.11	-1.00	32.69	26.00	31.00
Lochan Bac An Lochain	L009AIN	57.14	-5.66	720	6.32	27	11.64	10.91	1.65	56.16	4.10	49.00
Loch Carn A' Chaochain	L011AIN	57.17	-4.92	870	6.20	25	12.40	10.67	0.27	75.40	4.00	22.00
Un Named	L013MED	57.71	-5.59	570	6.13	19	11.50	10.17	1.08	65.19	0.70	18.00
Loch An Fhraoich Choire	L015IRE	57.50	-5.23	520	6.58	44	12.30	10.33	1.57	49.55	5.50	23.00
Fhearchair	L017AIR	57.68	-5.45	540	6.18	20	10.10	10.89	-0.79	20.98	24.00	30.00
Loch Bhuic Moir	L020OIR	57.81	-5.45	690	6.47	44	12.20	11.02	2.10	57.05	7.30	27.00
Loch Toll Lochan	L021HAN	58.19	-4.95	530	6.16	26	12.30	11.34	-0.43	52.92	13.00	25.00
Lochan A Chnapaich	L022ICH	56.83	-4.94	740	6.45	35	10.80	10.91	0.52	52.42	8.50	26.00
Loch Bealach Na H-Uidhe	L023DHE	56.95	-4.95	810	6.17	22	11.30	11.15	0.62	34.99	3.50	36.00
Loch Gorm	L026ORM	56.56	-4.58	720	6.15	19	12.30	11.76	1.18	49.44	3.80	33.00
Skredvatn	L033ATN	61.58	6.50	201	6.05	20	9.50	13.40	-2.20	15.97	7.20	42.00
OSDALSÆTER Vt.	L035RVT	61.98	6.33	362	6.37	38	11.00	12.40	-2.40	23.96	18.50	26.00
PAULS Vt.	L036SVT	61.61	6.51	130	5.98	25	10.00	13.80	-1.90	23.74	4.30	44.00
TÅBAKK Tj.	L041KTJ	61.26	8.83	934	6.13	32	15.00	10.90	-9.80	35.37	3.70	45.00
FLOT Vt.	L044TVT	61.01	7.33	1205	6.27	35	11.50	8.10	-8.50	7.49	2.60	24.00
LANGE Vt.	L046EVT	61.96	6.01	408	6.02	19	13.00	11.90	-2.00	38.27	6.80	22.00
Unnamed	L048MED	61.92	5.23	123	6.07	40	14.50	13.20	0.60	13.31	12.00	45.00
KONSDALS Vt.	L050SVT	61.87	5.08	110	6.33	43	13.00	13.20	0.80	31.24	6.50	44.00
Unnamed	L051MED	61.83	5.45	382	6.46	47	13.00	11.80	-1.00	10.36	26.00	27.00
Litle 147	L054147	61.57	5.61	147	5.9	23	16.00	13.30	-0.40	44.54	12.00	33.00
STOLS Vt.	L055SVT	61.82	6.04	416	5.95	19	15.50	11.90	-2.20	58.79	8.50	22.00
FULLSKJEGG Vt.	L056GVT	61.69	5.81	222	6.02	25	16.00	12.90	-1.00	24.82	13.50	28.00
SLÅTTESTOLS Vt.	L057SVT	61.69	5.79	181	5.82	22	15.50	13.20	-0.80	31.05	8.50	22.00
DALE Vt.	L058EVT	61.48	6.05	200	6.03	34	16.50	13.20	-1.50	36.57	13.00	31.00

SKOGSTAD Tj.	L060DTJ	61.51	6.00	160	6.16	28	16.50	13.40	-1.30	26.99	8.70	36.00
FAGREDALS Vt.	L063SVT	61.37	5.83	462	6.15	30	14.00	11.60	-2.20	46.21	21.00	22.00
STANGA Vt.	L065AVT	61.39	5.74	297	5.87	25	18.60	12.50	-1.40	37.50	11.50	22.00
Unnamed	L066MED	61.85	6.94	1020	6.43	47	12.00	9.00	-6.50	25.72	6.60	39.00
Røldalstjønn	L069ØNN	59.89	6.66	656	6.15	42	16.40	10.90	-4.30	64.71	6.10	35.00
Storemyrstjønn	L078ØNN	59.71	6.35	396	6.01	21	13.10	12.20	-2.50	39.41	8.50	40.00
Unnamed	L081MED	59.71	6.55	580	6.16	35	13.20	11.20	-3.70	50.61	18.50	28.00
Unnamed	L082MED	59.72	6.56	670	6.18	27	14.30	10.70	-4.10	33.19	7.80	29.00
Hermodholtjørni	L084RNI	59.81	7.25	1107	6.23	27	12.60	8.60	-7.40	33.25	5.00	54.00
Lintjønn	L088ØNN	59.53	5.66	125	6.23	28	16.50	13.30	0.00	29.34	7.50	70.00
Vatnedalsvatn	L091ATN	59.73	6.06	221	6.46	44	16.70	13.00	-1.30	28.31	15.00	53.00
Langareidtjønn	L092ØNN	59.73	6.12	178	6.49	53	17.30	13.30	-1.10	35.47	12.50	56.00
Grastjørni	L093RNI	59.91	6.56	426	6.01	23	17.70	12.10	-3.30	20.22	10.20	39.00
Midtre Søyletjønn	L095ØNN	59.96	6.57	460	6.01	30	18.30	11.90	-3.30	43.63	13.00	35.00
Sæsvasstjønn	L096ØNN	59.66	7.51	899	6.09	41	16.00	10.50	-7.70	34.40	12.00	30.00
Flotatjønn	L097ØNN	59.67	7.54	890	6.15	35	16.00	10.40	-7.60	31.12	8.10	26.00
Stokketjønn	L098ØNN	59.66	7.54	898	6.25	37	17.00	10.50	-7.70	44.69	4.50	20.00
Lisletjønn	L103ØNN	59.34	7.31	518	5.97	31	18.00	12.90	-5.00	44.72	7.10	67.00
Unnamed	L107MED	59.17	7.53	300	6.17	37	17.00	14.10	-4.10	37.05	12.00	57.00
Unnamed	L109MED	59.61	7.81	574	6.10	43	18.00	12.70	-6.00	40.98	4.10	21.00
Trolletjønn	L113ØNN	59.68	8.06	720	6.28	32	19.00	11.90	-6.70	56.92	3.30	10.00
Gregarstjønn	L114ØNN	59.58	8.02	660	5.81	28	20.00	12.20	-6.40	47.98	8.10	20.00
Histøl	L123TØL	58.33	7.79	245	6.34	52	19.00	14.30	-3.20	48.55	9.20	79.00
Jinninstjønn	L125ØNN	58.27	7.74	165	5.78	18	20.50	14.80	-2.70	37.42	6.30	68.00
Rypestøl	L131TØL	58.19	7.87	123	6.47	57	20.50	14.30	-1.90	44.56	11.00	94.00
Bærvannet	L134NET	58.34	7.79	315	6.04	26	20.00	14.10	-3.40	67.62	17.00	70.00
Un Named	L135MED	58.27	8.05	135	6.09	23	20.00	15.00	-2.40	53.57	8.70	97.00
Årstøl	L138TØL	58.14	7.72	195	6.19	40	20.50	13.90	-2.20	61.82	12.50	90.00
Un Named	L144MED	60.93	7.32	1290	6.27	32	9.20	7.60	-8.00	6.61	3.00	35.00
Hornsvatn	L145ATN	60.96	7.36	1289	6.15	28	8.90	7.60	-8.00	19.52	12.50	17.00
Un Named	L146MED	60.93	7.32	1240	6.22	29	8.00	7.80	-7.80	5.94	4.80	28.00
Vargebovatn	L148ATN	60.74	7.53	1400	6.4	37	7.50	5.90	-11.00	8.25	10.50	22.00
Bukkehammarstjønn	L162ØNN	61.47	8.71	1594	6.38	35	6.00	7.10	-12.70	7.83	13.00	18.00

Rasletjernet	L163NET	61.39	8.76	1461	6.15	31	8.50	7.90	-12.20	13.72	4.50	24.00
Stavtjern	L166ERN	61.32	8.82	1055	6.41	51	9.80	10.20	-10.40	20.21	6.50	22.00
Bjørnfjellvatnet	L169NET	68.43	18.07	510	6.33	36	9.00	10.50	-12.00	29.94	12.90	40.00
Nigardsbrevatnet	L171NET	61.68	7.23	285	6.96	24	5.00	13.60	-4.70	0.78	12.20	40.00
Un Named	L184MED	71.02	24.77	100	6.38	38	11.00	9.60	-4.00	19.36	10.50	75.00
Un Named	L186MED	71.05	25.77	232	6.34	44	7.50	8.80	-4.70	20.82	1.30	29.00
Un Named	L188MED	70.59	27.58	345	5.41	43	9.00	10.30	-13.70	27.06	1.00	49.00
Un Named	L190MED	70.32	31.04	110	5.35	45	11.80	8.60	-5.90	27.89	0.60	57.00
Un Named	L193MED	70.48	28.88	320	5.38	38	9.80	9.00	-6.90	14.03	0.50	69.00
Abbortjørn	L198ØRN	59.85	11.43	224	5.84	34	15.00	15.90	-7.50	57.18	11.50	60.00
Skiersjoen	L204ØEN	60.25	11.45	264	5.30	24	19.00	14.70	-7.70	60.92	18.50	37.00
Lochan Bealach Cornaidh	L221IDH	58.21	-5.00	430	6.41	33	12.88	11.72	1.06	37.80	13.40	45.00
Loch Coire Finonaraich	L223ICH	57.49	-5.01	235	6.34	33	14.75	12.97	0.81	32.16	14.00	24.00

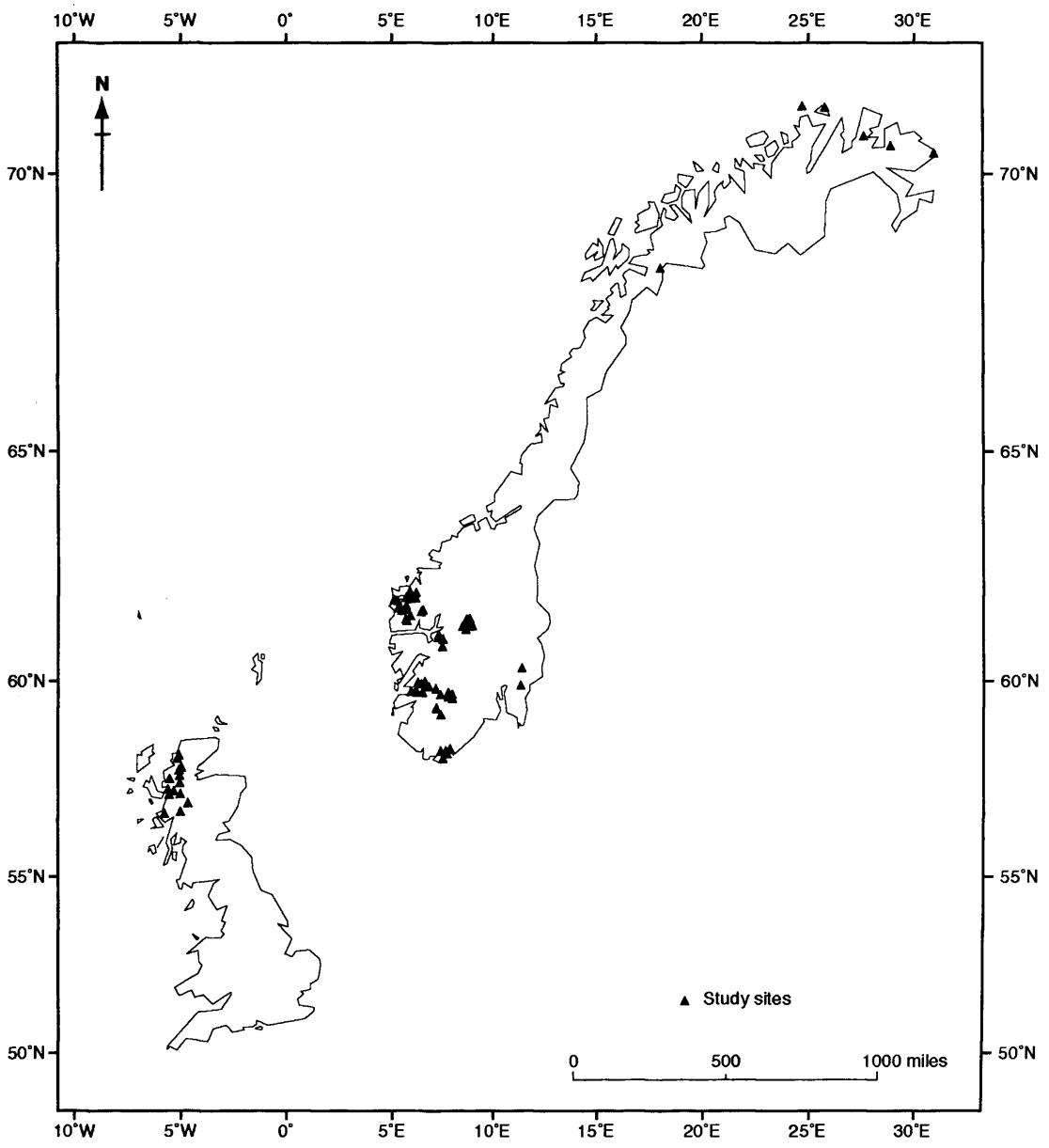


Figure 2.5: Map of Scotland and Norway showing selected training set sites.

impacts on these lakes are minimal. However, they are highly sensitive to meteorological forces and atmospheric deposition from long range transported trace metals such as Sb, Hg, Bi, As, and Pb in surface sediments (e.g. Catalan et al., 2002a). The major spatial and environmental variables of EMERGE sites are given in Table 2.2 and other environmental variables are presented in Appendix 2.2. Two other sites selected from the UKAWMN, Loch Coire Fionnaraich and Lochan Beleach Cornaidh, are located in lower altitudes of Northwest Scotland (Table 2.2, Figure 2.5). Both sites have similar physico-chemical gradients. Unlike EMERGE sites, they do not freeze during winter and the catchments of these sites are more vegetated with dominant littoral isoetids such as *Lobelia dortmanna*, *Litorella uniflora*, *Isoetes lacustris* and *Juncus bulbosus* along shorelines. As a result, the community dynamics of flora and fauna appears to be significantly different in these lakes compared to other high altitude EMERGE sites. Particularly, lakes associated with diverse micro-habitat structures (e.g. macrophytes, sand, rocks and open-water) provide increased diversity of littoral (e.g. Chydorids) and planktonic (e.g. Bosminids) Cladocera. Relationships between selected UKAWMN and EMERGE sites are presented in section 2.4.

2.3.2.2 Norwegian sites

A total of 58 sites were selected from Norway. Unlike the Scottish sites, the selected Norwegian lakes are distributed along a wide range of geography ranging from 58.14^{0}N to 71.05^{0}N latitude and 5.08^{0}E to 31.04^{0}E longitudes respectively (Table 2.2, Figure 2.5). The altitudinal range of the Norwegian sites also varies significantly with the lowest site at 100 m to the highest at 1461 m a.s.l. (Table 2.2). All measured environmental variables are presented in Appendix 2.2. Most of these sites are prone to atmospheric deposition from long range transported trace elements with high Sb, Hg, Bi, As, and Pb in surface sediments (Henriksen et al., 1998). Depending upon their catchments, the physico-chemistry of these sites varies considerably. Most lowland sites with forested catchments tend to have relatively high TOC. Most of these sites have littoral vegetation dominated by isoetids such as *L. dortmanna* , *L. uniflora*, *I. lacustris* and *J. bulbosus* (Lucassen et al., 1999). In recent years, many Norwegian lakes are recovering from the surface water acidification (e.g. Wright and Cosby, 2003) and it is expected that most of these sites should have regained populations of native flora and fauna. In general, most selected sites of Norway at higher latitude and altitudes have poor nutrient profiles. The climate of the Norwegian sites varies significantly. Sites located in southern Norway, those in particular away from the sea, appear to have

received influence from continental climate regimes, with cold winters and relatively warm summers (Økland, 1999). Precipitation is relatively high in the majority sites, but the amount of precipitation varies with distance from the sea being 5000 mm per year close to the coast in western Norway (orographic precipitation) to 300 mm per year in the driest areas in central part of Norway. The orographic precipitation is caused by steep topography across the western coast (Henriksen et al., 1998).

2.4 Relationship between LCFR and other selected training set sites

The PCA ordination of the 24 environmental variables of the combined 72 selected sites of Scotland and Norway show that Loch Coire Fionnaraich (LCFR) is closely associated with the PCA axis 1, where a large number of low altitude Norwegian sites with relatively high mean January air temperature and annual precipitation are also found (Figure 2.6). However, the other UKAWMN site, Lochan Bealach Cornaidh (L221IDH) is closely associated with mean July and summer lake surface water temperatures. Unlike LCFR, the Lochan Bealach Cornaidh is associated with the major physico-chemical variables such as Na, conductivity, TOC and SO_4 in the ordination (Figure 2.6). The altitudinal gradient appears to play a significant role in the ordination of the training set. Majority of sites in the ordination associated with altitudinal gradients is from Norway indicating that the altitudinal variations between Norway and Scotland are significantly high and should have an influence on the abundance and composition of Cladocera. The majority of sites from Norway have high latitudes as Norway lies further north than Scotland. However, the influence of latitudinal variation in the training set was not observed significantly in the ordination (Figure 2.6). At least five Norwegian sites were selected from the sub-Arctic region. It was considered that effects of these sites on the cladoceran growing season would probably be different from those of low latitude sites. However, the mean July and summer LSWT of these sites were very similar to those sites located in the high altitude regions of southern Norway. In the ordination, none of the high latitude sites was seen as outliers (Figure 2.6). However, the high altitude sites showed rather different characteristics with very low July and summer LSWT in the ordination. Since one of the main objectives of this study was to expand the climate gradient in order to understand the response of Cladocera to climate change, a decision to keep all sites was made. However, a close inspection will be given if there are any site-specific effects on ecology of Cladocera existed in the calibration set before the exclusion or inclusion of sites being carried out.

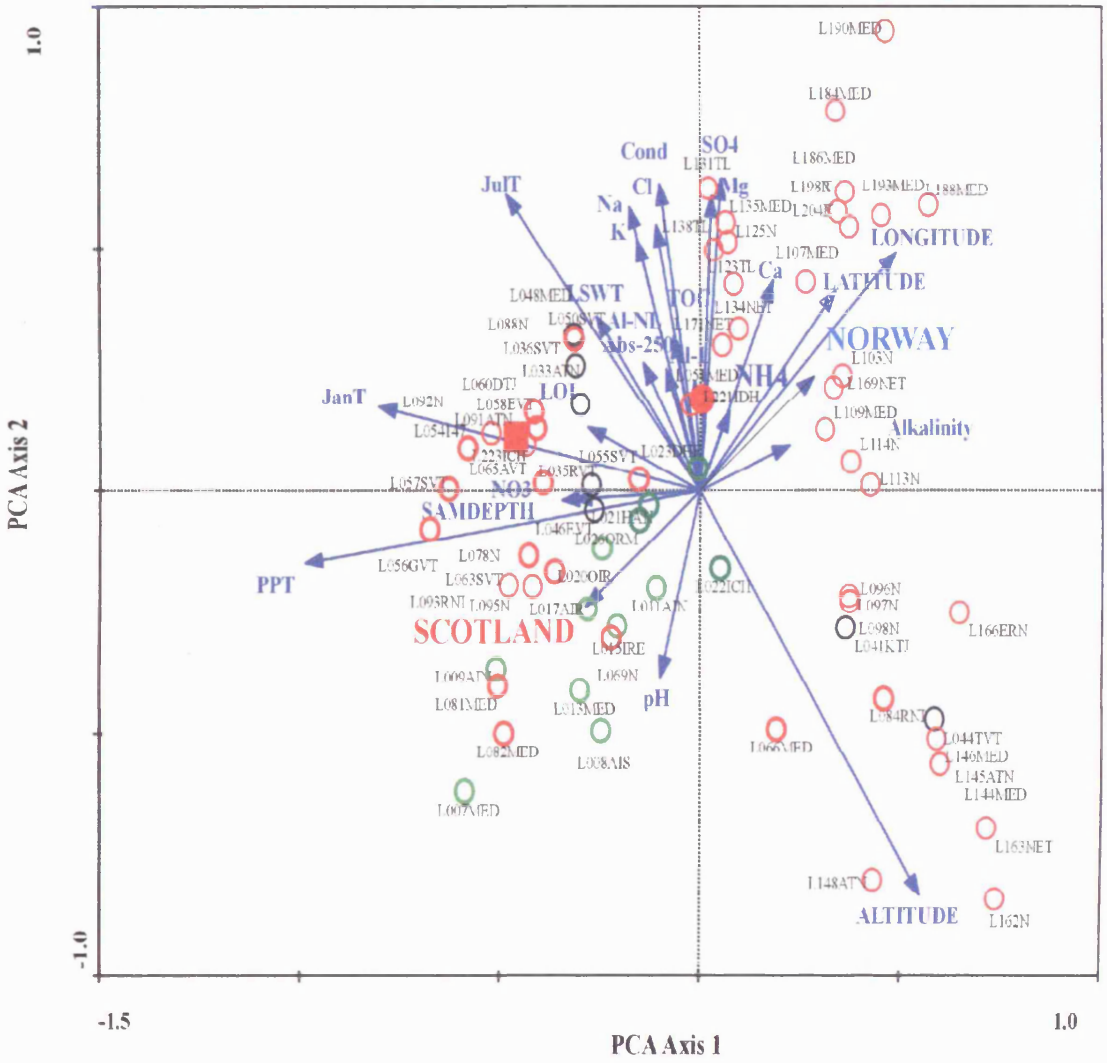


Figure 2.6: PCA ordination of the selected training set sites, where the Loch Coire Fionnaraich (LCFR) is compared with other sites in Scotland and Norway. Details are presented in Chapter 6. In ordination diagram, each group of lakes from different sources are given as various coloured-symbols. The two UK-AWMN sites, Loch Coire Fionnaraich (LCFR) and Lochan Belach Cornidh are presented as solid red square and solid oval-shaped circle and the EMERGE Scottish sites are presented as empty green circles. All Norwegian sites are presented as empty red circles.

Chapter 3

Methodology

3.1 Introduction

This chapter describes the sampling methods used in this study. The first section explains field methods, which include the survey of the contemporary Cladocera. This section also describes the collection of spatial surface sediment samples for taphonomic study of Cladocera, the collection of core sequence for studying subfossil assemblages of Cladocera in LCFR and the collection and measurement of the physico-chemistry of water samples, and the surface sediment samples of the training-set sites in Scotland and Norway. The second part focuses on the laboratory analyses of contemporary and fossil Cladocera in LCFR and the training-set sites. The final section describes the numerical analyses, in particular, the use of the multivariate techniques through ordinations. Numerical analyses used other than ordinations are described in each chapter.

3.2 Field Methods

Field methods include collection of live cladoceran samples, surface and core sediment samples and the environmental variables in Loch Coire Fionnaraich, and across the training set sites.

3.2.1 Survey of contemporary Cladocera in Loch Coire Fionnaraich

Cladocerans are important aquatic organisms inhabiting a variety of habitats. Planktonic Cladocera, Bosminids and Daphnids, are predominant in the open water habitat. They use both vertical and horizontal gradients of the lake extensively through diel and seasonal migrations. However, littoral Cladocera, mainly Chydorids, use a variety of substrates such as mud, vegetation and gravel for their food habitat. Thus a survey of live Cladocera provides insights into the spatial and temporal variability of the community dynamics of both groups of Cladocera. Because of their remoteness and cold climate, mountain lakes have been subject to rather limited studies on

contemporary dynamics of Cladocera, particularly for the littoral group. However, recently the survey of both group of Cladocera in mountain lakes has received more attention since the significance of their fossils on palaeolimnological studies has increased (Frey, 1958, 1960, 1986, 1988).

Unlike lowland lakes, most mountain lakes have bare catchments and limited shoreline littoral vegetation for Chydorid habitats. Growth of shoreline vegetation in these lakes is seasonal, particularly during summer. As a result, the seasonal sampling in mountain lakes could also vary significantly (Manca et al., 1999). A variety of factors can influence the sampling of live Cladocera in mountain lakes. The most important factors include which group or species of Cladocera is to be sampled and what methods and sampling devices are used during sampling. The number of cladoceran collection per unit volume or time of sampling may also vary due to quality, sampling efficiency and the speed of the net being drawn.

Random or uniform distributions are rather uncommon in cladoceran populations since their distributions tend to be patchy. While sampling, various scales of vertical and horizontal distance should be considered carefully (e.g. Wetzel & Likens, 2000). The fine nets around 100 μm mesh openings are suitable for filtering planktonic and littoral Cladocera in mountain lakes. Because of less productive with low macrophyte density, they are unlikely to be clogged by organisms or decayed debris while netting (Fott, 1996). In order to obtain a diverse sample of littoral species, Duigan (1992, 2001) suggested that littoral Cladocera could be sampled at a variety of shoreline substrates. In each substrate, a transect could be made with increased number of replications by pulling a plankton-net horizontally with a constant speed. Methods used for cladoceran zooplankton in this study were mainly based on the methods used by various authors such as Straškrabová et al. (1999), Caroni & Irvine (2000), Rautio et al. (2000) and Duigan (2001) and are outlined in detail below. Based on qualitative judgement, the littoral substrates along the shoreline of Loch Coire Fionnaraich were divided into three dominant microhabitat types, typical of chydorid microhabitats: (i) macrophytes, (ii) sand, and (iii) boulders. The macrophytes and sand habitats were dominant around the western part of the loch, while the boulder or rock dominated areas occurred mainly in the eastern end of the loch (Figure 3.1). A large open-water area, a typical habitat for pelagic cladocerans, was selected as a planktonic micro-habitat type (Figure 3.1).

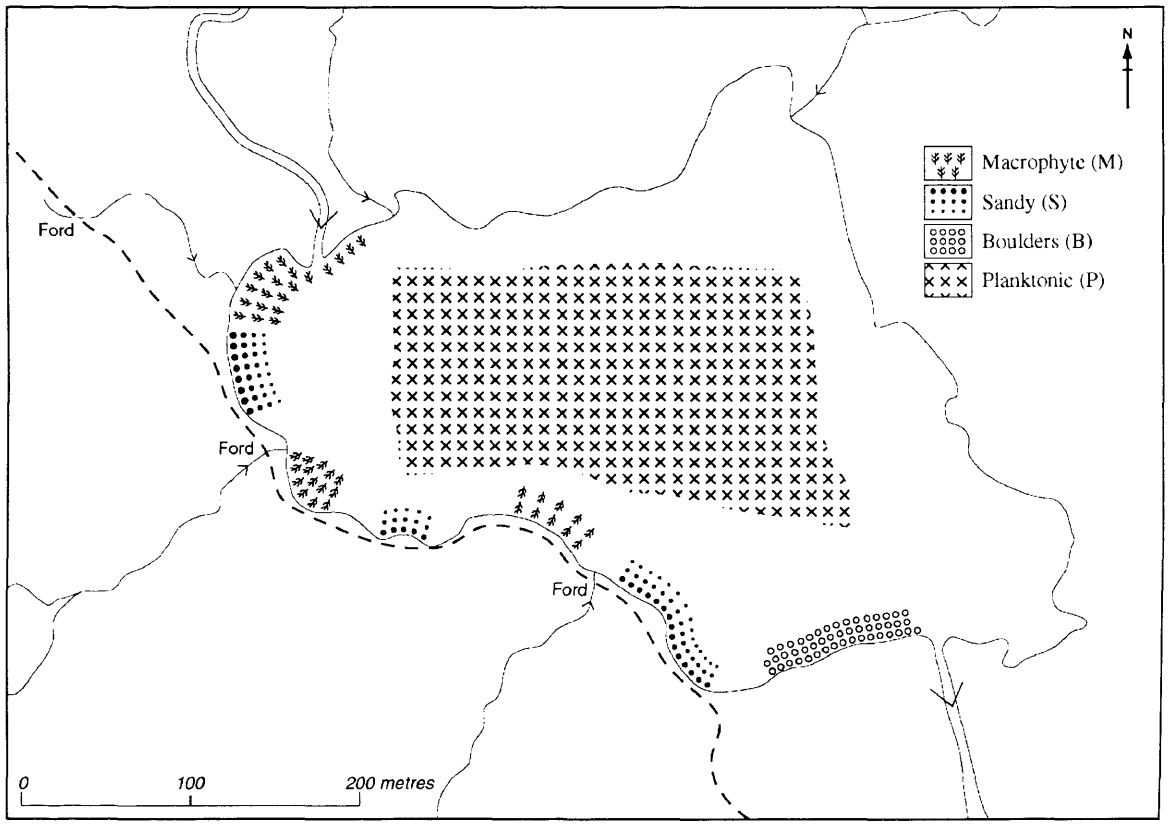


Figure 3.1: Micro-habitat types selected for sampling contemporary littoral and planktonic Cladocera in Loch Coire Fionnaraich, Scotland.

A net with 100 μm mesh size was used for sampling both littoral and pelagic zooplankton. The net was designed with a mouth-reducing cone measuring an average 40 x 20 cm^2 cross-section (Figure 3.2). The mouth of the net was attached with a light circular metallic-rod. The lower end of the net cone was attached with a funnel joined to a hollow rubber tube. A metal clip was used to block and release the sample through the rubber tube (Figure 3.2). The mouth of the net was supported by three short light ropes, which are knotted at a point using a coin-shaped metal disc with a hole at the middle so the net could be attached and detached for sampling pelagic and littoral Cladocera (Figure 3.2). In order to collect the open-water taxa the net was attached with a long bundle of rope with a scale marked on it, while for collecting the littoral taxa, the net was fixed to one end of a 1 m long extendable fibreglass landing pole (Figure 3.2).

3.2.1.1 Collection of cladoceran zooplankton

Open water samples were collected randomly at least 50 m apart, from three deep offshore locations on six occasions, 21 May 2001, 2 August 2001, 15 September 2001, 7 January 2002, 29 April 2002 and 10 August 2002. Seasonal samplings for year 2001 and 2002 were random considering that sampling in any month of summer, June, July or August would represent a summer sample and sampling in any month of winter December, January and February would represent a winter sample. Even though the month of sampling between 2001 and 2002 was similar, the date of sampling was not considered. However, all samples were taken only after the midday in the day of sampling. Samples were taken by hauling the net vertically (Figure 3.2) when the boat was anchored close to the sampling location. While collecting Cladocera, the net was towed approximately 1 m above the bottom to the lake surface at a towing speed of approximately 0.3 m sec^{-1}. After each haul, the inner surface of the net was rinsed several times by lowering the net into the water. Cladocerans were then collected and preserved in an acid washed bottle with 50% iso-propanol.

The total volume (cubic metre) of water filtered was calculated as:

$$V = \pi r^2 x L \qquad \textit{Equation 3.1}$$

Where, V = volume of water filtered, r = radius of the mouth of the net, L = towing length

The littoral zone was sampled by towing the net horizontally to a 5m length. Towing of net was carried out at three different shoreline locations (i) macrophytes, (ii) sand, and (iii) boulder-dominated habitats using the same plankton net as for collecting the pelagic zooplankton (Figure 3.2). While collecting zooplankton, the net was pulled horizontally at a constant speed (0.3 m sec^{-1}) using an extendable fibre rod (Fott, 1996; Straškrabová et al., 1999). Considering that planktonic taxa are also inhabiting the littoral substrata, samples were taken with one motion from different layers in the water column. Firstly, the net was fully submerged and pulled through just above the surface; secondly, the fully submerged net was pulled through the middle of the water column; and thirdly, the half submerged net was pulled through the water surface. The depth of each sampling location for each habitat type was taken. The zooplankton sample was then preserved in an acid washed bottle with 50% iso-propanol solution. The total volume of water filtered at each location was:

$$V = L(5\pi r^2 / 2) \qquad \textit{Equation 3.2}$$

Because of shallow water, the net was not fully submerged in the macrophyte habitat in August 2001 and January 2002, April 2002 and August 2002, while pulling through the middle of the water column, thus the net volume of water filtered in these samples is:

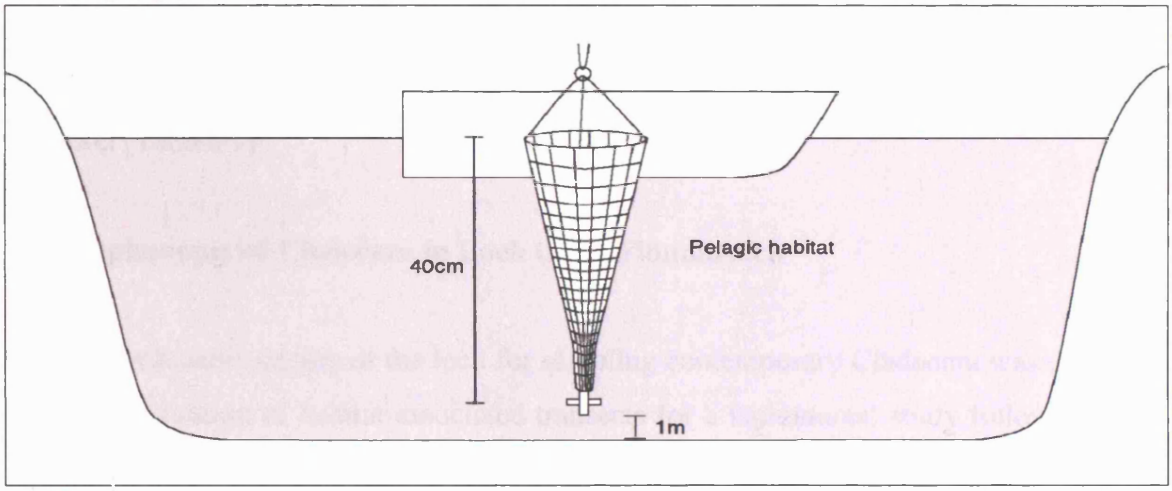
$$V = L(2\pi r^2) \qquad \textit{Equation 3.3}$$

At least three replicates for each planktonic habitat and one-two replicates for each littoral habitat were carried out in the loch depending upon availability of habitat types in a particular season. The sampling replicates for each habitat type are presented in Table 3.1.

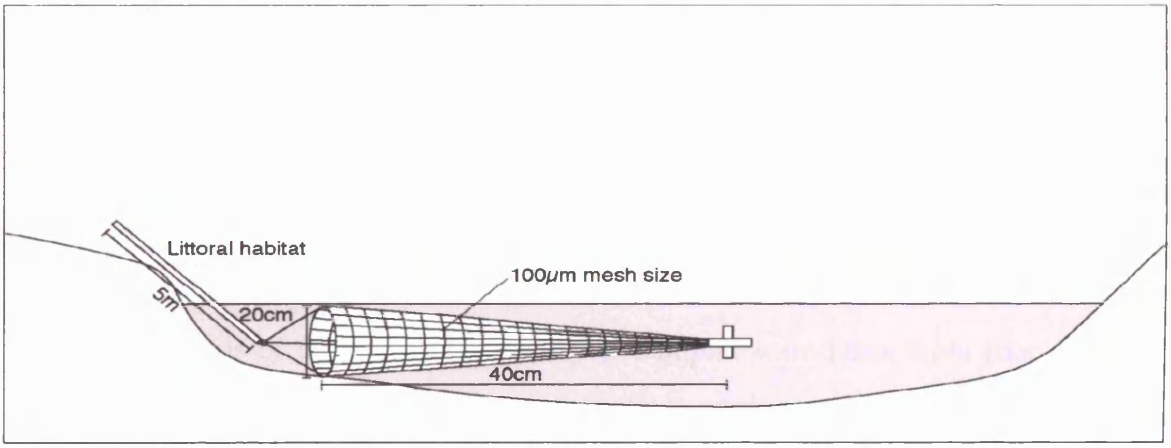
Table 3.1: Sampling replicate/s of live Cladocera for each habitat type among seasons.

Habitat type	**21 May'01**	**02 Aug'01**	**15 Sep'01**	**15 Jan'02**	**29 Apr & 7 May'02**	**10 Aug'02**
	Replicates	Replicates	Replicates	Replicates	Replicates	Replicates
Macrophyte	1	2	2	1	1	2
Sand	1	2	2	1	1	2
Boulder	1	2	2	1	1	1
Plankton	3	3	3	3	3	3

A. Sampling Planktonic Cladocera



B. Sampling Littoral Cladocera



C. Planktonic and Littoral Sampling Methods



Photograph: Gavin Simpson



Photograph: Ewan Shilland

Figure 3.2: Sampling methods of contemporary planktonic and littoral Cladocera in Loch Corie Fionnaraich, Scotland.

Since sampling depth often influences the community dynamics of Cladocera, the depth of sampling location was also recorded while sampling both planktonic and littoral Cladocera. A 'sample' was regarded as the sample taken from each micro-habitat type in one seasonal visit to the loch. Altogether six seasonal visits were made in year 2001 and 2002 (Table3.1).

3.2.2 Taphonomy of Cladocera in Loch Coire Fionnaraich

The comprehensive survey of the loch for sampling contemporary Cladocera was useful for the construction of habitat-associated transects for a taphonomic study followed by collection of spatial surface sediment samples and sediment trap installation.

3.2.2.1 Construction of transects

Cladoceran succession is influenced by the habitat they live in and by environmental conditions (Frey, 1986). In order to know how the remains of Cladocera from each habitat are represented the deep-water sediments, habitat-associated transects were constructed across Loch Coire Fionnaraich. At least three shoreline microhabitat types of Cladocera, macrophyte, sand and boulder, were identified and each transect was then drawn on the basis of these microhabitat types. Samples were taken from four depth points at 2 m, 5 m, 8 m and 11 m of each transect towards the lake centre, where the sediment core was taken at the deepest point of the loch (14 m) (Figure 3.3). The loch was visited twice in August and November 2002. Each time four transects were made. In a total of 8 habitat-associated transects, 3 transects were from shoreline macrophytes, 3 from boulder and 2 were made from sand dominated microhabitat types (Figure 3.3).

3.2.2.2 Collection of surface sediment samples from transects

While taking samples from each transect, at least two people were needed in the boat. At first, Transect 1 with shoreline macrophytes as the dominant microhabitat type was selected. A wooden pole with a yellow flag was placed as a shoreline marker. The straight line transect was made by using a 100 m long rope tied to the pole as well as the boat. The boat was then rowed back towards the centre of the loch where the sediment trap was installed. The desired location at 11 m depth was fixed by using an echo-sounder. A compass was used to make a straight line between the marker, location of the boat and the trap. A boat anchor was dropped as quickly as possible to avoid the possible change of the location of depth. The global positioning satellite (GPS) data and

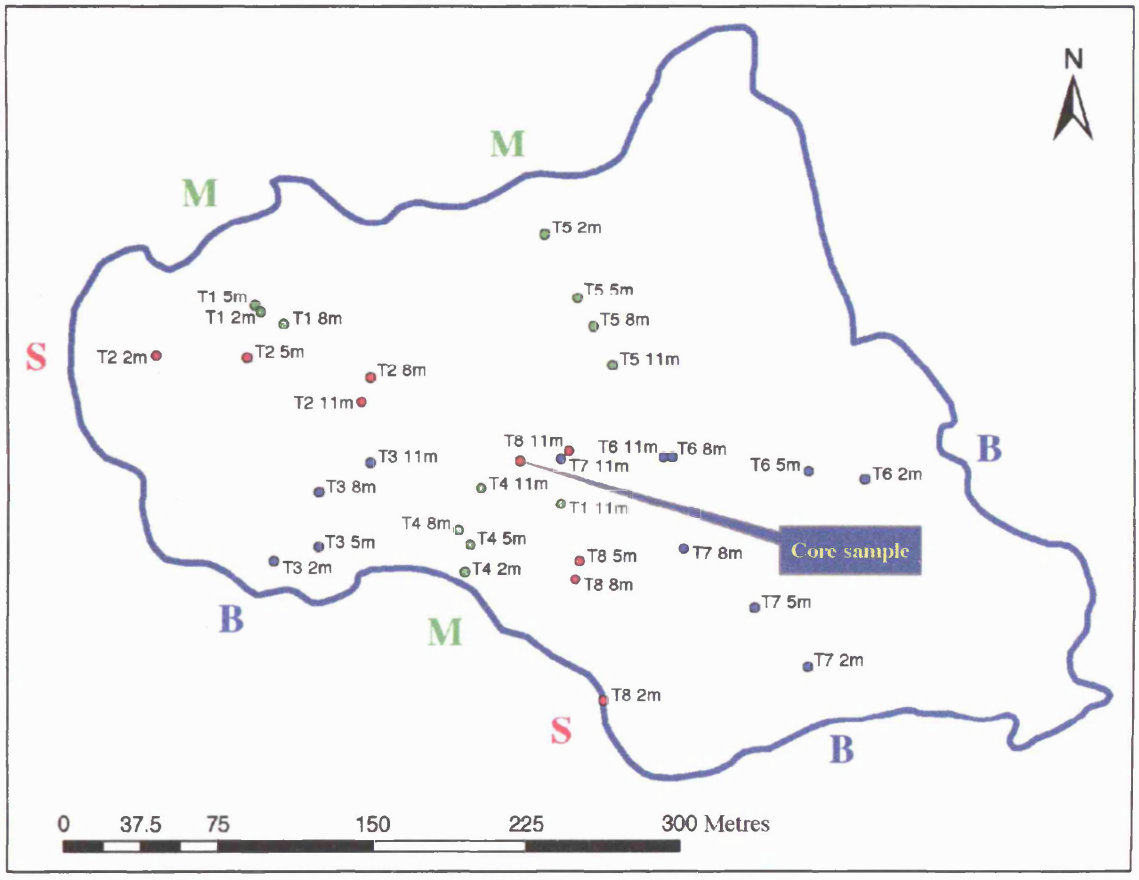


Figure 3.3: Spatial surface sediment samples of Cladocera were taken from 8 horizontal transects, each consisting of four depth points from Loch Coire Fionnaraich. The location of the core is shown as 'core sample' in the centre of the loch. Sampling locations at each transect with respective depths are presented as T1-2m, T1-5m, T-8m, T1-11m followed by other transects, T2, T3,...T8 respectively. The shoreline habitat types, from which each transect ran, was identified by different letters, M = Macrophyte, S= Sand and B = Boulder.

the exact depth of the location of the core were also recorded. Sediment cores were taken by using a Glew corer at the deeper portions of the loch, but at 2 m depth, an Ekman Grab was used. Once the coring was completed the boat was then rowed straight back to the 8m depths followed by 5m and 2m depths. A similar method was used in the rest of the transects. Altogether a total of 32 surface sediment samples was taken from all transects (Figure 3.3).

3.2.2.3 Design of sediment trap

Simple cylindrical sediment traps were built in the ECRC for trapping fossil Cladocera, diatoms and chrysophyte cysts from the water column. The collecting cylinders were constructed by using modified PVC grey drainpipes. The internal diameter of the trap was approximately 10 cm, which was cut to 50 cm lengths to give a 5:1 aspect ratio. Cylinder bases were made from a PVC sheet cut into circular sections and bonded to the pipe with suitable PVC adhesive as described by Cameron (1990). Trap holders were constructed from 15 cm internal diameter PVC grey drainpipe cut to 40 cm sections and secured to a plastic frame containing foam to keep the trap buoyant. The collecting cylinders were secured in these holders by gravity and stainless steel bolts lightly secured against the sides (Figure 3.4). As a result, the collecting cylinders were held securely, but could be removed easily when sampling.

3.2.2.4 Installation of the sediment trap

In order to recover the diatoms, chrysophyte cysts and cladoceran zooplankton fossil remains on a seasonal basis, a trap, with three cylinders, was installed in the central part (14 m) of the loch in May 2001. Even though the trap was anchored on the lake-bed and supported by a float, this trap went missing during the subsequent visits to the loch in August and September 2001. A second sediment trap with three cylinders was therefore installed in parallel in September 2001 at the same location where the first (missing) trap was installed. Finally, both sediment traps were retrieved and reinstalled when the loch was visited in January and May 2002. The first trap was used for diatom analysis by Don Monteith and Roger Flower, while the second trap was used for chrysophyte and Cladocera analysis. The second trap was emptied in August 2002 for the last visit (Table 3.2). Out of three cylinders of the second trap, the material collected in only one cylinder was used for Cladocera analysis in each season, and the remaining two cylinders were analysed by Sergi Pla for chrysophytes. Each time, the sediment trap contents were stored at 4 ^{0}C until analysis.

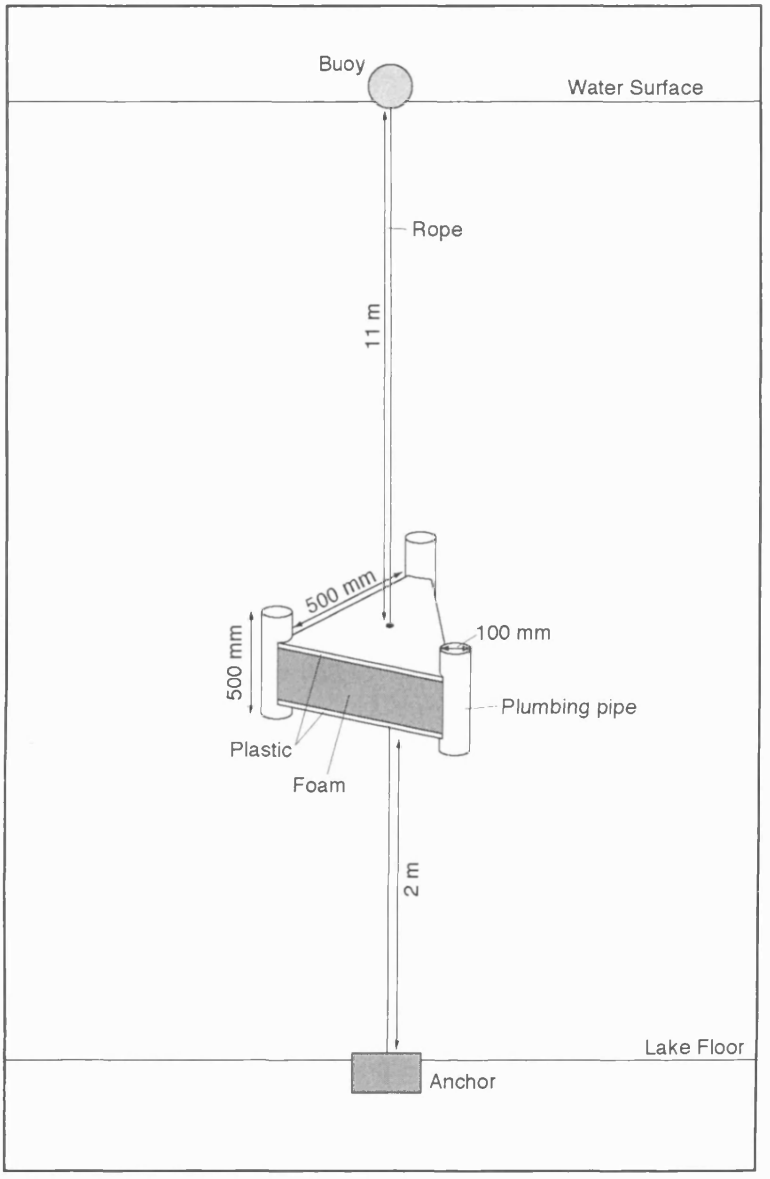


Figure 3.4: Sediment trap installed in the Loch Coire Fionnaraich for a taphonomic study of Cladocera.

Table 3.2: Exposure dates for sediment traps in Loch Coire Fionnaraich, Scotland.

Trap instalment period	From	To	Total exposure days
Period 1	15 September 2001	15 January 2002	122 days
Period 2	15 January 2002	7 May 2002	112 days
Period 3	7 May 2002	10 August 2002	95 days
			Total = 329 days

3.2.3 Training set sites

Similar sampling methods were used for sampling environmental variables between Scottish and Norwegian training set sites (John Birks & Martin Kernan pers. comm.). Methods of collecting samples for most environmental parameters from the EMERGE sites are described in the EMERGE report (1999). The most important methods for the measurement of the physico-chemical variables of water related to this study are described in the following sections.

3.2.3.1 Measurement of environmental variables

July and January air temperatures

There were no temperature stations within the study areas. Therefore, the air temperature was taken from the nearest neighbouring stations using correction for the respective temperature lapse rate with altitude of training set sites. In the case of Norwegian sites, the Botanical Institute, the University of Bergen, already did the correction of the mean July and January air temperatures with respect to temperature lapse rate. However, the correction for the temperatures for the Scottish sites was done as described in Table 3.3.

'Temperature lapse rate' denotes the decrease of temperature per unit increase of height, taken to be positive when temperature decreases with height. The temperature lapse rate is of fundamental significance in atmospheric adiabatic vertical motion and static stability (Livingstone et al., 1999). An adiabatic process (thermodynamic) is one in which heat does not enter or leave the system. Since the atmosphere is compressible and pressure varies with height, adiabatic processes determine changes of vertical temperature distribution within the troposphere. Such adiabatic temperature changes proceed at definite rates. For dry (unsaturated) air the change in temperature per unit height change (lapse rate) is given by the expression:

$$\frac{\gamma - 1}{\gamma} \frac{g}{R} \text{ or } \frac{g}{c\rho} \qquad \textit{Equation 3.4}$$

Where R is the gas constant for air (287 JKg^{-1} ^0K), g the acceleration of gravity (9.8 m s^{-2}) and γ the ratio of specific heats of dry air at constant pressure (c_ρ) and constant volume (c_v) respectively (1.4), from which the 'dry adiabatic lapse rate' (DALR) is about 0.98 ^0C per 100 m or, with sufficient accuracy, 1 ^0C per 100m (5.4 ^0F per 100ft) (http://farside.ph.utexas.edu/teaching/sm1/lectures/node55.html). The lapse rate averages about 0.6 ^0C per 100m in the troposphere, where, however, it is very variable in space and time; over a limited interval of time it may be negative corresponding to an inversion.

The mean July and January air temperatures of Scottish training set sites were estimated after calculation of the temperature from the nearest neighbouring meteorological stations (Table 3.3). The temperatures taken in the nearest neighbouring station vary from the last 7-32 years period depending upon the station. Temperatures were taken in degree C with daily high and daily low-temperatures. These were then averaged as monthly high and monthly low temperature. The monthly high and low temperatures of the nearest neighbouring stations were then averaged for a single mean temperature for July and January air temperatures. The lapse rate for mean July and January air temperatures were given as 0.57 ^0C and 0.44 ^0C every 100 m increasing height (Odland & Birks, 1999).

The lapse rate equation is as follows:

$$T^0C_{(site)} = T^0C_{(nearest\ station)} - (X - Y) * lapse\ rate/100 \qquad \textit{Equation 3.5}$$

Where X and Y are elevation of site and stations respectively.

The mean July and January air temperatures of Norwegian sites were estimated for each lake using 1961-1990 Climate Normals data from 11 nearby climate stations and applying consistent regional lapse rates and a linear interpolation procedure to allow for the small but statistically significant trend in mean July and January air temperatures (e.g. Odland & Birks, 1999; Olander et al., 1999).

Table 3.3: Calculation of mean July and January air temperatures, and mean summer LSWT of Scottish lochs with respect to the nearest meteorological station and lapse rates. For Loch Coire Fionnaraich (L223ICH), air temperature data are obtained from the two nearest sites, Kinlochewe and Plockton, however, the temperature derived from the station, Plockton is more realistic for the lapse rate calculation.

Lake code	Altitude	Nearest station in Scotland	Altitude of the nearest site	Difference	Nearest site temp July (^{0}C)	Nearest site temp January (^{0}C)	Lapse rate (July) every 100m	Lapse rate (Jan ^{0}C) every 100m	Mean Jul T (^{0}C)	Mean Jan T (^{0}C)	Mean summer LSWT (^{0}C)
L007MED	740	Dalwhinnie	351	389	12.73	1.01	0.57	0.44	10.51	-0.70	11.20
L008AIS	810	Dalwhinnie	351	459	12.73	1.01	0.57	0.44	10.11	-1.00	10.99
L009AIN	590	Eilanreach	8	582	14.23	4.22	0.57	0.44	10.91	1.659	11.60
L011AIN	660	Ft Augustus	21	639	14.32	3.09	0.57	0.44	10.67	0.278	12.40
L013MED	720	Eilanreach	8	712	14.23	4.22	0.57	0.44	10.17	1.087	11.50
L015IRE	660	Plockton	12	648	14.03	4.43	0.57	0.44	10.33	1.578	12.30
L017AIR	600	Kinlochewe	25	575	14.17	1.74	0.57	0.44	10.89	-0.79	10.10
L020OIR	540	Plockton	12	528	14.03	4.43	0.57	0.44	11.02	2.106	12.20
L021HAN	520	Kinlochewe	25	495	14.17	1.74	0.57	0.44	11.34	-0.43	12.30
L022ICH	690	Glascarnoch	264	426	13.34	2.4	0.57	0.44	10.91	0.525	10.80
L023DHE	530	Cassley	99	431	13.61	2.52	0.57	0.44	11.15	0.623	11.30
L026ORM	540	Glascarnoch	264	276	13.34	2.4	0.57	0.44	11.76	1.185	12.30
L221IDH	430	Cassley	99	331	13.61	2.52	0.57	0.44	11.72	1.063	11.95
L223ICH	235	Kinlochewe	25	210	14.17	1.74	0.57	0.44	12.97	0.81	13.50
L223ICH	235	Plockton	12	223	14.03	4.43	0.57	0.44	12.76	3.44	13.50

Mean summer lake surface water temperature (LSWT)

Miniature thermistors with integrated data loggers were employed to measure lake surface water temperatures (LSWTs) in EMERGE sites providing at least 1 hour sample interval. The data capacity of Vemco 8-TR Minilogs was 8064 temperature readings; assuming a sampling interval of 1 hour, this corresponds to 11 months of data. Theoretically, it was possible to leave the mini-thermistors in a lake for at least a year, however, it was not possible to visit the site within the given time period to reset them. The mini-thermistors were used to measure LSWT using sensors about 5 cm under the lake surface. It was achieved by inserting them into the undersides of rectangular styrofoam blocks. Acting as floats, the Styrofoam blocks shade the temperature sensor from direct solar radiation. The mini-thermistors were also attached with a string to a small buoy.

The LSWT data were missing for at least four selected EMERGE sites (L008AIS, L013MED, L015IRE and L026ORM) in Scotland due to a loss of thermistors. The LSWT was also not recorded for Lochan Bealach Cornaidh (L221IDH). Thus the mean summer LSWTs of these sites were estimated on the basis of surface water temperature lapse rates in EMERGE Scottish sites in three summer months (June, July and August) as described by Livingstone & Dokulil (2001). The mean summer LSWT of Loch Coire Fionnaraich (L223ICH) was recorded using a portable field thermometer for summer seasons. The mean summer LSWT for Norwegian sites were obtained from the Botanical Institute, University of Bergen, and were also measured using a portable field thermometer under a few centimetres of lake surface water as described in Brook & Birks (2000).

Precipitation

The mean annual rainfall records of the training-set sites were also obtained from the nearest meteorological stations of Scotland and Norway.

Maximum depth

Coring depth was taken as the maximum sampling depth for each site. The maximum depth was recorded by using an echo-sounder.

Physico-chemistry of water

The physico-chemistry data were obtained directly from the Botanical Institute, University of Bergen, Norway and from the EU-EMERGE database for Scotland. Each sample was taken from the shore using acid-washed polyethylene bottles. Collected samples were then stored at 4 ^{0}C until analysis. For European EMERGE (Scotland) and UKAWMN sites, the conductivity was measured directly in the field by placing a probe (ELE Model No.: 4070) in the lake water. Similarly, the pH of these sites was measured using a pH meter (ELE Model No.: 4070) in unstirred water after calibration of the electrode with two buffers, in which buffers with low ionic strength were used. Analysis of other physico-chemistry variables is described later in section 3.3.3.1 (laboratory methods).

3.2.3.2 Collection of surface sediment samples across the training set sites

The surface sediment samples in Scottish EMERGE sites were collected from the upper portion (0.25 cm) of the core sequence at the central part of each lake (EMERGE, 1999) using a Glew corer. The Glew Corer is a simple gravity-operated sampling device, which is well established for recovery of lacustrine sediments. In such operations, the weight of the coring device is used to drive an open-ended core tube into the sediment (Glew, 1991, 1995; Glew and Last, 2001). The extrusion was best achieved by using two sampling rings of differing sizes. The top 0.5 cm section of the core was taken from the UKAWMN sites for surface sediment analysis. The surface sediment samples from the Norwegian sites were collected during summers between 1996 and 1997. Each sample consisted of the 0-1 cm layer of the lake sediment. Samples from Norway were taken from the deepest point in each lake using a modified HON-Kajak corer (Renberg, 1991) following a rapid survey of the bathymetry with an echo-sounder (Brooks & Birks, 2000). The samples were stored in sealed and labelled polythene bags, kept cool in transit to the laboratory, and then stored at +4 ^{0}C as described by Brooks & Birks (2000).

3.2.4 Sediment cores from Loch Coire Fionnaraich

Two short sediment cores, LCFR1 (24.9 cm) and LCFR2 (27.5 cm) were retrieved from the deepest points (14.5 m and 14 m) of Loch Coire Fionnaraich, Scotland in May 2001

using a Glew corer. Even though no earlier comprehensive study had been carried out, it was assumed that the sediment accumulation rate was greatest at these points. Both cores were sub-sampled in the field within 24 hours at 0.2 cm and 0.5 cm intervals respectively. Each sediment sub-sample was transferred into a labelled plastic bag. The plastic bag was then sealed and stored in the laboratory at 4 ^{0}C until further analysis.

3.3 Laboratory methods

Laboratory methods include analyses of contemporary zooplankton and fossil Cladocera for Loch Coire Fionnaraich as well as water chemistry, and preparation of fossil Cladocera across the training set sites in Scotland and Norway.

3.3.1 Contemporary Cladocera analysis

Quantitative zooplankton analysis was carried out by using a 1 ml sub-sample volume of lake water sample on a glass cover plate and examined under a binocular microscope at x100 magnification. For samples with rich zooplankton abundance, a minimum of 100 individuals were counted from each sub-sample, for which about 2-5 sub-sample volumes were needed. However, for samples with poor zooplankton abundance, counting was continued until the count of subsequent sub-sample volumes was constant. For this, an average of 7-10 sub-sample volumes was needed. Then the total count of the sample was estimated as the number of zooplankton per cubic metre of water using the sub-sample count of zooplankton. A detailed method for zooplankton counting through sub-sampling is described in Wetzel & Likens (2000).

All contemporary cladoceran zooplankton were identified to species level. Identification was carried out by using Scourfield & Harding (1958) and Flößner (1972). Non-cladoceran zooplankton were not identified to species level, but they were given as the group name such as 'copepods' and 'rotifers'. According to Filter and Manuel (1995) and Olsen et al. (2001), the dominant genera of copepods in the loch were identified as *Diaptomus* and *Cyclops* and the dominant genus for rotifer was identified as *Keratella*.

3.3.2 Taphonomy of Cladocera

3.3.2.1 Spatial surface sediment samples

The analyses of DW, LOI and fossil Cladocera of spatial surface sediment samples along the various transects are described below.

Dry weight (DW) and loss-on-ignition (LOI) analysis

The spatial surface sediment samples were subjected to analysis for percentage dry weight and loss-on-ignition. Between 1 and 2 g of wet sediment was added to empty pre-weighed crucibles carefully avoiding any drops of sediment around the rim of the crucible. The crucibles were reweighed and placed in oven overnight at 105 ^{0}C. The crucibles were then removed from the oven and kept in the desiccator before reweighing to prevent re-absorption of moisture. The percentage weight remaining after drying (DW) was then calculated. The crucibles with dried sediments were placed in a furnace (Carbolyte) and kept at 550 ^{0}C for 2 hours in order to estimate the percentage loss on ignition (LOI). Methods for calculating the dry weight (DW) and loss on ignition are presented in detail in Meyers & Teranes (2001).

Fossil Cladocera analysis

The analysis of fossil Cladocera was based mainly on Frey (1986) and recently revised procedures by Korhola & Rautio (2001). However, a slight modification, on selection of sieve and duration of KOH solution in hotplate, was made for this study, which is described below.

Approximately 4-8 g of sub-sample volume of sediment was taken for the Cladocera analysis. Each sub-sample volume was then treated with 100ml, 10% KOH solution and heated with 60 ^{0}C (adjusted temperature) on a hotplate for at least 45 minutes. Each sub-sample mixture was constantly and gently stirred by a glass-rod to deflocculate all organic materials without damaging the remains. The sub-sample mixture was then sieved through a 38 μm sieve. Sieving was continued with running tap water until the rinse was clear. The sediment residue was then flushed gently into a pre-weighed and labelled tube, using a squeezer and a funnel, then stored in a freezer overnight to settle down the remains completely. Once the supernatant fluid was removed, a few drops of methanol were added into the tube for preservation. A few drops of safranin were also added to stain the remains. The tube with remains was weighed and quantitative slides

were prepared by pipetting 0.1 ml of each sub-sample volume on a microscope slide. The remains in an object glass were well spread out and allowed to dry gently on a hot plate before it was covered with a cover slip (22 mm x 50 mm) to make a permanent slide using warm glycerol jelly. All slides were then examined in a microscope under 100 and 400x magnification.

All Cladocera remains found (carapaces, head-shields, post abdomen, ephippia, and post-abdominal claws) were tabulated separately, but only the most frequent body parts for each taxon were used for estimating the species abundance; if the two halves of the bilateral carapace came apart, one half was counted as half an individual. Badly fragmented remains were counted if they contained a clear diagnostic feature as described by Goulden (1969). The dry weight percentage of each sediment sample was used to calculate the counted portion of remains present in per gram of dry sediment. Identification was carried out by using Frey (1958, 1959); Whiteside et al., (1978); Frey (1986), Korhola & Rautio (2001). The identification of cladoceran remains is described in detailed and presented in Appendix 3.1.

3.3.2.2 Sediment traps

The Cladocera remains in the sediment traps were analysed using a slightly different method from the analysis of fossil Cladocera described in the previous section (3.3.2.1). First, a filter paper was weighed and dried in an oven at 150 ^{0}C overnight. Trap material was then filtered through a pre-weighed-dried filter paper. The filter paper with filtrate (residue) was then transferred to a dryer at 50 ^{0}C for at least three days. Once the residue was completely dry, the net dry weight of trap materials was calculated. The materials were then subjected to Cladocera analysis as described above. The number of cladoceran remains was calculated as number per gram of dry material.

3.3.3 Training set sites

3.3.3.1 Analysis of physico-chemical variables of water samples

The laboratory methods for the physico-chemical analysis of water of training set sites were carried out in the EU-EMERGE project Scotland, the UKAWMN and the Botanical Institute, University of Bergen. Methods used by all three institutes were very similar, and are described briefly below.

The measurements of conductivity and pH of Norwegian sites were carried out in the laboratory (Brooks and Birks, 2000). The alkalinity measurement was carried out using Gran titration techniques (Gran, 1950; Marcheto, 1997). Alkalinity is the capacity to neutralise strong acids such as HCl, H_2SO_4 and HNO_3 (Wetzel & Likens, 2000). The concentration of ammonium ions (NH_4^+) was estimated by using a membrane electrode (ABB Kent-Taylor) following the method developed by Beckett & Wilson (1974). Measurements of anions such as nitrate, sulphate, phosphate and chloride concentrations were carried out by using an ion chromatography method as described in Tartari et al. (1995). The concentrations of cations, Ca^{2+}, Mg^{2+}, Na^+, K^+, Mn^{2+}, Al^{3+} were measured by using the techniques described by Jennins et al. (1997).

3.3.3.2 Dry weight (DW) and loss-on-ignition (LOI) analysis

The surface sediment samples from each training set site were subjected to analysis for percentage DW and LOI. The analyses of DW and LOI were carried out on the basis of methods described in the previous section 3.3.2.1.

3.3.3.3 Fossil Cladocera analysis

The analysis of fossil Cladocera was carried out on the basis of methods described in section 3.3.2.1. The method for the identification of remains is described in Appendix 3.1.

3.3.4 Core sequence

The analysis of DW, LOI and fossil Cladocera were carried out on the basis of methods described in section 3.3.2.1. Of the two cores which were taken from Loch Coire Fionnaraich (see section 3.2.4), the first core, LCFR1, was used for lithostratigraphy, bulk sediment analyses, ^{210}Pb dating and the analysis of subfossil assemblages of diatoms and chrysophytes (Flower and Pla, unpublished), while the second core, LCFR2 was mainly used for bulk sediment analyses and analysis of Cladocera. The dating of LCFR1 was carried out by P.G. Appleby at the Department of Mathematics, Liverpool University. The dating of LCFR2 was, however, conducted by core correlation technique with LCFR1. Core details and dating are further described in Chapter 7.

3.4. Numerical analyses

Numerical analyses were performed on multivariate data from a large number of environmental and biological samples collected from Loch Coire Fionnaraich, and training set sites across Scotland and Norway. From Loch Coire Fionnaraich, mainly the biological data-sets of contemporary Cladocera, spatial surface sediment samples, and subfossil assemblages of Cladocera, and environmental variables (e.g. depth, micro-habitats) associated with the loch were used for data analyses, while from the training set sites, both environmental (e.g. spatial and physico-chemical) and biological data-sets were used for numerical analyses. Most of these data were used for indirect and direct gradient analyses in ordination using CANOCO 4.5 (ter Braak & Šmilauer 2002). Data from training set sites were also used for multiple regression analyses. Generalized linear models (GLM) and weighted averaging (WA) methods were used to explore species-environment relationships using Huismann-Olff-Fresco (HOF) models (Oksanen and Minchin, 2002), and CALIBRATE (version 0.81, Juggins and ter Braak, 1997). The contemporary samples in Loch Coire Fionnaraich, were classified in two-way indicator species analysis (TWINSPAN, Hill, 1979). Zonation of sediment core data was performed by cluster analyses (e.g. CONISS) using the program ZONE (Juggins, 1991, University of Newcastle-upon-Tyne).

Data manipulation and transformation were performed in WinTran (1.5) and Excel (2000). The graphical presentations of contemporary and modern fossil assemblages of Cladocera were made in ordination using CANODRAW 4.5 (ter Braak & Šmilauer 2002). Stratigraphic diagrams were made in C2 (Juggins, 2003). Representation (taphonomy) of Cladocera in Loch Coire Fionnaraich was presented as thematic maps using the Arc-GIS program (version 2.0). Methods, including the theoretical backgrounds of gradient analyses used in this study are described briefly in the following sections.

3.4.1 Ordination

Ordination techniques were used to explore the assemblage structures of contemporary and fossil Cladocera across the environmental gradients of Loch Coire Fionnaraich as

well as the training set sites of Scotland and Norway. Ordination is the multivariate technique used to arrange a large number of samples (sites) in two-dimensional scales on the basis of data on species composition. In such arrangement, samples are represented as points, where points close together are similar in species composition and points far apart are dissimilar in composition.

3.4.1.1 Principal components analysis (PCA)

PCA is an ordination technique, which involves an eigen-analysis of the correlation matrix. In eigen-analysis, eigen-vector and eigenvalues of the matrix are calculated. The eigenvector and eigenvalues are the key concepts of matrix algebra, in which the sample scores are regarded as eigenvectors, while eigenvalues measure the strength of an ordination axis (Cliff, 1987). PCA relates to a linear response model in which the abundance of any species either increases or decreases with the value of each of the latent environmental variables or eigenvalue (ter Braak, 1995). PCA is useful for the analysis of samples in environmental space since, unlike species data, environmental variables are monotonically related to each other (ter Braak, 1995; Leps and Smilauer, 2003).

PCA was used to explore the major patterns of variation in the contemporary zooplankton data-set collected across the various micro-habitats of Loch Coire Fionnaraich. PCA was also used for the taphonomic study of Cladocera in Loch Coire Fionnaraich. The representation of Cladocera was evaluated by comparing the variation in their assemblage structures in the core sample and the surface sediment samples across the sediment-transects. The patterns of variations in physico-chemical variables and modern fossil assemblages of Cladocera across the training set sites of Scotland and Norway were also summarised using PCA. PCA was also used for a time-track analysis of the sub-fossil assemblages of Cladocera in the sediment core, LCFR2.

3.4.1.2 Detrended correspondence analysis (DCA)

DCA was used to assess the gradient lengths or the standard deviation units of the contemporary and fossil assemblages of Cladocera in Loch Coire Fionnaraich as well as the modern assemblages of fossil Cladocera across the training set sites of Scotland and Norway. It was also performed to explore the principal patterns of compositional variations of the assemblage structures of live Cladocera along temporal and spatial scales in Loch Coire Fionnaraich. Since correspondence analysis (CA) suffers from two

major problems: arch effect and gradient compression, Hill & Gauch (1980) developed a new ordination method, DCA, to correct such problems by 'detrending' and 'rescaling' the first axis. Detrending is the process of removing the arch effect, in which the first axis is divided into segments, and then the second axis is centred on zero. In rescaling the positions of the samples along the ordination axis are shifted to make the beta diversity constant (Gauch, 1982; ter Braak & Šmilauer 2002; Leps and Smilauer, 2003).

3.4.1.3 Redundancy analysis (RDA)

RDA was used to explore the patterns of species-environment relationships of total contemporary zooplankton assemblages along temporal and spatial scales of Loch Coire Fionnaraich. It was also performed to explore the relationships between the modern fossil assemblages of Cladocera and the measured physico-chemical variables across the training set sites of Scotland and Norway. RDA is a multivariate direct gradient analysis method in which species are presumed to have a linear relationship to environmental gradients. Thus RDA is also called reduced-rank regression since its application in community variance is within a narrow range (ter Braak & Prentice, 1988). In RDA, linear combinations of independent environmental variables are formed that account for successively maximal proportions of the total sum of squares over the set of biological response variables, where it gives the smallest total residual sum-of-squares (Birks, 1995). The results of RDA can be expressed in a tri-plot, i.e. a plot of sample scores, species scores and environmental arrows. The arrows in RDA can represent species scores more accurately, in which the direction of the arrows is an increasing abundance of species (ter Braak & Šmilauer 2002; Leps and Šmilauer, 2003).

3.4.1.4 Detrended canonical correspondence analysis (DCCA)

DCCA is an integration of regression and ordination (e.g. ter Braak, 1987; ter Braak and Juggins 1993; Birks 1995, Korhola 1999). This was used to assess the mode of response (i.e. gradient lengths) of cladoceran assemblages across the mean summer lake surface water temperature gradients in training set site. This was also used as a guide for identifying the large secondary gradients (e.g. Lotter et al. 1997). DCCA was performed with detrending-by-segments, non-linear rescaling and square-root transformation of percentage data and down weighting of the rare taxa (e.g. Korhola, 1999).

3.4.1.5 Partial ordination

Partial RDA was used to partial-out the effects of co-variables in cladoceran assemblages in calibration data-set in Scotland and Norway. Partial ordination is called a 'residual regression' or 'variance partitioning' (Qinghong & Bråkenhielm, 1995). Borcard et al. (1992) argued that in ordination, some species and environmental variables often share a common spatial structuring, this might be due to the impact of spatially structured environmental predictors on the response variable, which is not included in the model. As a result, a common spatial structure appears in both the independent and dependent variables of the model. In partial ordination, the amount of variation in the species data that is due to this common spatial structuring is extracted by both the environmental and the spatial sets of explanatory variables (Borcard et al., 1992).

Chapter 4

Variations in patterns of cladoceran community in littoral and open water habitats of Loch Coire Fionnaraich, Scotland

4.1 Introduction

This chapter describes the variations in patterns of cladoceran community in littoral and planktonic habitats of Loch Coire Fionnaraich (LCFR). Loch Coire Fionnaraich presents ideal habitats for both littoral and planktonic Cladocera with a variety of shoreline substrata for chydorid Cladocera and an open-water habitat for planktonic Cladocera. Replicated samples were taken from shoreline littoral micro-habitats (macrophyte, sand, boulder) as well as open-water habitats (Figure 3.1) on a seasonal basis. Patterns of variations in the assemblage structure of Cladocera in the loch were assessed using indirect gradient analyses in CANOCO 4.5 (ter Braak and Šmilauer, 2002).

4.2 Materials and methods

4.2.1 Field methods

Details of the Cladocera sampling methods are presented in Chapter 3, Section 3.2.1. Altogether 24 samples were collected from four micro-habitat types (macrophyte, sand, boulder and plankton) in six seasonal visits to Loch Coire Fionnaraich (Table 3.1). The coding for the sample was given as month-year of sampling-habitat type. For example, the sample collected in May 2001 from macrophytes was coded as May'01M. Similarly, the sample collected in September 2001 from a sandy habitat was coded as Sep'01S (see Appendix 4.1 for details).

4.2.2 Laboratory methods

Sub-sample (1 ml) volumes of a sample were counted one at a time. The number of sub-samples to be counted was decided by whether the sub-samples had more than 100

counts of the dominant taxa or if the sub-sample had a poor representation of Cladocera. Sub-samples were counted until the cumulative number of dominant taxa present per sub-sample volume was constant for at least 7 sub-samples. The total number of zooplankton present in a sample was then estimated by multiplying the mean number of zooplankton present in a sub-sample volume and the total volume of the sample. The number of zooplankton per cubic metre was calculated by dividing the total number of zooplankton counted in a sample by the volume of water filtered. The number of zooplankton counted from different locations of the same micro-habitat type was harmonized following the estimation of percentage counts of zooplankton in each sample for ordination analyses.

4.2.3 Numerical analyses

Since the data-set was rather small and irregular, the direct gradient analysis in ordination was not considered appropriate. However, the patterns of the cladoceran community structure along seasonality and habitat gradients in Loch Coire Fionnaraich were carried out using indirect gradient analysis such as DCA in CANOCO 4.5 (ter Braak & Šmilauer, 2002). The DCA ordination method is described in Chapter 3 in detail. Cladoceran samples were also classified using a two-way indicator species analysis (TWINSPAN) (Hill, 1979). TWINSPAN is one of the most widely used programs in community ecology. The program classifies the samples and it also constructs an ordered two-way table from a sites-by-species matrix.

4.3 Results

4.3.1 Species richness, occurrences and composition of Cladocera in LCFR

A total of 36 cladoceran taxa was recorded in Loch Coire Fionnaraich in six seasonal visits to the loch between May 2001 and August 2002. The highest number of species was recorded in 21 May 2001 in the boulder habitat, when a total of 15 cladoceran taxa was recorded (Figure 4.1). The lowest species richness was recorded in 29 April 2002 in sand and boulder habitats where only 4 cladoceran taxa were recorded (Figure 4.1). Number of species recorded between spring and summer 2001 and 2002 varied considerably. The number of species recorded for spring 2001 was higher than that of

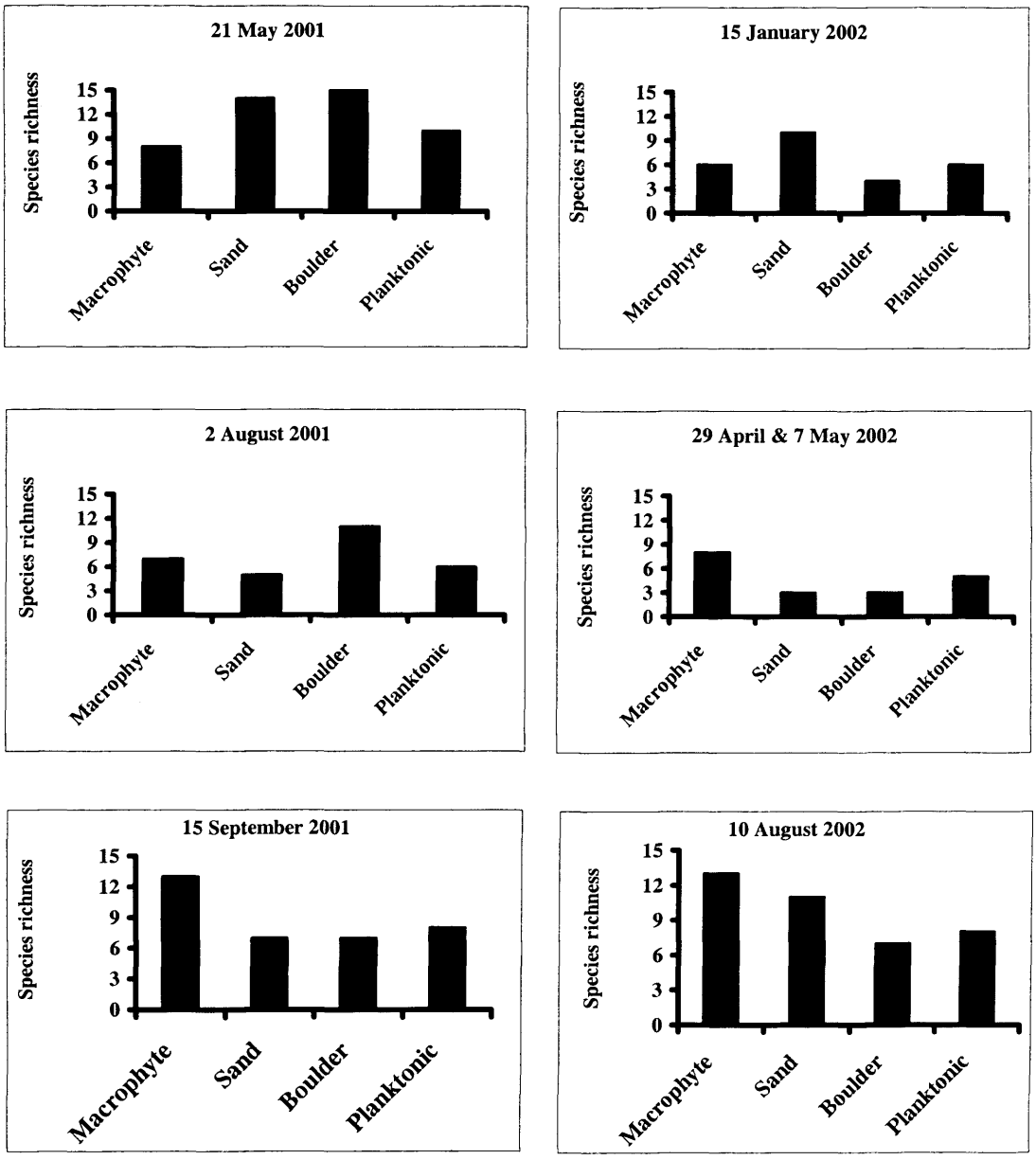


Figure 4.1: Species richness (total number of species) of Cladocera along seasons and habitat types in Loch Coire Fionnaraich, Scotland. The sampling replicates for each microhabitat type from each season have been given in Table 4.1.

spring 2002, but the number of species recorded in summer 2001 was lower than the number of species recorded in summer 2002 (Figure 4.1).

The occurrences of Cladocera in Loch Coire Fionnaraich are presented in Table 4.1. The highest Cladocera count was recorded on 02 August 2001 for the macrophyte habitat, where a total of 16,568 individuals were recorded (Table 4.1). The lowest count was recorded in 29 April 2002 for the boulder habitat, where only 12 Cladocera were counted (Table 4.1). A large number of planktonic Cladocera such as *Bosmina* and *Daphnia* was recorded in the planktonic habitat while most littoral taxa were recorded for the macrophyte, sand and boulder habitat (Table 4.2).

The mean density of littoral and planktonic Cladocera recorded per cubic metre of water sampled in Loch Coire Fionnaraich from the four micro-habitat types, regardless of season, is presented in Figure 4.2a. The highest density of littoral Cladocera was recorded in the macrophyte habitat followed by sand, boulder and plankton. The density of littoral Cladocera recorded in the macrophyte zone was approximately 3000 individuals per cubic metre of water sampled, where the number of Cladocera recorded in this habitat alone was more than the total number of Cladocera recorded in the other three microhabitat types, sand, boulder and plankton combined (Figure 4.2a). The highest density of planktonic Cladocera was recorded in the plankton samples followed by macrophyte, sand and boulder samples. The density of planktonic Cladocera in the open water habitat was less than 1000 individuals per cubic metre water filtered, which is far less than the density of littoral Cladocera recorded in the macrophyte zone (Figure 4.2a).

The mean density of Cladocera per cubic metre of water sampled in Loch Coire Fionnaraich from six seasonal visits regardless of micro-habitat types is presented in Figure 4.2b. The density of planktonic Cladocera was rather low in all seasons being lowest (~40 individuals per cubic metre) in winter 2002 and highest (>500 individuals per cubic metre) in autumn 2001 (Figure 4.2b). However, the density of littoral Cladocera was highly variable in seasonally being high (1500-2300 individuals per cubic metre) in spring and summer 2001 and 2002 and low (90-200 individuals per cubic metre) in autumn and spring 2001 and spring 2002 (Figure 4.2b).

Table 4.1: Seasonal occurrence (total count) of total Cladocera among four micro-habitat types (M= Macrophyte, S = Sand, B = Boulder, P = Planktonic or Open Water) in Loch Coire Fionnaraich, Scotland. The numbers in brackets represent the sampling replicates.

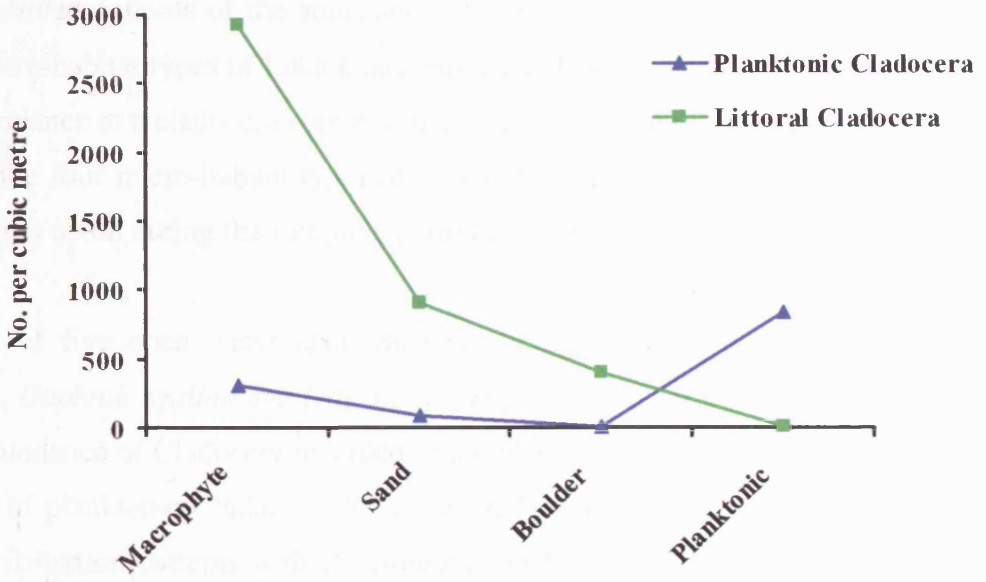
Cladocera/Seasons	21 May 2001				02 August 2001				15 September 2001				15 January 2002				29 April & 7 May 2002				10 August 2002			
Microhabitats	**M (1)**	**S (1)**	**B (1)**	**P (3)**	**M (2)**	**S (2)**	**B (2)**	**P (3)**	**M (2)**	**S (2)**	**B (2)**	**P (3)**	**M (1)**	**S (1)**	**B (1)**	**P (3)**	**M (1)**	**S (1)**	**B (1)**	**P (3)**	**M (2)**	**S (2)**	**B (1)**	**P (3)**
Bosmina coregoni	-	14	4	1909	-	5	19	533	635	122	-	1456	-	11	12	209	-	-	4	3627	760	187	18	405
Bosmina longispina	-	76	10	521	-	-	15	1283	1435	-	-	1897	-	-	-	-	8	-	4	1148	2280	1143	18	468
Bosmina longirostris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	240	-	-	52
Daphnia glaeata	-	-	2	538	-	-	-	80	-	-	-	-	-	-	-	-	-	-	-	13	-	-	-	13
Daphnia hyalina	-	-	-	395	-	-	-	219	-	-	-	29	-	-	-	-	-	-	-	25	-	-	-	-
Daphnia longispina	-	-	-	298	-	-	-	43	-	30	-	104	11	22	12	174	-	-	-	930	-	-	-	74
Daphnia magna	-	-	-	-	-	-	-	-	-	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Daphnia culculata	-	-	-	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Daphnia ambigua	-	-	-	-	-	-	-	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diaphanosoma brachyurum	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ceriodaphnia dubia	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	4	-	-	-	-	-	-	-
Acroperus elongatus	8388	28892	39	-	3830	650	1672	-	684	507	164	6	130	56	70	-	140	9	4	-	9458	6038	1818	90
Monospilus dispar	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	74	28	-	-
Polyphemus pediculus	72	248	23	45	11078	6050	386	-	14	-	-	-	-	-	-	-	-	-	-	-	274	157.5	36	-
Chydorus piger	36	124	4	-	32	-	-	-	47	15	-	-	-	11	-	2	-	-	-	-	40	26	-	21
Chydorus sphaericus	-	-	6	-	-	-	-	-	17	-	-	-	11	11	-	-	-	-	-	-	-	-	-	-
Alonella exigua	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alonella excisa	-	-	7	-	-	-	11	-	-	-	12	4	-	-	-	-	-	-	-	-	-	54	54	-
Alonella nana	144	496	19	-	224	-	15	-	149	-	-	-	22	11	-	-	4	-	-	-	40	28	-	-
Acroperus harpae	216	744	10	15	734	183	252	-	295	172	19	14	140	11	-	-	12	-	-	-	886	400	342	-
Alona guttata	-	0	8	-	350	9	-	-	132	-	12	-	-	37	12	-	4	-	-	-	-	-	-	-
Alona intermedia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18	-
Alona rustica	-	-	-	12	320	-	-	-	176	77	120	-	-	22	-	-	12	18	-	-	-	-	-	-
Eurycercus lamellatus	72	248	-	-	-	-	-	-	17	-	-	-	-	-	-	-	-	-	-	-	40	-	-	14
Alona affinis	-	-	-	-	-	-	-	-	17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Camptocercus rectirostris	-	-	2	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	21 May 2001				02 August 2001				15 September 2001				15 January 2002				29 April & 7 May 2002				10 August 2002			
Rhynchotalona falcata	-	-	-	-	-	-	-	-	-	30	12	-	11	-	-	-	4	-	-	-	40	-	-	-
Oxyurella tenuicaudis	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pleuroxus truncatus	-	-	-	-	-	-	37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1575	-	-
Lathonura rectirostris	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Macrothrix sps	36	-	-	-	-	-	4	-	-	-	-	-	-	-	-	18	-	-	-	-	-	-	-	-
Leptodora kindtii	36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-	-	-	-	-	-	-	-
Bythotrephes longimanus	-	-	-	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sida crystallina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1160	-	-	-
Graptoleberis testudinaria	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-	-	-	-	-	-	440	-	-	-
Streblocerus serricaudatus	-	-	-	-	-	-	-	-	14	-	12	-	-	-	-	-	-	-	-	-	-	27	-	-
Total Cladocera	**9000**	**30849**	**144**	**3778**	**16568**	**6897**	**2419**	**2183**	**3631**	**968**	**351**	**3517**	**325**	**203**	**106**	**415**	**188**	**36**	**12**	**5743**	**15732**	**9661**	**2304**	**1137**

Table 4.2: Occurrence (total count) of Cladocera among four microhabitat types in Loch Coire Fionnaraich, Scotland.

Taxa	Abbreviation	Macrophyte	Sand	Boulder	Planktonic
Bosmina coregoni	Bos cor	1403	337	56	8139
Bosmina longispina	Bos lspn	3715	916	864	4955
Bosmina longirostris	Bos lngr	240			52
Daphnia galeata	Dap gal			2	620
Daphnia hyalina	Dap hya				668
Daphnia longispina	Dap lon	7	53	12	1624
Daphnia magna	Dap mag		16		
Daphnia cucullata	Dap cul				15
Daphnia ambigua	Dap amb				25
Diaphanosoma brachyurum	Diap bra		7		
Ceriodaphnia dubia	Cer dub	1			7
Acroperus elongatus	Acr elo	22629	7457	3766	96
Monospilus dispar	Mon dis	74	93	2	0
Polyphemus pediculus	Pol ped	11438	6267	445	45
Chydorus piger	Chy pig	155	59	4	21
Chydorus sphaericus	Chy sph	27	28	6	12
Alonella exigua	Alo exi			6	
Alonella excisa	Alo exc		57	87	4
Alonella nana	Alo nan	582	54	34	
Acroperus harpae	Acr har	2283	795	280	371
Alona guttata	Alo gut	486	53	31	
Alona intermedia	Alo int			18	
Alona rustica	Alo rus	508	121	120	12
Eurycercus lamellatus	Eur lam	129	3		13
Alona affinis	Alo aff	17			
Camptocercus rectirostris	Cam rec			6	
Oxyurella tenuicaudis	Oxy ten			2	
Rhynchotalona falcata	Rhy fal	55	1610	12	
Pleuroxus truncatus	Ple tru			37	
Latothonura rectirostris	Lat rec			4	
Macrothirx sp	Macrothrix	36		4	12
Leptodora kindtii	Lep kin	36			18
Graptoleberis testudinaria	Gra tes		37		
Streblocerus serricaudatus	Str ser	454		12	
Sida crystallina	Sid cry	1160			
Bythotrephes longimanus	Byt lon				30

(a)



(b)

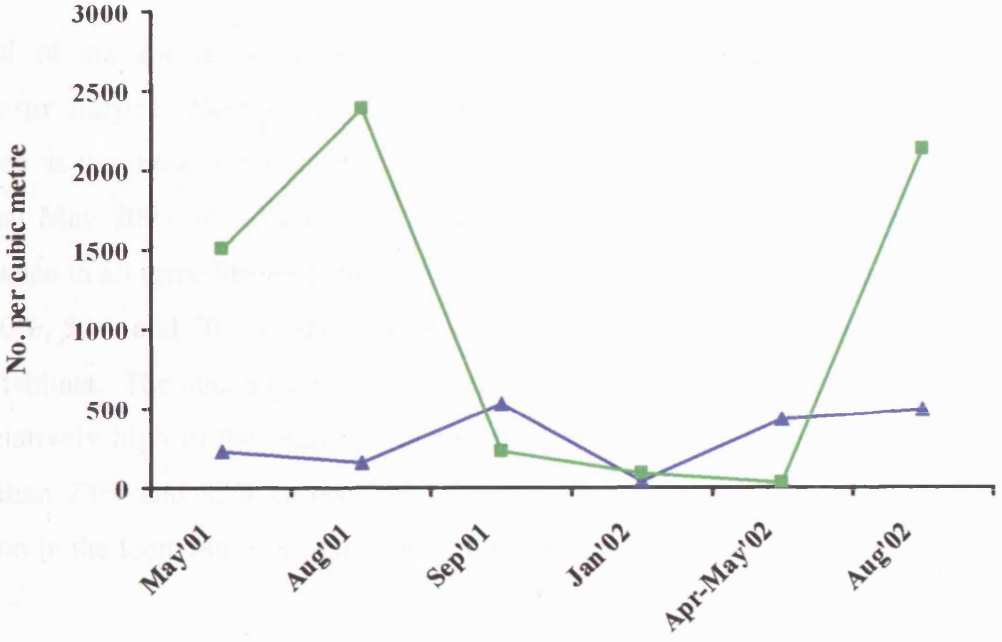


Figure 4.2: Composition of planktonic and littoral Cladocera in Loch Coire Fionnaraich. (a) composition with respect to microhabitat, (b) composition with respect to season.

4.3.2 Observed patterns of the abundance of the common species of Cladocera

The observed patterns of the abundance of the most common species of Cladocera in four micro-habitat types of Loch Coire Fionnaraich are presented in Figure 4.3a & b. If the abundance of a cladoceran taxon was at least 1% of the total cladocerans recorded in one of the four micro-habitat types of LCFR, this taxon was regarded as the common cladoceran taxon during the sampling period between May 2001 and August 2002.

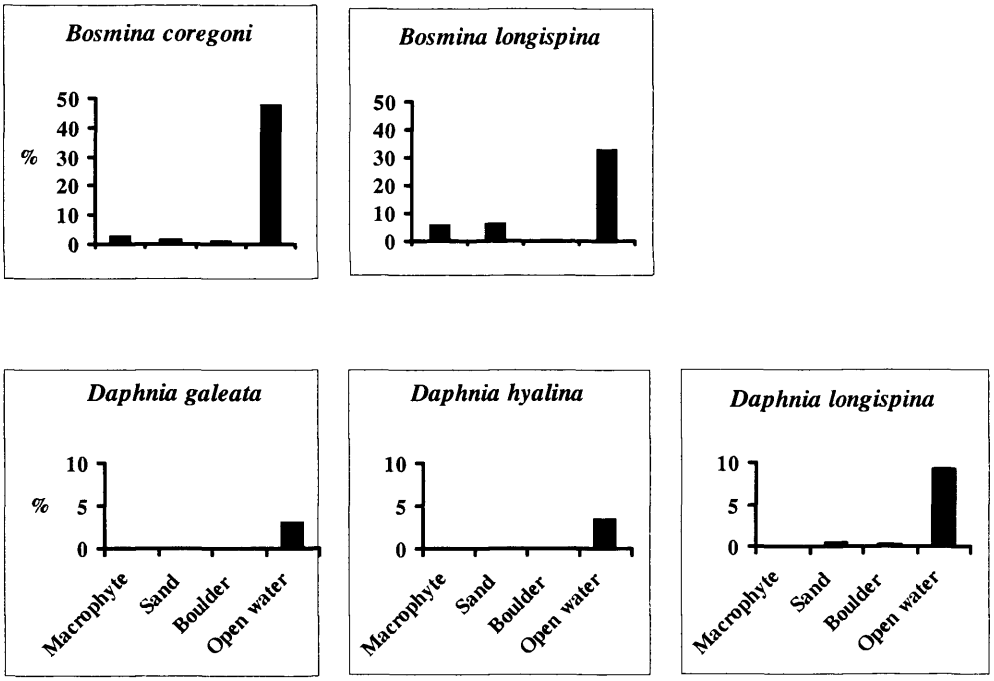
A total of five open water taxa, *Bosmina coregoni*, *Bosmina longispina*, *Daphnia galeata*, *Daphnia hyalina* and *Daphnia longispina* had more than 1% abundance of the total abundance of Cladocera recorded in the plankton of the loch. However, only three species of planktonic Cladocera, *B. coregoni*, *B. longispina* and *D. longispina* showed clear distribution patterns with *B. coregoni* and *B. longispina* dominating contributing more than 30% of the total Cladocera in the open water habitat (Figure 4.3a). The three species, *B. coregoni*, *B. longispina* and *D. longispina* contributed only small fractions to the littoral habitats (Figure 4.3a).

A total of six species of Cladocera, *Acroperus elongatus*, *Polyphemus pediculus*, *Acroperus harpae*, *Rhynchotalona falcata*, *Alonella excisa* and *Alona rustica* was recorded as the most common species in the littoral habitat during the sampling period between May 2001 and August 2002. Only one littoral taxon, *A. elongatus,* showed dominance in all three littoral habitats, sand, macrophyte and boulder, contributing more than 40%, 50% and 70% of the total abundance respectively of Cladocera recorded in those habitats. The abundance of the second most dominant littoral taxon, *P. pediculus* was relatively high in the macrophyte and sand habitats, where this taxon contributed more than 23% and 33% respectively (Figure 4.3b). The taxon, *A. harpae* was also common in the loch, but was significantly lower than *A. elongatus* and *P. pediculus*.

4.3.3 TWINSPAN classification and patterns of Cladocera in ordinations

A TWINSPAN statistical analysis was performed to classify the 24 samples into various divisions showing the most sensitive indicator species in each division. The number of pseudo-species cut levels was used as, 0, 2, 5, 10 and 20. A TWINDEND analysis was then used to calculate the within-group variance or dispersion of all the TWINSPAN groups ranging from no groups (all data) to the maximum number at level 6

a. Common planktonic Cladocera



b. Common littoral Cladocera

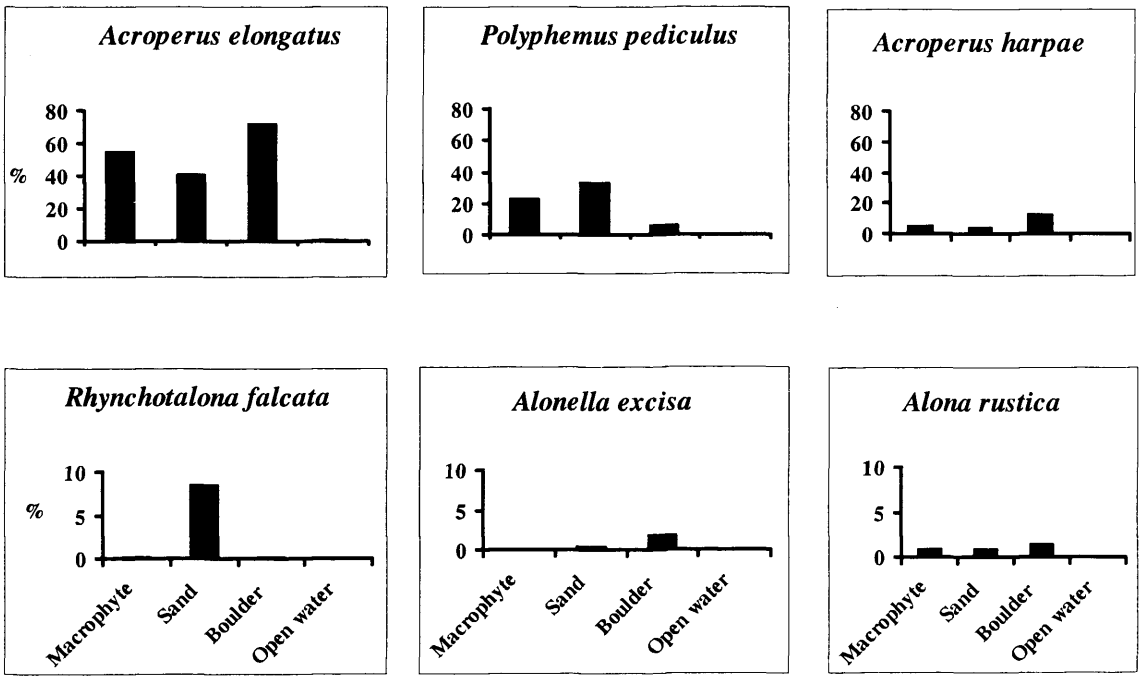


Figure 4.3: Relative abundances of the most common (a) planktonic and (b) littoral crustacea in the four available microhabitats (macrophyte, sand, boulder and open water) of Loch Coire Fionnaraich, Scotland

(Hill, 1979). Except for sample Apr'02B, all littoral samples (-ve group) were distinctly separated from samples collected from planktonic (open water) habitats (+ve group) (Figure 4.4). *Bosmina coregoni* was the indicator species for the planktonic group. The mean dispersion or within group variation under TWINDEND statistical analysis (ter Braak and Birks, Unpublished) for group 2 was more than 50%, so it was further divided into a second division. Most littoral samples collected in autumn 2001, winter 2002 and spring 2002 fell into group 4 (-ve), while other littoral samples taken in spring and summer 2001 and 2002 fell into group 5 (+ve) (Figure 4.4). *Polyphemus pediculus* was the indicator species for group 5 indicating their relationships with summer 2001 and 2002. Group 3 did not have mean dispersion >50%, so this group was not further divided. Both groups 4 and 5 showed within group variations >50% so they were further divided. In division 4, only one sample taken from sand in April 2002 fell into group 8 (-ve), and the remaining samples were in group 9 (-ve) (Figure 4.4). Here, *Monospilus dispar* was the negative indicator species. In division 5, *Bosmina longispina* was the negative indicator species and at least 4 samples fell into group 10 (-ve) and 6 samples fell into group 11 (+ve) (Figure 4.4). Only group 11 had a mean dispersion >50%, so it was further divided. *Daphnia galeata* was the positive indicator species for division 11 (Figure 4.4).

A detrended correspondence anaysis (DCA) was performed for understanding the patterns of Cladocera assemblages in 24 samples collected from Loch Coire Fionnaraich with detrending by segments and down-weighting the rare taxa. The gradient length, or the standard deviation (SD) of cladoceran species was 3.61 units (Table 4.3) indicating that they had unimodal distribution in the ordination data-set (e.g. Birks, 1995).

Table 4.3: Summary of DCA ordination of Cladocera assemblages estimated from a total of 24 planktonic and littoral samples in various seasons in Loch Coire Fionnaraich, Scotland.

DCA axes	1	2	3	4
Eigenvalues (λ)	0.530	0.0196	0.096	0.050
Lengths of gradient (standard deviation units)	3.619	2.033	1.796	1.007
Cumulative percentage (%) variance of species data	25.4	34.8	39.3	41.7
Sum of all unconstrained eigenvalues				**2.089**

In DCA ordination, relatively large number of both planktonic and littoral Cladocera are associated with DCA axis 1 while a few number of littoral taxa are associated with DCA axis 2 (Figure 4.5). Most littoral taxa with a higher weight are positioned at the

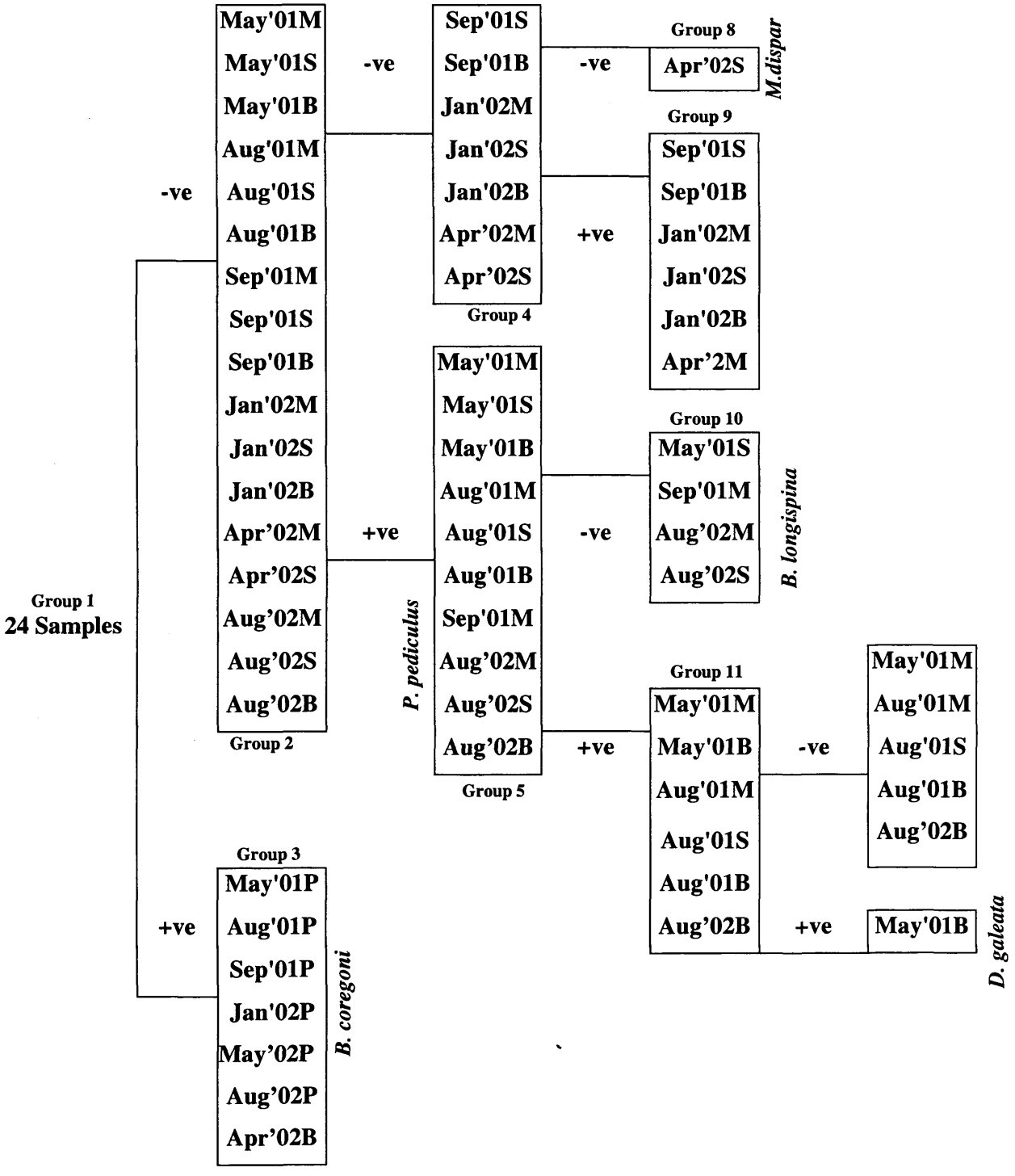


Figure 4.4: TWINSPAN classification of 24 samples collected from Loch Coire Fionnaraich. The groups were retained after TWINDEND statistical analysis with mean dispersion or within group variation of each group were equal or more than 50%.

centre of the ordination while species with a lower weight such as *Streblocerus serricaudatus* (Str ser) are positioned at the edge of the ordination diagram (Figure 4.5). The 24 samples were also grouped into their habitat and seasonal classes in order to determine the size structure of each habitat type regardless of TWINSPAN classification in DCA. The group shape and structure made by planktonic samples were different and separated completely from that of the other three littoral classes (Figure 4.6). Among the three littoral classes, samples collected from macrophytes were different from the other two littoral samples, from sand and boulder habitats (Figure 4.6). Among seasonal classes, variation was not so obvious though summer 2001 (Aug'01) and winter 2002 (Jan'02) were very similar in shape (Figure 4.6).

4.4 Discussion

4.4.1 Diversity, abundance and composition

This study provides insights into the qualitative and quantitative structure of the cladoceran community in LCFR. Species diversity reflects the nutrient status and habitat structure of the loch and its variability seasonally is related also to climatic factors. George & Winfield (2000) argued that inter-annual variation in temperature, probably related to the NAO, is characteristic of many Scottish lochs and it influences the growth rates and reproduction of phytoplankton and zooplankton significantly.

Shoreline habitats are essential for littoral specialists. Aquatic macrophyte beds, in particular, are used by most chydorid Cladocera. The density of littoral Cladocera in macrophyte beds in LCFR is greater than the density of littoral and planktonic Cladocera in other habitats (sand, boulder and open water). Various authors have argued that the density and abundance of Chydorid Cladocera are significantly related to the species composition and abundance of macrophytes per unit area (Hamsworth and Whiteside, 1968; Quade, 1969). The dynamics of vegetation in LCFR has not yet been studied quantitatively, though the increased diversity of vegetation in shoreline habitats during summer can have contributed to a significantly high density of phytophylous Cladocera. The increased significance of the littoral vegetation in summer is indicated by the observed patterns of the abundances of littoral and planktonic Cladocera in LCFR during six seasonal visits. Unlike planktonic Cladocera, the densities of littoral Cladocera are very high during both summers of 2001 and 2002 (Figure 4.2b).

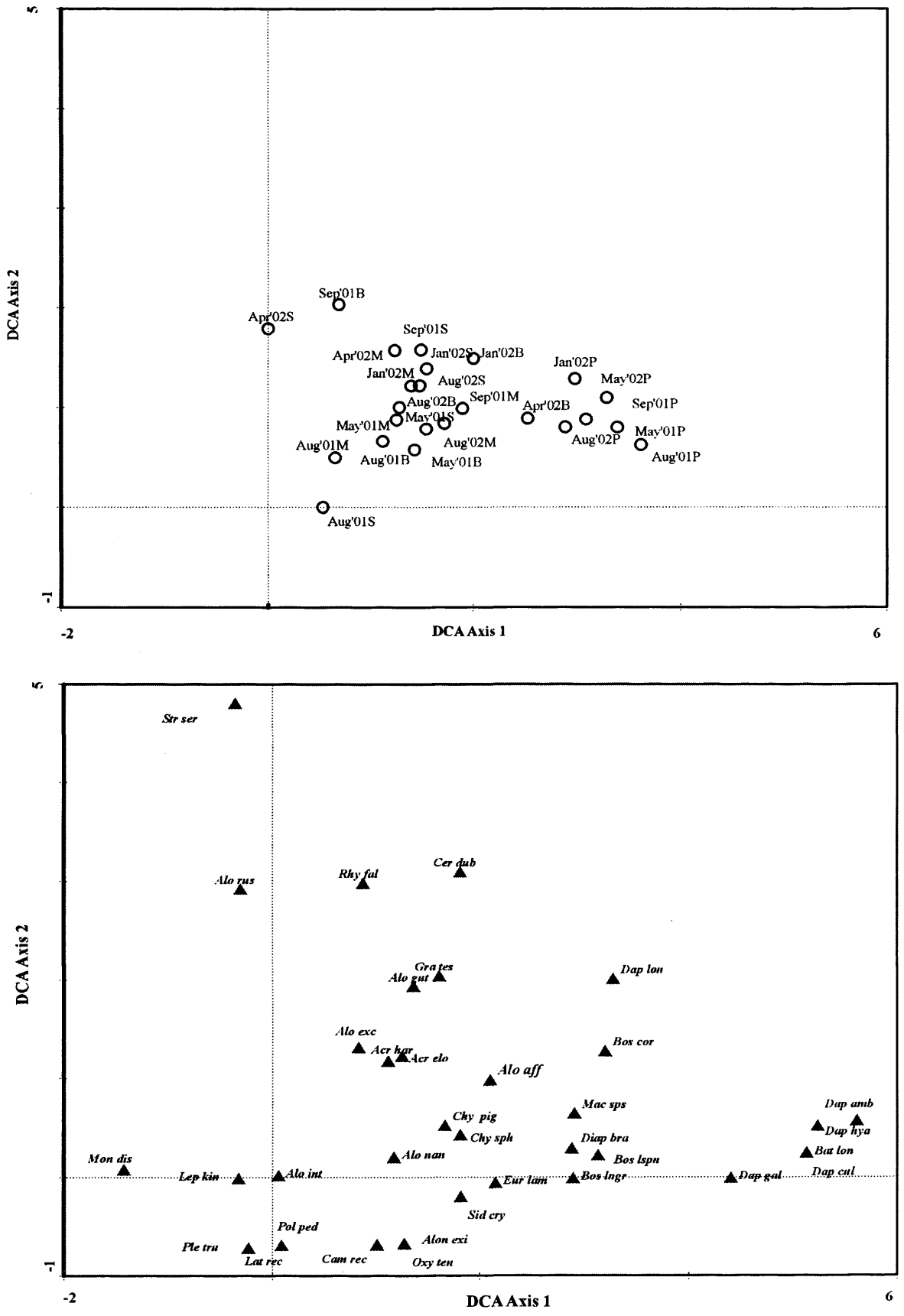


Figure 4.5: DCA of cladoceran zooplankton in 24 contemporary samples. The abbreviation for species data is given in Table 4.2. The coding for sample stands for month-year of sampling-habitat type. For example, the sample taken in May 2001 from the macrophyte habitat is May'01M. Four habitat types are given as M = Macrophyte, S = Sand, B = Boulder and P = Planktonic respectively.

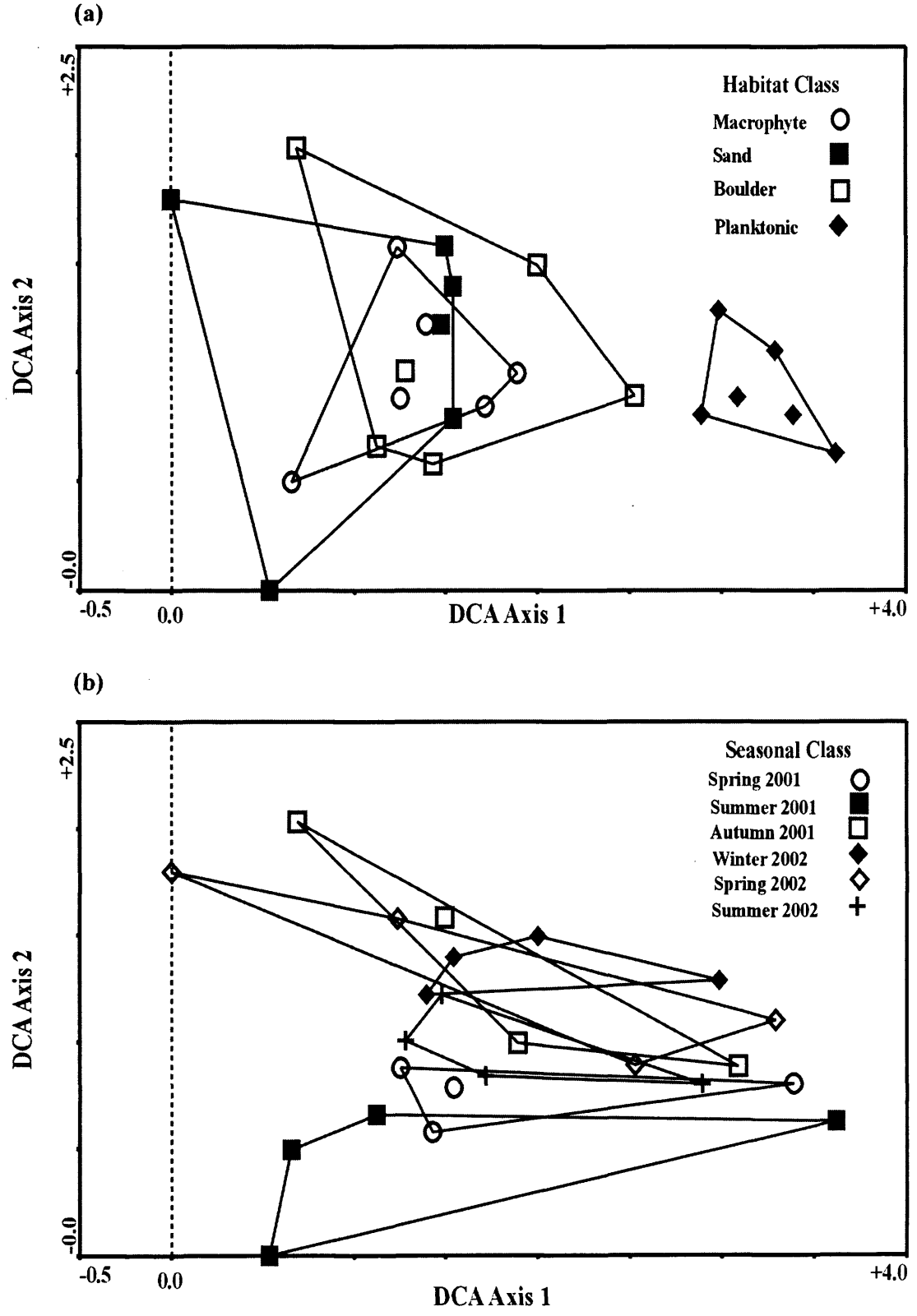


Figure 4.6: Classification of 24 contemporary Cladocera samples collected from Loch Coire Fionnaraich, Scotland, (a) with respect to micro-habitat types, (b) with respect to seasons.

4.4.2 Autoecology of dominant Cladocera

It emerges from this survey that all six common pelagic taxa recorded in the loch are restricted to the open water habitat. However, variations in the patterns of the abundance among these taxa suggest that *Bosmina coregoni* and *Bosmina longispina* are the two most dominant species. These two taxa commonly co-occur. However, they appear to show differences in response to certain environmental change such as eutrophication and climate change. *B. coregoni* prefers rather nutrient rich (mesotrophic) environments compared to *B. longispina,* which prefers clearer, oligotrophic conditions (Hofmann, 1996). The presence of *B. coregoni* and *B. longispina* in littoral habitats suggest that both taxa often utilize the littoral substrata of LCFR, in contrast to *Daphnia.* Loch Coire Fionnaraich has low fish abundance judging from neighbouring lochs (Adams, 1994; Monteith & Evans, 2000) suggesting that there is a relatively low predation risk for small-bodied Cladocera (*Bosmina* and *D. longispina*) from fish in the open-water habitat (e.g. Dal-Hansen, 1995).

This survey reveals that the shoreline habitats are important for littoral Cladocera to the loch. The taxon, *A. elongatus* is the most dominant taxon in the littoral community. Various studies suggest that *A. elongatus* is one of the most common cladoceran taxa in the British Isles. Fryer (1993) argued that this taxon requires low summer temperature to reproduce. However, reasons for the exceptionally high abundance of *A. elongatus* in LCFR is not known yet, although its occurrence in a range of habitats could be one of the main reasons for its high density (e.g. Whiteside, 1970; Flössner; 1972; Fryar, 1974). *A. harpae*, a closely related species of *A. elongatus,* is also common in all littoral habitats in LCFR (Figure 4.3b), although its abundance is far lower than *A. elongatus. A. harpae* is also one of the most widely distributed taxa in Europe and is reported from a variety of micro-habitats including vegetation beds, sands and rocks (e.g. Whiteside, 1970; Whiteside et al.; 1978; Duigan, 1992). *R. falcata* is common in sandy substrata its abundance reflects the widespread occurrence of sandy habitats in LCFR. The very small amount of *A. excisa* and *A. rustica* in each of the three littoral substrate types indicates that some taxa are not specific to habitat. In many northwest European lakes, these taxa are often found feeding on detritus and predominant in bogs with *Sphagnum*-dominated vegetation (Nillsen and Sandøy, 1990; Duigan, 1992). The occurrence of *A. rustica* in LCFR was not expected. Its presence reflects some nutrient enrichment in the loch. Duigan (1992) argued that presence of *A. rustica* indicates

dystrophic condition of a lake with relatively high DOC. *P. pediculus* was the only non-chydorid taxon recorded predominantly in the littoral zone of LCFR. It is a common littoral taxon found in many Scottish lochs during summer (Maitland et al., 1981).

4.4.3 Assemblage structure of Cladocera

In general, Cladoceran assemblages in Loch Coire Fionnaraich suggest that the open water habitat regulates the lake community structure. This is indicated by a niche separation of littoral and planktonic habitats by the planktonic taxon, *B. coregoni* in the TWINSPAN classification and by the association to the planktonic Cladocera with DCA axis 1 in the ordination. However, the significance of the littoral habitats is also indicated by the TWINSPAN classification very clearly. In particular, the littoral taxa, *Polyphemus pediculus* and *Monospilus dispar* play a significant role. Because of its seasonal emergence, particularly during summer, and its significant predation effects on other Cladocera in Scottish lochs (e.g. Maitland et al., 1981), *P. pediculus* appears to be an important indicator species in the cladoceran community in LCFR with respect to season. Increased precipitation over recent years may have altered the habitat available for a variety of littoral communities, possibly increasing sandy substrates favouring *M. dispar* (Figure 4.4).

From the limited temporal data available in this study, it is difficult to assess whether the community dynamics of Cladocera in LCFR have been influenced by the NAO (e.g. George et al., 2004). The NAO can cause changes in water column, mixing and nutrient supply, which in turn can influence chlorophyll$_a$ production and the distribution of phytoplankton and zooplankton (e.g. Jenkin, 1942; Jones et al., 1995; George & Winfiled, 2000). On this basis and by comparison with other studies (e.g. George et al., 2004) it is probable that at least the planktonic cladocerans in LCFR are subjected to the NAO effect.

The littoral community in LCFR is mainly influenced by the composition and abundance of the most structurally diverse marginal habitats comprising macrophyte beds, mud, sand and rocky substrata, that support many littoral cladoceran specialists (Whiteside, 1974; Hann & Turner, 1999; Tremel et al., 2000). Climate change can play an indirect role on these communities by regulating habitat structure (e.g. Monteith and

Evans, 2000). Colonisation of littoral habitats by Cladocera often occurs after high precipitation and flooding effects, when a variety of micro-habitat structures form due to catchment erosion and littoral modification. Changes in seasonality can also affect habitat structure, particularly, with respect to the growth and development of shoreline macrophytes. Whilst the data collected in this study are not accurate to demonstrate these influences at LCFR it is apparent that the LCFR cladoceran populations will be sensitive to them.

4.5 Conclusions

This study provides an insight of the contemporary dynamics of Cladocera in Loch Coire Fionnaraich, a Northwest Scottish mountain loch. Unlike some remote high mountain lochs in Scotland, LCFR is an important site for both planktonic and littoral Cladocera. Data on species diversity, composition and abundance of planktonic and littoral Cladocera in this loch suggest that the loch contains diverse micro-habitats However, the community structure is dominated by open water taxa where *Bosmina coregoni* is the most abundant. The littoral communities are dominated by *A. elongatus* and *P. pediculus*, and *R. falcata* is abundant in sandy habitats. These observations not only contribute to an understanding of the ecology and distribution of Cladocera in upland lakes but also provide the basis for studying the sediment record of Cladocera which is addressed in the following chapters.

Chapter 5

Taphonomy of Cladocera in a remote Scottish mountain loch, Loch Coire Fionnaraich

5.1 Introduction

This chapter describes the taphonomy or representation of Cladocera in Loch Coire Fionnaraich. The assessment of representation of Cladocera is carried out using a variety of approaches. Firstly, the composition of the sedimentary assemblages of Cladocera in the core sample is compared with the samples recovered from each transect using an ordination approach. Secondly, the sedimentary assemblages in the core sample are compared with the composition of remains in the trap sample using the approaches of loss and representation rates. Thirdly, the percentage composition of Cladocera in the contemporary or source sample and the percentage composition of sedimentary assemblages in the core sample are compared using the 'taxon rates' approach. Finally, how effectively the remains in the core sample represent the cladoceran species present in the loch is assessed by integrating the core sample, the spatial surface sediment samples, the trap sample and the source sample using both ordination and the 'integration of percentage compositions' techniques.

5.2 Materials and methods

5.2.1 Collection of fossil remains and live Cladocera

The collection of surface sediment samples for taphonomic studies is described in detail in Chapter 3 (section 3.2.2). A total of 8 horizontal transects, 3 associated with macrophytes, 3 associated with boulders and 2 associated with sand, were aligned towards the sediment core site in the deepest basin (14 m) of the loch in August and October 2001 (Figure 5.1). From each horizontal transect, at least four surface sediment samples (top 1 cm) at 2 m, 5 m, 8 m and 11 m water depths were taken using an Ekman grab or Glew corer. Abbreviations for surface sediment samples are presented in Appendix 5.1. The surface sediment (core-top) sample of a short core (hereafter 'core

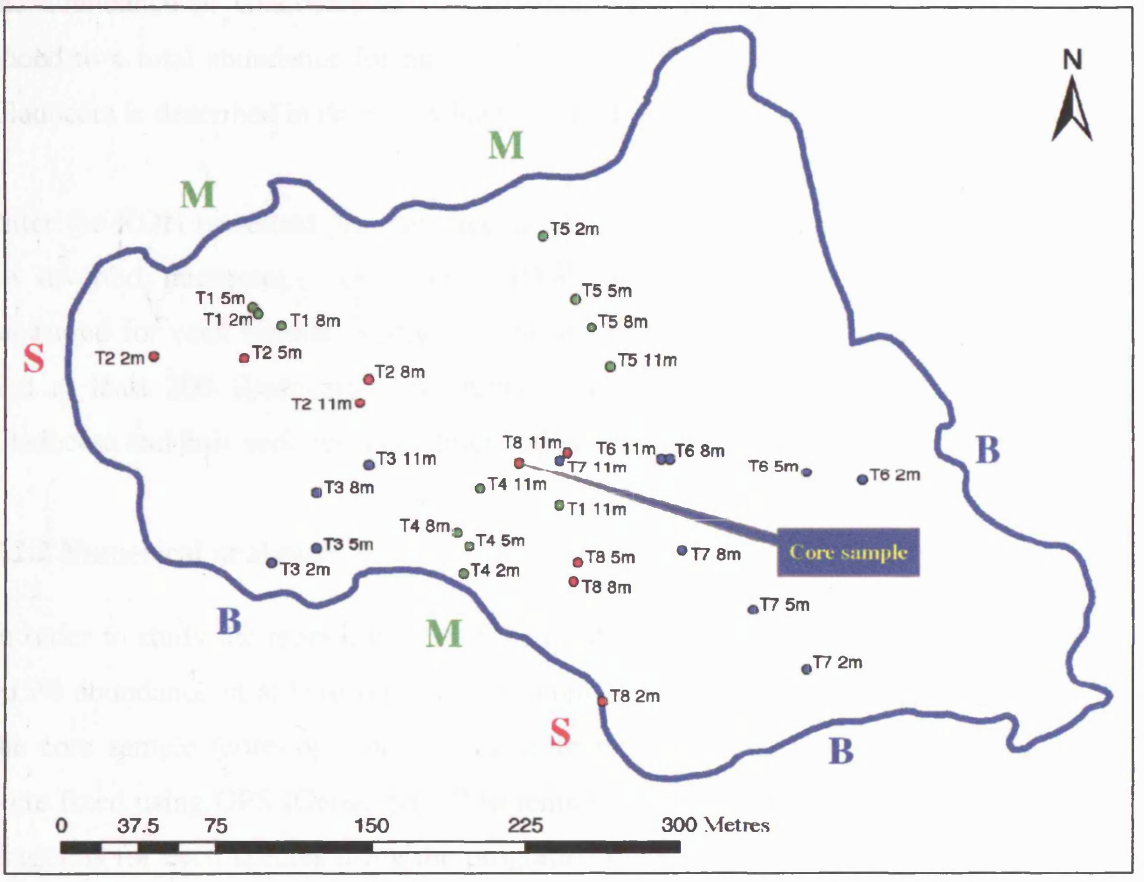


Figure 5.1: Spatial surface sediment samples of Cladocera were taken from 8 horizontal transects, each consisting of four depth points from Loch Coire Fionnaraich. The location of the core is shown as 'core sample' in the centre of the loch. Sampling locations at each transect with respective depths are presented as T1-2m, T1-5m, T-8m, T1-11m followed by other transects, T2, T3,...T8 respectively. The shoreline habitat types, from which each transect ran, was identified by different letters, M = Macrophyte, S= Sand and B = Boulder.

sample') taken from the deepest point of the loch (14 m) was also used to compare the spatial distribution of fossil assemblages. Including the core sample, there was a total of 33 spatial surface sediment samples.

In order to compare trap assemblages with fossil assemblages, a sediment trap was also installed at 2 m above the lake floor at the centre of the loch (Figure 3.4). Data for contemporary assemblages in the source sample were derived from Chapter 4, where the abundance of Cladocera in an individual sample (i.e. micro-habitat-season) was added to a total abundance for numerical analysis. The method of collection of living Cladocera is described in detail in Chapter 3 (section 3.2.1).

After the KOH treatment, the most identifiable Cladocera remains were counted using an inverted microscope. Dry weight (DW) and loss-on-ignition (LOI) were also measured for each sample. Surface sediment samples were analysed in the laboratory and at least 200 Cladocera fossil remains were counted. Laboratory analyses for Cladocera and bulk sediments are described in detail in Chapter 3 (sub-section 3.3.2.1).

5.2.2 Numerical analyses

In order to study the representation of the most common cladoceran (taxa with at least ≥15% abundance in at least one surface sample) Cladocera in Loch Coire Fionnaraich, the core sample (core-top) and surface sediment samples across the various transects were fixed using GPS (Geographic Positioning Satellite) and linked to generate the bar diagrams for each species using the program Arc-GIS (2.0). The absolute count of the individual Cladocera in each sample was estimated as the number per gram dry sediment (gdw^{-1}) and data were entered in Microsoft Excel and stored in comma delimited (*csv) format (Appendix 5.4) to facilitate the data for producing bar charts on a digital map of Loch Coire Fionnaraich (http://edina.ac.uk/digimap). The projected co-ordinate systems in ArcMap were selected as the British National Grid. The species data file was then added in ArcMap as species shape file format (*shp).

The extent of fossil deposition of Cladocera in different water depths (2m, 5m, 8m and 11m) in Loch Coire Fionnaraich was assessed by using the correlation between the remains of Cladocera in two subsequent depth points (2m v 5m, 5m v 8m and 8m v 11m) of all transects.

The representation of Cladocera in the loch was also examined through ordination techniques, in which the core sample was compared with a total of 32 spatial surface sediment samples collected across 8 transects. Both direct and indirect gradient analyses were used to identify the patterns of 33 (32 surface sediment and 1 core sample) samples along environmental gradients using CANOCO 4.5 (ter Braak & Šmilauer, 2002). Detrended correspondence analysis (DCA) was used with detrending by segments, down-weighting of rare taxa and non-linear rescaling of axes (Hill & Gauch, 1980) to assess the standard deviation (SD) of the cladoceran species data among the 33 spatial samples. Since the SD of species in DCA was less than 2, principal component analyses (PCA) and redundancy analysis (RDA) were appropriate to explore the species, and species-environment relationships followed by the Monte Carlo permutation tests in CANOCO 4.5 (ter Braak & Šmilauer, 2002). Although a number of important factors (e.g. lake-water chemistry and temperature, bioturbation) are involved in the taphonomy of Cladocera, only 6 environmental or so-called 'taphonomic' factors were available for this study. The three shoreline littoral habitats (macrophyte, sand and boulder) and the 1 central (i.e. for the core sample) were taken as dummy variables using binary codes (1/0) and other two environmental variables (depth and LOI) were taken as quantitative taphonomic variables (Table 5.1). Depth is one of the foremost components influencing transportation and deposition of fossil remains of Cladocera in lake sediments. The type of the sediment itself also plays a significant role. It has been assumed that cladoceran fossils associated with sediments richer in organic matter would probably have a different rate of deposition and composition than those associated with low organic matter and the assemblage composition of Cladocera would also be influenced by the proximity to their source habitats. For example, it has been argued that the remains of most littoral Cladocera preferentially accumulate in the lake basin close to littoral habitats, such as macrophytes, sand and boulders, while the planktonic Cladocera are deposited in the deepest basin of the lake (Frey, 1960, Frey, 1988).

The Cladoceran representation was also evaluated by comparing the compositions in the core sample with the compositions in the trap and contemporary assemblages. The numerical analyses for how well the trap and contemporary assemblages were represented by the fossil assemblages in the core sample, are described in the results section. The representation of Cladocera in the loch was also examined using ordination

Table 5.1: Sampling design for physico-chemical variables used in ordination analyses of 33 spatial surface sediment samples. Transects are represented as T1, T2.....T8. M, S, and B are samples associated with macrophyte, sand and boulder habitats. Samples were recovered from 2m, 5m, 8m and 11m depths of each transect. The core sample was collected from the central point (14m) of the loch, Loch Coire Fionnaraich, Scotland.

TRANSECTS	MACROPHYTE	SAND	BOULDER	CENTRAL	DEPTH	LOI
T1M2m	1	0	0	0	2	28.14
T1M5m	1	0	0	0	5	21.06
T1M8m	1	0	0	0	8	24.87
T1M11m	1	0	0	0	11	21.43
T2S2m	0	1	0	0	2	1.75
T2S5m	0	1	0	0	5	25.49
T2S8m	0	1	0	0	8	26.45
T2S11m	0	1	0	0	9.5	23.51
T3B2m	0	0	1	0	2	20.83
T3B5m	0	0	1	0	4.7	13.36
T3B8m	0	0	1	0	7.2	28.31
T3B11m	0	0	1	0	11	33.81
T4M2m	1	0	0	0	2	24.55
T4M5m	1	0	0	0	4.8	15.57
T4M8m	1	0	0	0	7.7	14.45
T4M11m	1	0	0	0	11	24.36
T5M2m	1	0	0	0	1.9	23.68
T5M5m	1	0	0	0	5.6	19.30
T5M8m	1	0	0	0	8.3	25.73
T5M11m	1	0	0	0	11	28.75
T6B2m	0	0	1	0	2	20.78
T6B5m	0	0	1	0	5.6	20.88
T6B8m	0	0	1	0	8.2	24.93
T6B11m	0	0	1	0	11.5	29.74
T7B2m	0	0	1	0	2	20.29
T7B5m	0	0	1	0	5	21.26
T7B8m	0	0	1	0	8	16.54
T7B11m	0	0	1	0	12	28.09
T8S2m	0	1	0	0	2	22.67
T8S5m	0	1	0	0	5	25.37
T8S8m	0	1	0	0	7.7	26.23
T8S11m	0	1	0	0	10	19.99
CORE-SAMPLE	0	0	0	1	14	32.16

by comparing the core sample with the combination of spatial, trap and contemporary assemblages of Cladocera using PCA in CANOCO 4.5 (ter Braak & Šmilauer, 2002).

5.3 Results

In the following sections, primarily the dry weight (DW) and the loss-on-ignition (LOI) of the overall spatial surface sediment samples are presented. Then the species number, concentration and the littoral:planktonic ratio of Cladocera in the spatial surface sediments samples are discussed. The deposition of Cladoceran remains in each successive depth of loch is also presented using bar and charts in the Arc-GIS program. The extent of the deposition of Cladocera in subsequent depths of LCFR is then assessed by correlation of the concentration of the remains deposited in between two successive depths. The representation of Cladocera in the sediments of Loch Coire Fionnaraich is assessed by comparing the fossil assemblages in the core sample with spatial surface sediment samples; sediment trap, and contemporary assemblages; and the integration of all samples in ordination.

5.3.1 Percentage dry weight (DW) and loss-on-ignition (LOI)

The percentage dry weight (DW) and loss on ignition (LOI) data from the surface sediment samples are presented in Figure 5.2. In general, the proportion of LOI was found high in offshore (8m, 11m and 14m depths) samples indicating that the surficial sediments in these samples contain relatively high amount of organic matter. The highest percentage of LOI was measured in the sample recovered from 11m-depth (33%) in Transect 3 followed by the core sample (32%). In T1, the highest LOI was measured in the 2m-depth due to proimity of a macrophyte bed. In contrast, the percentage LOI in the 2m depth sample of T2 was exceptionally low (1%) due to the nature of the sample, which was taken exclusively from the sand-dominated habitat. The lowest percentages of LOI (other than in T2), were measured in the 5m-depth samples of T3 (13%) and in T4 (14%) respectively (Figure 5.2).

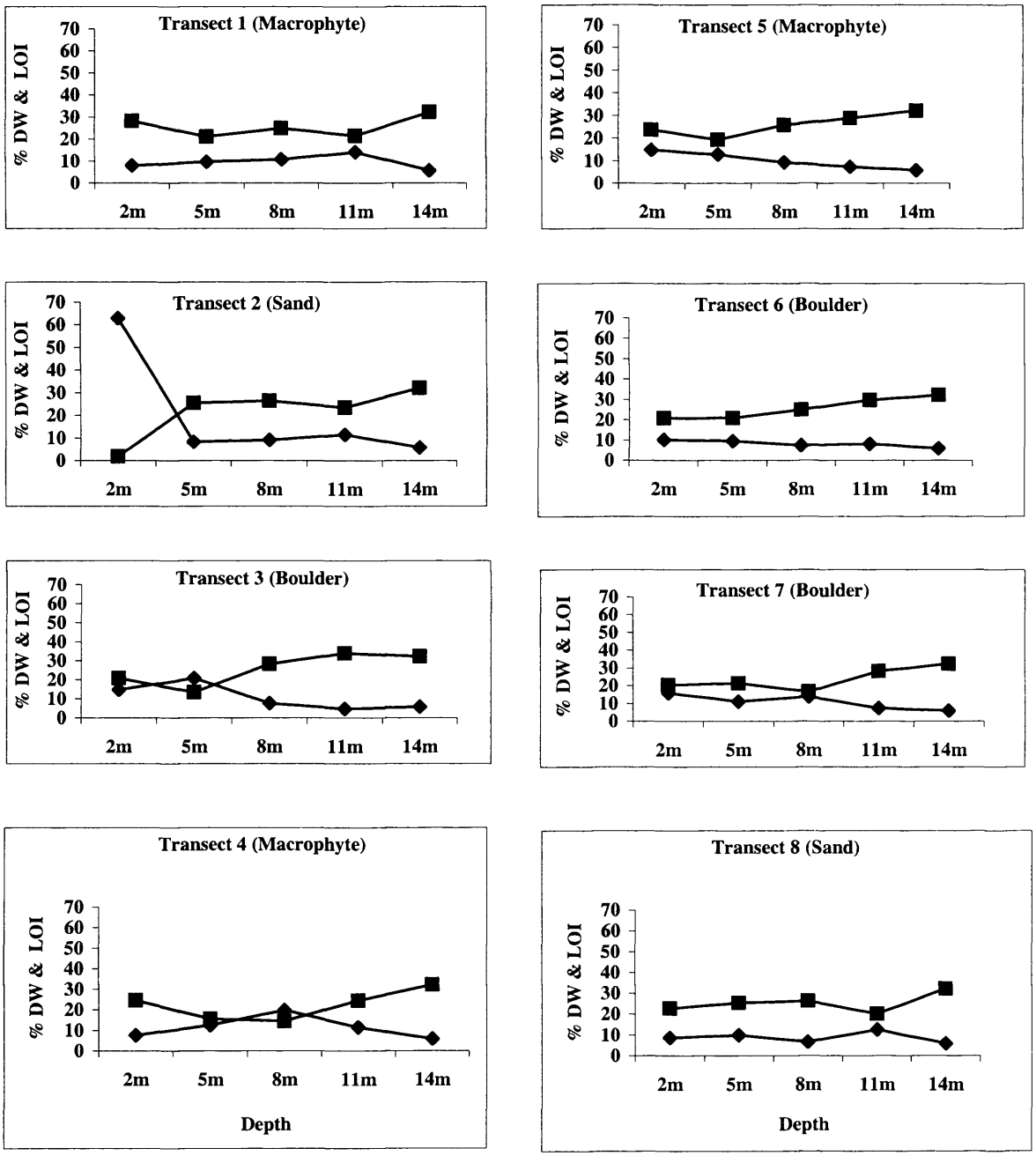


Figure 5.2: Percentage dry weight (DW) and loss on ignition (LOI) of surface sediment of 8 transects consisting of 32 samples and core sample at the deepest location in Loch Coire Fionnaraich, Scotland. Diamonds (♦) and squares (■) represent DW and LOI respectively.

5.3.2 Transportation and deposition of cladoceran remains in Loch Coire Fionnaraich

One of the important questions in taphonomy is to understand how the remains of Cladocera from their source habitat are transported towards the lake centre. One assumption is that the remains follow the most shortest distance to reach the lake centre due to the law of gravity. However, the remains are also assumed to be transported by the wind-induced water currents and the most remains can stay in the water column for a long time period before deposition. As a result, the integration of remains in the lake centre can vary largely depending upon seasons and the weather conditions. One way of evaluating the transportation of the remains of the individual Cladocera from their source habitat to the lake centre is to compare the assemblage structure, richness and the littoral:planktonic ratio of the Cladocera in various depth points of the each habitat-associated transect and the core sample.

The concentration of remains of Cladocera in each depth point of each habitat-associated transect in LCFR can also be presented by bars and charts using the program Arc-GIS. This can provide accurate information on the distribution and deposition of remains and is also useful in comparing the deposition of remains between habitat-associated transects and the core sample. In GIS, the comparisons of fossil deposition between species can be made for an individual lake.

5.3.2.1 Transects vs core sample

Comparison of fossil assemblages from the surface sediment samples along the transects with the core surface sample reveals that the accumulation of total Cladocera (planktonic and littoral) remains is considerably higher in the core sample: the remains of planktonic Cladocera were almost 4 times higher than the littoral ones (Table 5.2 a, b, c, d). A total of 5 planktonic species was recorded in the lake sediments but only two taxa, *Bosmina coregoni* and *B. longispina,* were abundant. The representation of remains of *Daphnia*, *Ceriodaphnia* and *Bosmina longirostris* was low in most samples and *Ceriodaphnia* and *B. longirostris* were absent in the core sample. Remains of a total of 25 species of littoral Cladocera were recovered from the lake sediments of which only one was a non-chydorid Cladocera (*Sida crystallina*). Most Chydorids were

Table 5.2: Number of cladoceran remains recorded per gram of dry sediment (gdw^{-1}) sample derived from the each depth points, 2m, 5m, 8m and 11m of 8 transects and the core sample (14m) in Loch Coire Fionnaraich, Scotland.

(a) Transect 1 (T1), Transect 2 (T2) vs Core sample

Species/depth	T1 (Macrophyte)					T2 (Sand)					Core
Species/depth	**2m**	**5m**	**8m**	**11m**	**Sum**	**2m**	**5m**	**8m**	**11m**	**Sum**	**14m**
Daphnia spp	46	0	0	0	**46**	0	16	18	13	**47**	**53**
Bosmina longirostris	46	78	57	10	**191**	2	16	0	0	**18**	**0**
Bosmina longispina	551	1028	1701	461	**3741**	10	581	792	535	**1918**	**7159**
Bosmina coregoni	1241	970	2098	666	**4975**	24	957	1918	1070	**3969**	**11968**
Planktonic Cladocera	**1884**	**2076**	**3856**	**1137**	**8953**	**36**	**1570**	**2728**	**1618**	**5952**	**19180**
Sida crystallina	138	39	57	29	**263**	2	16	18	25	**61**	**106**
Non-chydorid Cladocera	**2022**	**2115**	**3913**	**1166**	**9216**	**38**	**1586**	**2746**	**1643**	**6013**	**19286**
Graptoleberis testudinaria	827	58	76	39	**1000**	3	31	88	25	**147**	**267**
Eurycercus lamellatus	46	39	38	10	**133**	0	31	18	0	**49**	**320**
Camptocercus rectirostris	276	19	19	10	**324**	2	16	18	0	**36**	**0**
Acroperus harpae	1333	155	132	59	**1679**	12	94	141	76	**323**	**480**
Acroperus elongatus	184	233	189	78	**684**	24	126	158	166	**474**	**374**
Alona rectangula	46	97	19	39	**201**	3	0	35	115	**153**	**160**
Alona guttata	322	155	95	39	**611**	12	63	44	25	**144**	**160**
Alona guttata tuberculata	46	58	19	0	**123**	0	0	0	0	**0**	**0**
Alona rustica	368	349	340	108	**1165**	19	204	246	115	**584**	**748**
Alona intermedia	230	272	302	176	**980**	28	110	229	102	**469**	**374**
Alona affinis	46	58	19	10	**133**	14	31	0	25	**70**	**160**
Alona quadrangularis	0	19	0	0	**19**	0	16	70	0	**86**	**106**
Alonella nana	689	369	227	108	**1393**	21	126	88	115	**350**	**748**
Alonella excisa	1884	272	151	59	**2366**	19	31	123	76	**249**	**213**
Monospilus dispar	1562	116	529	147	**2354**	54	188	158	217	**617**	**801**
Rhynchotalona falcata	0	19	19	10	**48**	38	16	0	13	**67**	**106**
Chydorus sphaericus	46	39	57	10	**152**	16	31	35	51	**133**	**267**
Chydorus piger	919	407	265	147	**1738**	44	251	176	115	**586**	**480**
Chydorid Cladocera	**8824**	**2734**	**2496**	**1049**	**15103**	**309**	**1365**	**1627**	**1236**	**4537**	**5764**
Littoral Cladocera	**8962**	**2773**	**2553**	**1078**	**15366**	**311**	**1381**	**1645**	**1261**	**4598**	**5870**
Total Cladocera	**10846**	**4849**	**6409**	**2215**	**24319**	**347**	**2951**	**4373**	**2879**	**10550**	**25050**
Number of species	**21**	**22**	**21**	**20**	**22**	**19**	**21**	**19**	**18**	**22**	**20**
Littoral:planktonic ratio	**4.76**	**1.34**	**0.66**	**0.95**	**1.72**	**8.64**	**0.88**	**0.60**	**0.78**	**0.77**	**0.31**

contd.

Table 5.2 contd.

(b) Transect 3 (T3), Transect 4 (T4) vs Core Top

Species/depth	T3 (Boulder)					T4 (Macrophyte)					Core
Species/depth	**2m**	**5m**	**8m**	**11m**	**Sum**	**2m**	**5m**	**8m**	**11m**	**Sum**	**14m**
Daphnia spp	0	0	19	55	**74**	0	0	0	11	**11**	**53**
Bosmina longirostris	0	0	0	27	**27**	0	0	0	11	**11**	**0**
Bosmina longispina	24	75	984	1181	**2264**	205	120	113	798	**1236**	**7159**
Bosmina coregoni	65	143	1448	3049	**4705**	243	131	179	951	**1504**	**11968**
Planktonic Cladocera	**89**	**218**	**2451**	**4312**	**7070**	**448**	**251**	**292**	**1771**	**2762**	**19180**
Sida crystallina	16	10	74	55	**155**	37	11	13	22	**83**	**106**
Non-chydorid Cladocera	**105**	**228**	**2525**	**4367**	**7225**	**485**	**262**	**305**	**1793**	**2845**	**19286**
Graptoleberis testudinaria	41	23	111	82	**257**	429	22	6	33	**490**	**267**
Eurycercus lamellatus	24	6	37	0	**67**	75	5	0	0	**80**	**320**
Camptocercus rectirostris	82	0	37	27	**146**	112	5	6	22	**145**	**0**
Acroperus harpae	204	26	204	192	**626**	467	27	9	77	**580**	**480**
Acroperus elongatus	33	19	260	604	**916**	112	33	35	120	**300**	**374**
Alona rectangula	7	10	37	192	**246**	56	5	13	22	**96**	**160**
Alona guttata	27	19	111	82	**239**	112	33	25	55	**225**	**160**
Alona guttata tuberculata	0	0	0	0	**0**	56	5	3	0	**64**	**0**
Alona rustica	65	55	371	330	**821**	187	137	60	142	**526**	**748**
Alona intermedia	24	36	204	220	**484**	112	16	25	131	**284**	**374**
Alona affinis	8	6	111	27	**152**	0	5	3	33	**41**	**160**
Alona quadrangularis	0	3	19	55	**77**	0	0	3	22	**25**	**106**
Alonella nana	106	42	223	165	**536**	317	66	47	79	**509**	**748**
Alonella exigua	8	0	0	0	**8**	0	0	0	0	**0**	**0**
Alonella excisa	376	10	111	247	**744**	429	33	22	55	**539**	**213**
Monospilus dispar	261	127	371	82	**841**	336	356	94	109	**895**	**801**
Rhynchotalona falcata	8	3	19	55	**85**	19	11	9	0	**39**	**106**
Chydorus sphaericus	33	19	56	55	**163**	75	22	6	0	**103**	**267**
Chydorus piger	82	49	241	302	**674**	355	93	38	109	**595**	**480**
Chydorid Cladocera	**1389**	**453**	**2523**	**2717**	**7082**	**3249**	**879**	**404**	**1009**	**5541**	**5764**
Littoral Cladocera	**1405**	**463**	**2597**	**2772**	**7237**	**3286**	**890**	**417**	**1031**	**5624**	**5870**
Total Cladocera	**1494**	**681**	**5048**	**7084**	**14307**	**3734**	**1141**	**709**	**2802**	**8386**	**25050**
Number of species	**20**	**19**	**21**	**22**	**23**	**19**	**21**	**20**	**18**	**22**	**20**
Littoral:planktonic ratio	**15.79**	**2.12**	**1.06**	**0.64**	**1.02**	**7.33**	**3.55**	**1.43**	**0.58**	**2.04**	**0.31**

contd.

Table 5.2 contd.

(c) Transect 5 (T5), Transect 6 (T6) vs Core Top

Species/depth	T5 (Macrophyte)					T6 (Boulder)					Core
Species/depth	**2m**	**5m**	**8m**	**11m**	**Sum**	**2m**	**5m**	**8m**	**11m**	**Sum**	**14m**
Daphnia spp	0	23	93	161	**277**	13	30	32	31	106	**53**
Ceriodaphnia sp.	26	23	0	0	**49**	0	15	0	31	46	**0**
Bosmina longirostris	0	23	0	0	**23**	0	30	0	0	30	**0**
Bosmina longispina	182	1277	1430	1800	**4689**	193	529	1315	1941	3978	**7159**
Bosmina coregoni	312	1209	3078	3342	**7941**	128	861	2502	4899	8390	**11968**
Planktonic Cladocera	**520**	**2555**	**4601**	**5303**	**12979**	**334**	**1465**	**3849**	**6902**	**12550**	**19180**
Sida crystallina	52	23	31	32	**138**	26	30	128	31	215	**106**
Non-chydorid Cladocera	**572**	**2578**	**4632**	**5335**	**13117**	**360**	**1495**	**3977**	**6933**	**12765**	**19286**
Graptoleberis testudinaria	520	91	31	161	**803**	77	76	160	123	436	**267**
Eurycercus lamellatus	78	46	31	64	**219**	103	15	96	62	276	**320**
Camptocercus rectirostris	0	23	0	0	**23**	39	15	32	31	117	**0**
Acroperus harpae	416	274	93	129	**912**	501	181	321	216	1219	**480**
Acroperus elongatus	26	182	218	225	**651**	77	106	385	277	845	**374**
Alona rectangula	78	68	155	32	**333**	26	15	96	62	199	**160**
Alona guttata	572	228	62	96	**958**	103	60	128	92	383	**160**
Alona guttata tuberculata	26	46	62	0	**134**	0	15	32	0	47	**0**
Alona rustica	208	525	342	353	**1428**	103	257	449	401	1210	**748**
Alona intermedia	208	342	187	386	**1123**	39	181	128	308	656	**374**
Alona affinis	26	68	62	32	**188**	51	106	64	62	283	**160**
Alona quadrangularis	26	46	31	32	**135**	0	15	32	0	47	**106**
Alonella nana	312	433	280	193	**1218**	154	257	481	92	984	**748**
Alonella excisa	961	251	280	64	**1556**	462	91	449	308	1310	**213**
Monospilus dispar	1247	228	591	482	**2548**	308	106	641	585	1640	**801**
Rhynchotalona falcata	0	23	31	32	**86**	0	15	32	31	78	**106**
Chydorus sphaericus	208	137	93	129	**567**	90	45	96	123	354	**267**
Chydorus piger	1325	525	311	289	**2450**	436	287	257	308	1288	**480**
Kurzia lattisima	0	46	0	0	**46**	0	0	0	0	0	**0**
Chydorid Cladocera	**6237**	**3582**	**2860**	**2699**	**15378**	**2569**	**1843**	**3879**	**3112**	**11403**	**5764**
Littoral Cladocera	**6289**	**3605**	**2891**	**2731**	**15516**	**2595**	**1873**	**4007**	**3143**	**11618**	**5870**
Total Cladocera	**6809**	**6160**	**7492**	**8034**	**28495**	**2929**	**3338**	**7856**	**10045**	**24168**	**25050**
Number of species	**20**	**25**	**21**	**20**	**25**	**19**	**24**	**22**	**22**	**24**	**20**
Littoral:planktonic ratio	**12.09**	**1.41**	**0.63**	**0.51**	**1.20**	**7.77**	**1.28**	**1.04**	**0.46**	**0.93**	**0.31**

contd.

Table 5.2 contd.

(d) Transect 7 (T7), Transect 8 (T8) vs Core Top

Species/depth	T7 (Boulder)					T8 (Sand)					Core
Species/depth	**2m**	**5m**	**8m**	**11m**	**Sum**	**2m**	**5m**	**8m**	**11m**	**Sum**	**14m**
Daphnia spp	24	21	53	0	**98**	50	20	41	39	150	**53**
Ceriodaphnia sp.	0	0	0	0	**0**	0	0	0	20	20	**0**
Bosmina longirostris	0	0	0	0	**0**	0	0	0	39	39	**0**
Bosmina longispina	284	662	7159	2508	**10613**	350	663	1571	1379	3963	**7159**
Bosmina coregoni	308	939	11968	4355	**17570**	650	1045	2812	1537	6044	**11968**
Planktonic Cladocera	**616**	**1622**	**1892**	**6863**	**10993**	**1050**	**1729**	**4424**	**3014**	**10217**	**19180**
Sida crystallina	47	43	18	66	**174**	150	60	124	20	354	**106**
Non-chydorid Cladocera	**663**	**1664**	**1910**	**6929**	**11166**	**1200**	**1789**	**4548**	**3034**	**10571**	**19286**
Graptoleberis testudinaria	260	85	73	99	**517**	1050	60	124	79	1313	**267**
Eurycercus lamellatus	142	0	37	66	**245**	350	40	83	20	493	**320**
Camptocercus rectirostris	260	21	18	33	**332**	50	40	41	20	151	**0**
Acroperus harpae	710	192	202	363	**1467**	2150	141	538	236	3065	**480**
Acroperus elongatus	47	149	147	231	**574**	250	161	372	236	1019	**374**
Alona rectangula	71	21	0	33	**125**	50	20	83	99	252	**160**
Alona guttata	237	64	92	132	**525**	700	181	496	197	1574	**160**
Alona guttata tuberculata	24	0	0	33	**57**	50	0	0	0	50	**0**
Alona rustica	189	341	257	495	**1282**	600	302	620	512	2034	**748**
Alona intermedia	95	171	165	363	**794**	650	141	992	158	1941	**374**
Alona affinis	24	128	37	0	**189**	0	201	41	20	262	**160**
Alona quadrangularis	0	0	0	33	**33**	0	20	0	20	40	**106**
Alonella nana	710	171	312	429	**1622**	2100	261	827	394	3582	**748**
Alonella excisa	804	149	110	264	**1327**	1350	161	289	99	1899	**213**
Monospilus dispar	828	982	202	363	**2375**	1900	704	1034	414	4052	**801**
Rhynchotalona falcata	0	21	0	0	**21**	0	40	41	20	101	**106**
Chydorus sphaericus	47	85	18	66	**216**	200	20	83	39	342	**267**
Chydorus piger	497	171	312	297	**1277**	700	422	786	335	2243	**480**
Chydorus globusus	0	0	0	0	**0**	0	0	0	20	20	**0**
Chydorid Cladocera	**4992**	**2795**	**2002**	**3365**	**13154**	**12303**	**2975**	**6574**	**2936**	**24788**	**5764**
Littoral Cladocera	**4992**	**2795**	**2002**	**3365**	**13154**	**12303**	**2975**	**6574**	**2936**	**24788**	**5870**
Total Cladocera	**5608**	**4417**	**3893**	**10228**	**24146**	**13353**	**4704**	**10998**	**5950**	**35005**	**25050**
Number of species	**20**	**18**	**18**	**19**	**22**	**19**	**21**	**20**	**24**	**25**	**20**
Littoral:planktonic ratio	**8.10**	**1.72**	**1.06**	**0.49**	**1.20**	**11.72**	**1.72**	**1.49**	**0.97**	**2.43**	**0.31**

recorded in the spatial surface sediment samples, of which 20 species were recorded in the core sample (Table 5.2). The littoral:planktonic ratios in each depth points of all transects suggest that the 2m depth has the highest deposition of the remains of Chydorid Cladocera followed by the subsequent depth points in each transect (Table 5.2).

Transects, T1, T4 and T5 began from the macrophyte-associated habitats (Figure 5.1, also see Figure 3.1 for habitat details). The number of Cladocera recorded in various depths of these transects suggest that the deposition of the remains of littoral Chydorids is related to the proximity of the source habitat. However, the remains of each species of chydorid Cladocera showed evidence of different patterns of transportation within the transect. *Alonella excisa*, *Monospilus dispar* and *Acroperus harpae* in T1, and *Chydorus piger* and *M. dispar* in T2 were highly abundant in the 2m-depth sample followed by the decrease of the assemblage in subsequent depths of 5m, 8m and 11m and the core sample indicating that the remains of these taxa are transported towards the lake centre with respect to the proximity of the source habitat by sediment focusing (Table 5.2 a, c). Even though the abundance of aquatic vegetation such as *Isoetes, Lobelia* and *Juncus bulbosus* was dominant in the source habitat, the transect, T4 had rather poor concentration of chydorid Cladocera compared to T1 and T5 in 2m and subsequent depths (Table 5.2b). Transects, T2 and T8 began from the sandy substrata (Figure 5.1) but the distribution pattern of transportation of the chydorid remains betweem these transects was different. The number of chydorid remains recorded in the 2m depth of T2 was rather poor, while the deposition of the remains of chydorids such as, *A. harpae*, *A. nana* and *M. dispar* in the same depth of T8 was high (Table 5.2 a, d). Transects T3, T6 and T7 started from the boulder-dominated habitat with exposed bedrock (Figure 5.1). The remains of the most species of Chydorid Cladocera were distributed evenly across these transects indicating that the remains are transported and deposited regularly in the various depth points of these transects (Table 5.2 b, c, d). In all transects, the remains of many species of chydorids deposited in the core sample were rather low, though the remains of large bodied chydorids such as *Eurycercus lamellatus, Alona affinis* and *Allona quadrangularis* were still higher in the core sample than in the source habitats indicating that their transportation is influenced by sediment focusing.

5.3.2.2 Arc-GIS approach

Variations in remains are influenced largely by a variety of factors such as sediment focusing, lake morphometry, depth, water currents, bioturbation, geochemical processes, shoreline habitats and the species-specific habitat preferences of Cladocera. Lake morphometry, in particular, has a significant influence on sediment focusing in lake basins (Blais & Kalff, 1995). Thus the bathymetry of Loch Coire Fionnaraich (Figure 5.3) is assumed to be important for taphonomy of Cladocera.

Remains of the most common species of Cladocera mainly *Bosmina coregoni*, *Bosmina longispina*, *Acroperus harpae*, *Alonella nana*, *Alonella excisa*, *Monospilus dispar* and *Chydorus piger* each representing more than 15% of the total Claodcera in at least one sample in the loch were presented as bar-charts individually by concentration (gdw^{-1}), and the distribution of the remains of each species was assessed on the basis of the number of remains recovered in each depth. Figures 5.4-5.10 show the patterns of the key taxa. The distribution of other less dominant taxa is presented in Appendices 5.5-5.15.

B. coregoni

The deposition of the remains of *B. coregoni* was highly concentrated in the core sample (core-top) being 10,000-12,000 remains collected gdw^{-1} (Figure 5.4). Shoreline microhabitat types do not appear to be important for the deposition of *B. coregoni.* However, the deposition of fossils occurs in a wide range of shoreline to offshore areas particularly related to lake depth and morphometry. Offshore pelagic habitat is important for *B. coregoni.* This taxon has vertical migration patterns to locate their food resources and avoid predators. As a result, the majority of individuals leaves their exoskeletons or die in the pelagic zone. Thus the remains of *B. coregoni* deposited at the lake centre are very high.

B. longispina

Deposition of the remains of *B. longispina* in the loch shows that the highest concentrations are deposited around the lake centre being 6000-7000 individuals (gdw^{-1}) (Figure 5.5). The wide range of low values shown across a large area of the loch suggests that the remains of this taxon are also widely deposited in the offshore region. *B. longispina* and *B. coregoni* have many similarities in food habit and reproduction. Hofmann (1978) argued that *B. longispina* prefers rather deep, large and clear water

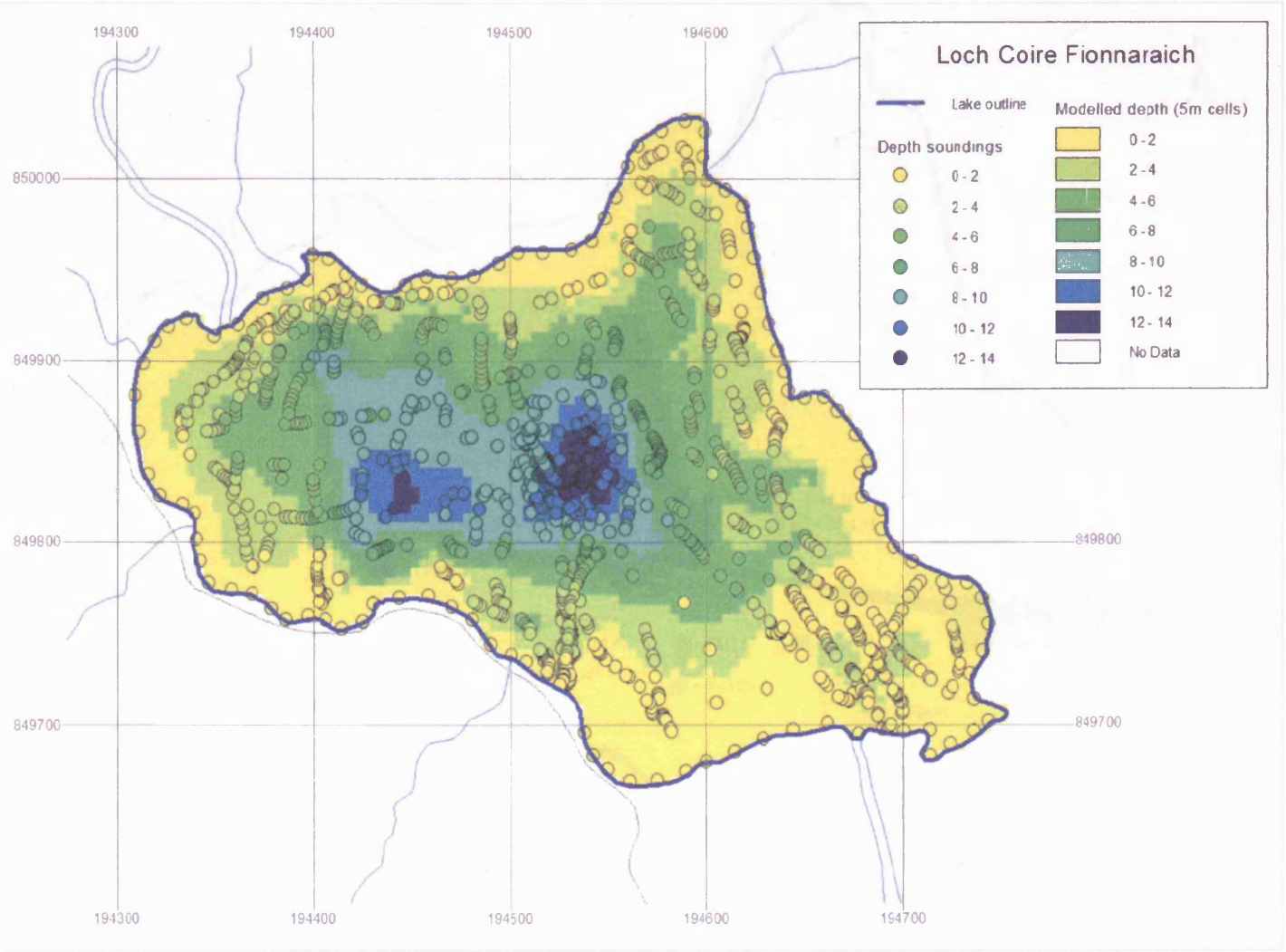


Figure 5.3: Bathymetric measurements in Loch Coire Fionnaraich, Scotland based on Arc-GIS. Each grid has 100 m spacing (Source: Mike Hughes).

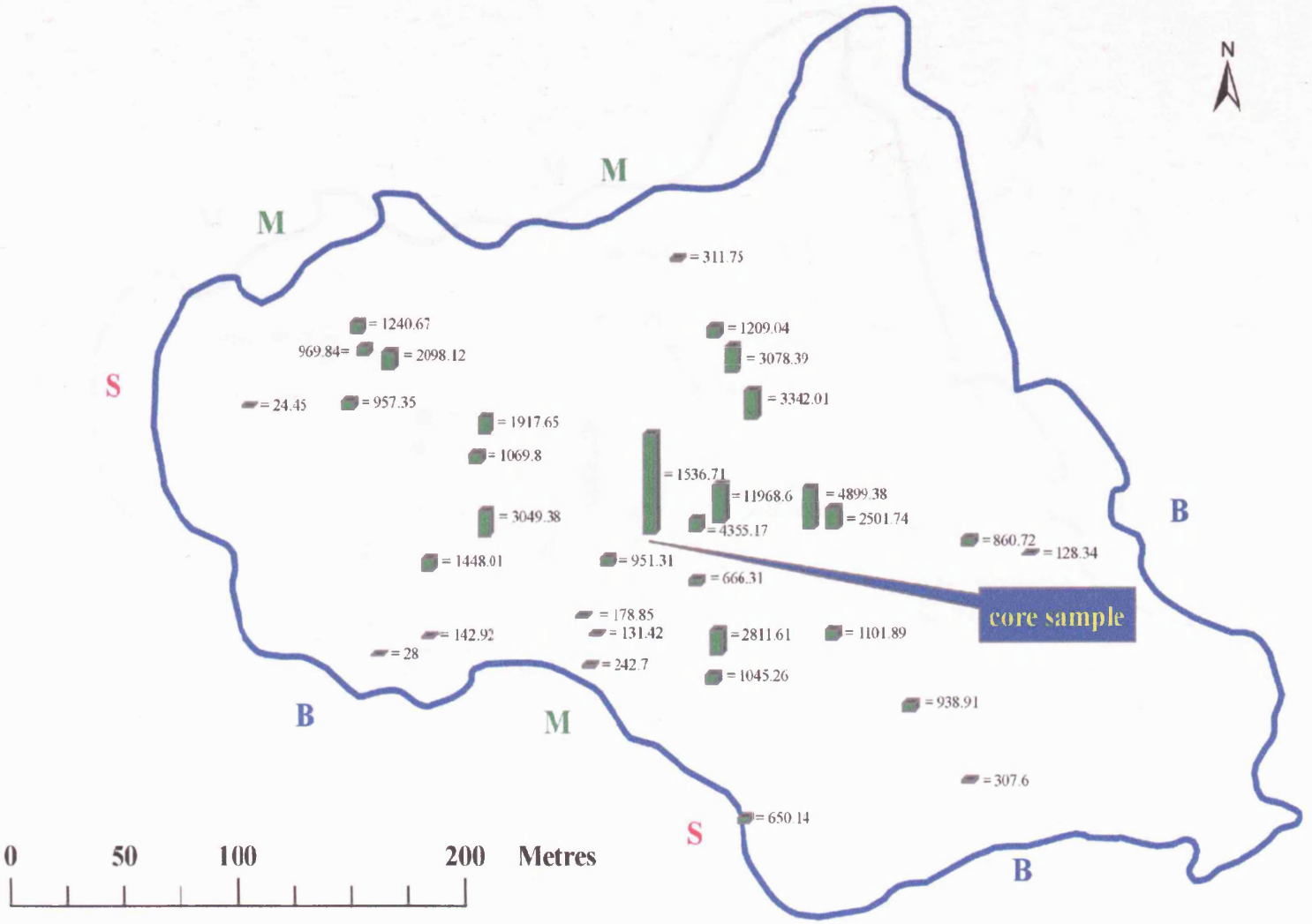


Figure 5.4: Deposition of the remains of *Bosmina coregoni* in Loch Coire Fionnaraich, Scotland. The concentration of remains, number per gram of dry weight sediment (gdw^{-1}) in each sampling point is presented as bars. The sampling points are the GPS co-ordinates, which are described in detail in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran, are identified by M = Macrophyte, S = Sand and B = Boulder respectively.

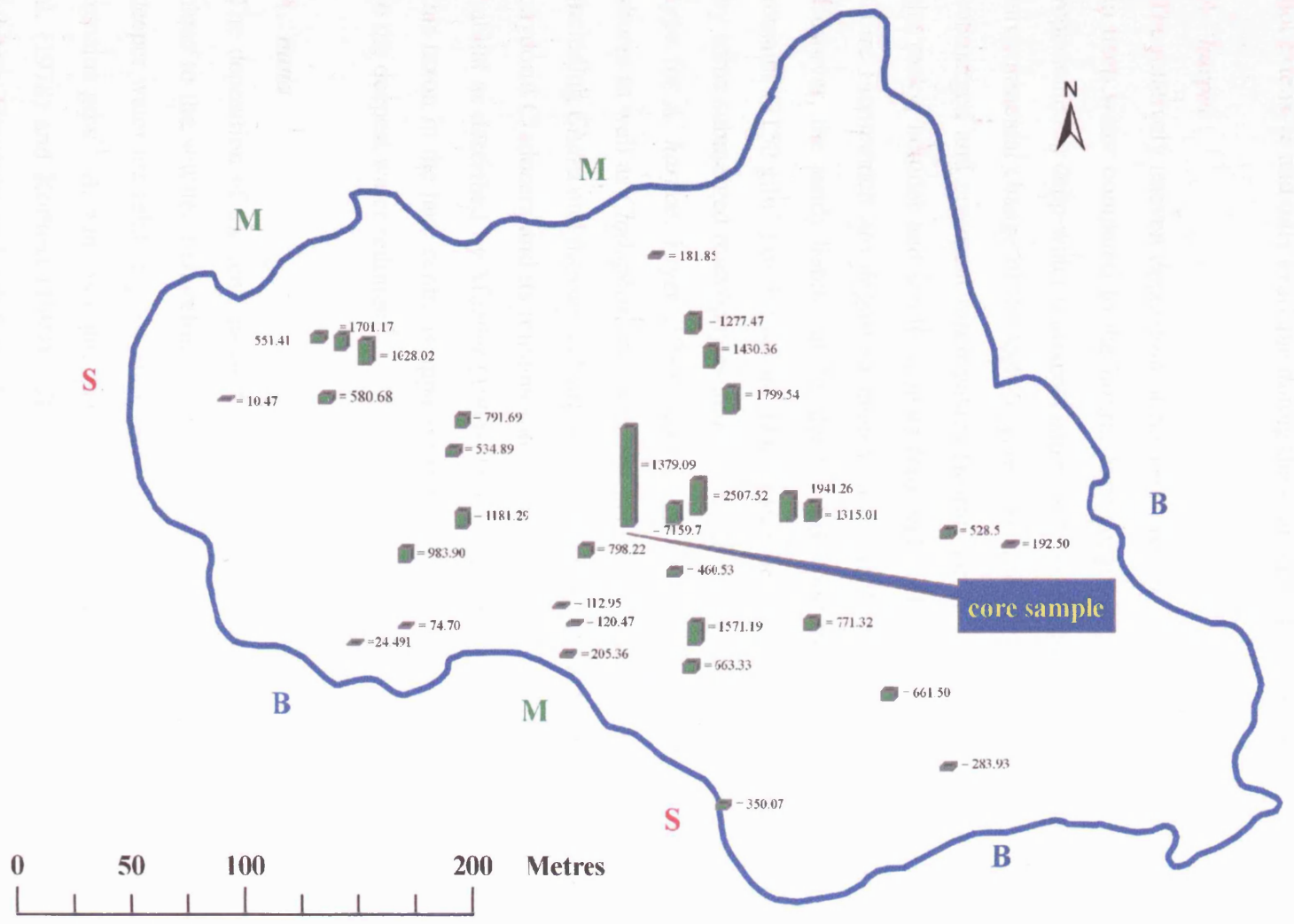


Figure 5.5: Deposition of the remains of *Bosmina longispina* in Loch Coire Fionnaraich, Scotland. The concentration of remains, number per gram of dry weight sediment (gdw^{-1}) in each sampling point is presented as bars. The sampling points are the GPS co-ordinates, which are described in detail in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran, are identified by M = Macrophyte, S = Sand and B = Boulder respectively.

lakes suggesting that its remains could be disarticulated most in the pelagic zone followed by its transportation and deposition towards the deep water zone. However, Korhola (1992) reported that the vegetation substrates in Finnish wetlands have been found to support *B. longispina* indicating that shoreline macrophytes may play an important role for this species. In Loch Coire Fionnaraich, macrophyte substrates are not extensive and only available during the short period in summer.

A. harpae

The relatively uneven deposition of the remains of *A. harpae* and its low concentration in deep water compared to the littoral zone suggesting that this taxon may be under-represented in deep-water sediments and might cause biases in the reconstruction of past environmental change of the loch (Figure 5.6). *A. harpae* is reported to be dominant in submerged and emergent macrophytes (Korhola et al., 2000). This taxon also utilises the rocky, boulder and sandy habitats frequently. The remains of this taxon in Loch Coire Fionnaraich are deposited mainly in macrophyte and sand dominated habitats. However, the sandy habitat at 2m depth contributed the highest concentration of the remains (2150 gdw^{-1}) of this taxon. During summer sandy substrata are often colonized by some submerged macrophytes and this could have also become a significant habitat type for *A. harpae*. Fryer (1993) reported its abundance in bare gritty bottoms and shores as well as *Cladophora*-covered rocks, sandy patches, vegetation of several kinds, including *Chara* and mosses and angiosperms. In LCFR, *A. harpae* is a rather common chydorid Cladocera and its remains should be deposited at the proximity to the original habitat as described by Mueller (1964). However, limited occurrence of the remains of this taxon in the lake centre is apparent indicating some transportations from the shore to the deepest water sediment.

A. nana

The deposition of the remains of *A. nana* shows that the highest concentrations occur close to the southeast shoreline (1700-2100 gdw^{-1}) (Figure 5.7). Concentrations in the deeper water are relatively low although the core sample (core-top) had more than 700 remains gdw^{-1}. *A. nana* is found mainly in macrophyte beds according to Whiteside et al. (1978) and Korhola (1999). Thus its remains should be deposited close to such habitats. However, in Loch Coire Fionnaraich, the remains of this taxon are also found abundantly in other localities, such as sandy and rocky substrata. Fryer (1993) has

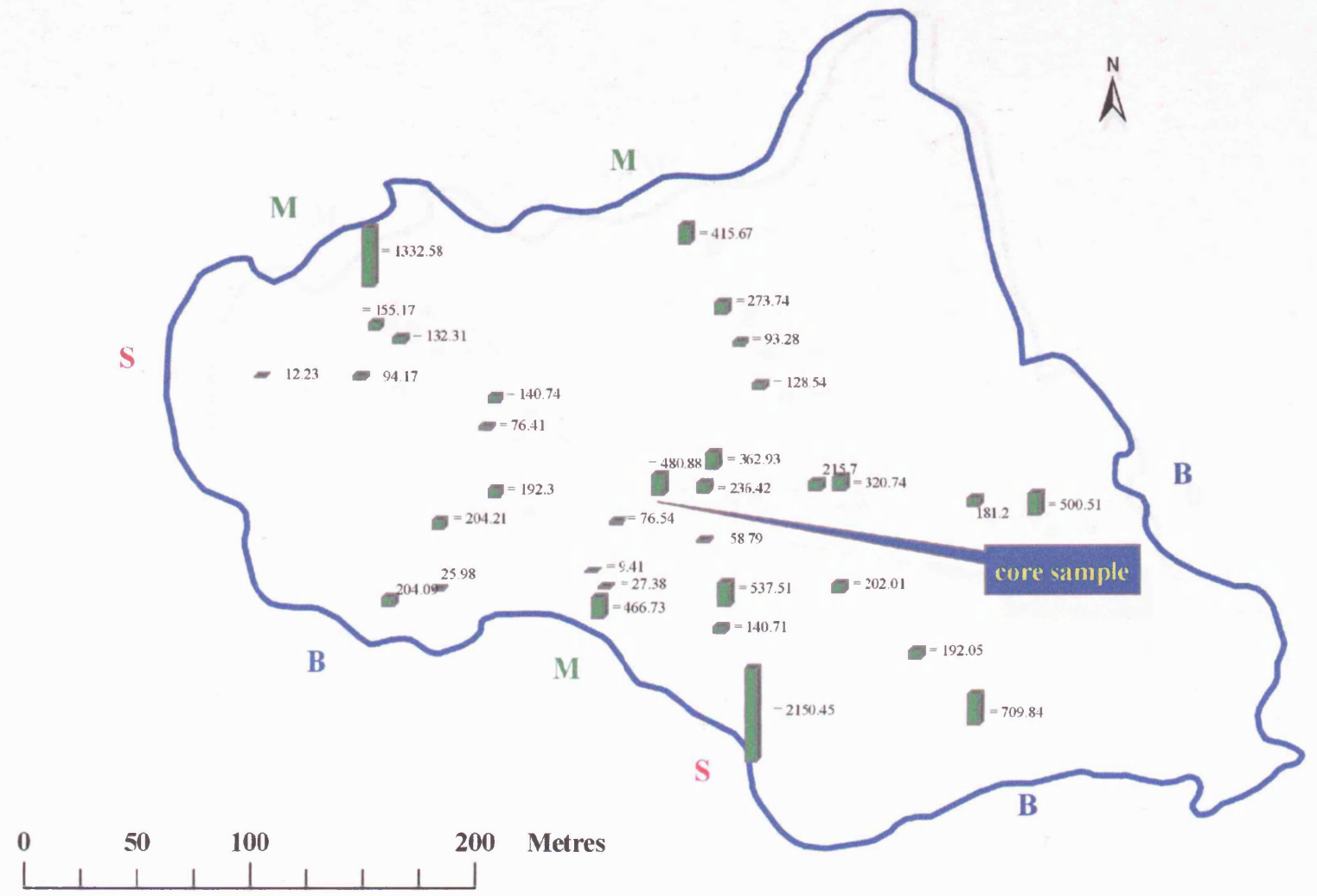


Figure 5.6: Deposition of the remains of *Acroperus harpae* in Loch Coire Fionnaraich, Scotland. The concentration of remains, number per gram of dry weight sediment (gdw^{-1}) in each sampling point is presented as bars. The sampling points are the GPS co-ordinates, which are described in detail in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran, are identified by M = Macrophyte, S = Sand and B = Boulder respectively.

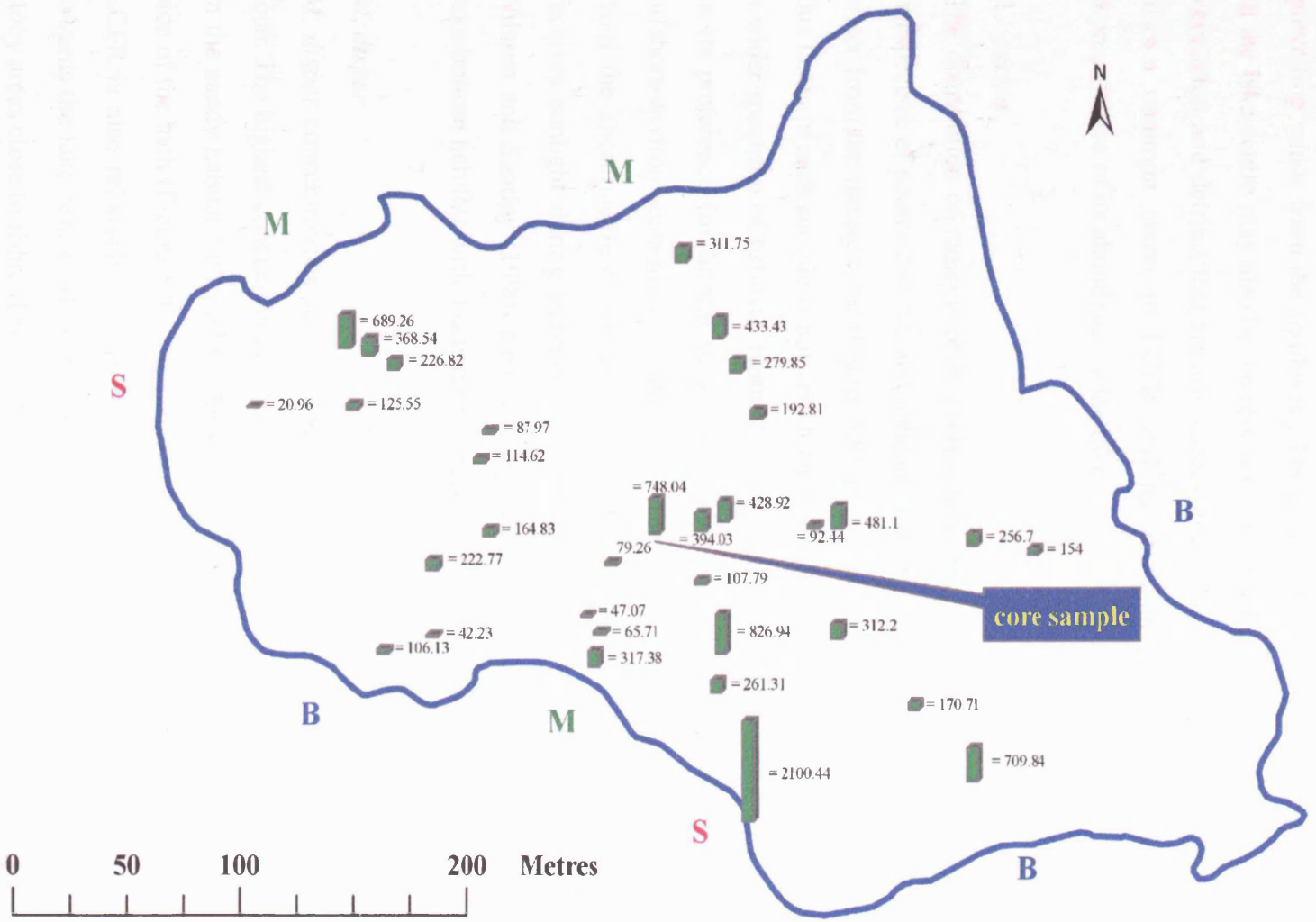


Figure 5.7: Deposition of the remains of *Alonella nana* in Loch Coire Fionnaraich, Scotland. The concentration of remains, number per gram of dry weight sediment (gdw^{-1}) in each sampling point is presented as bars. The sampling points are the GPS co-ordinates, which are described in detail in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran, are identified by M = Macrophyte, S = Sand and B = Boulder respectively.

recorded this taxon in different situations including small pools with *Sphagnum,* sandy substrates, boggy places, a *Sphagnum*-choked runnel, and even in wet *Sphagnum.*

The concentration of the remains of this taxon deposited in 5m, 8m, 11m and the lake centre (14m) shows that it distribution in the sediment is liely to be influenced by the prevailing winds from the southwest. The relatively higher concentration of this taxon in the lake centre may also be the relsult of the resuslt small size occupying crevices in vegetation and detritus that are are inaccessible to larger taxa (Fryer, 1974). *A. nana* is also a common taxon in LCFR and its abundance in the lake centre is quite representative of its abundance in the lake.

A. excisa

The distribution of remains of *A. excisa* shows that this taxon occurs across the basin irrespective of source habitat, and indicates that it is effectively transported into deeper water from the littoral zone (Figure 5.8). However, the concentration of the remains of this taxon in each sample is not very high. Fryer (1993) argued that this taxon colonises a wider spectrum of habitats. Normally it does not colonise the open water habitat due to its preference for littoral substrata. However, higher deposition of its remains in offshore environments indicates that it may also occupy the shallow water habitats away from the shoreline (e.g. 5m and 8m) of LCFR, especially where the lake bottom receives sunlight during summer and supports the growth of emergent macrophytes. Nilssen and Sandøy (1990) have also reported that this taxon can be predominant in lake-bottom habitats with a detritus rich feeding environment.

M. dispar

M. dispar concentrations suggest that this taxon was one of the most common in the loch. The highest concentration (1500-1900 gdw^{-1}) was close to the southeast shoreline in the sandy habitat followed by the shoreline macrophyte substrates in the northwest side of the loch (Figure 5.9). The concentration of remains of this taxon in the centre of LCFR is also relatively high (800 gdw^{-1}) indicating that it is effectively transported towards the lake centre. M. dispar thrives in sandy habitats although it is also found in stony areas close to shore (Fryer, 1993).

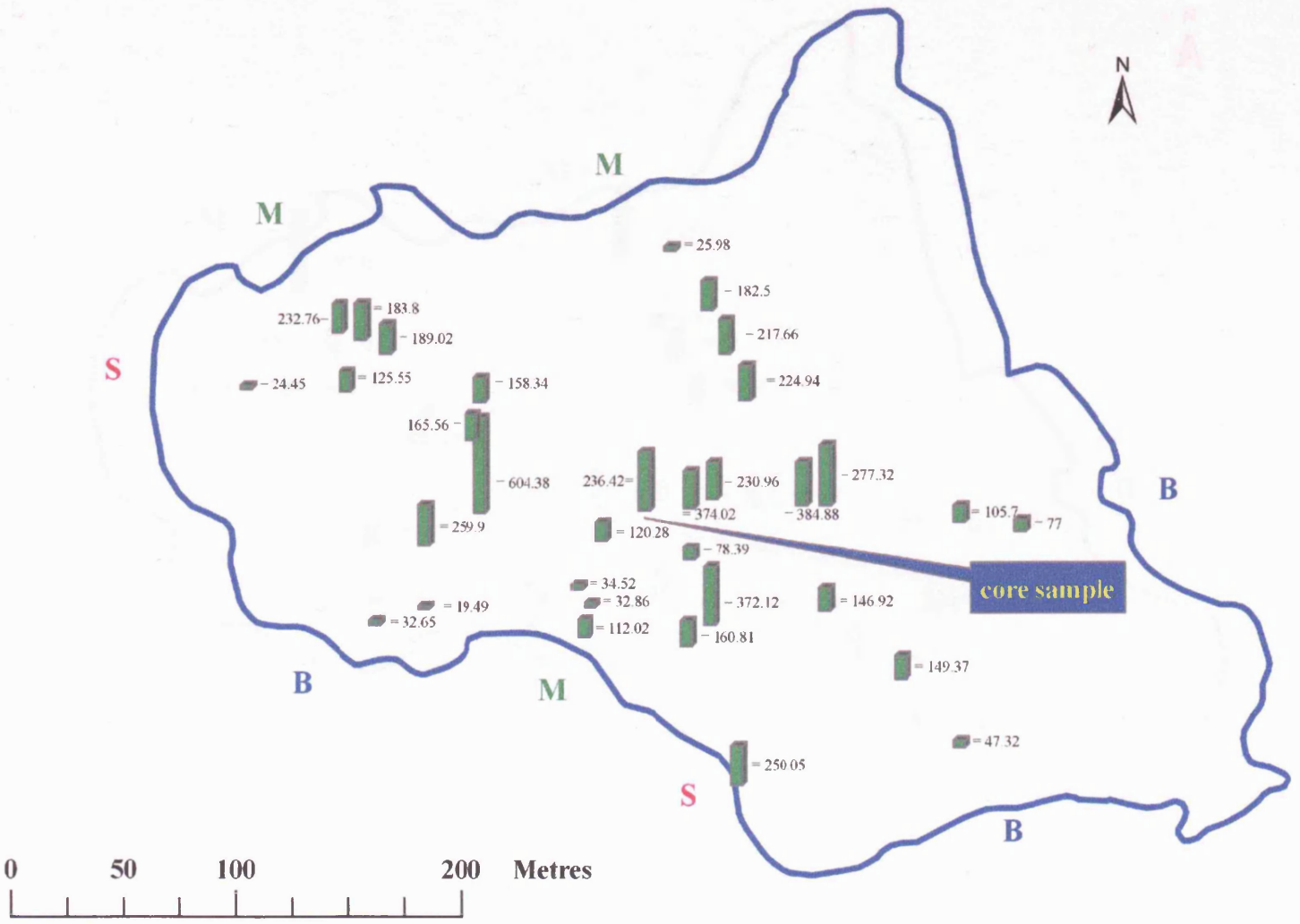


Figure 5.8: Deposition of the remains of *Alonella excisa* In Loch Coire Fionnaraich, Scotland. The concentration of remains, number per gram of dry weight sediment (gdw^{-1}) in each sampling point is presented as bars. The sampling points are the GPS co-ordinates, which are described in detail in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran, are identified by M = Macrophyte, S = Sand and B = Boulder respectively.

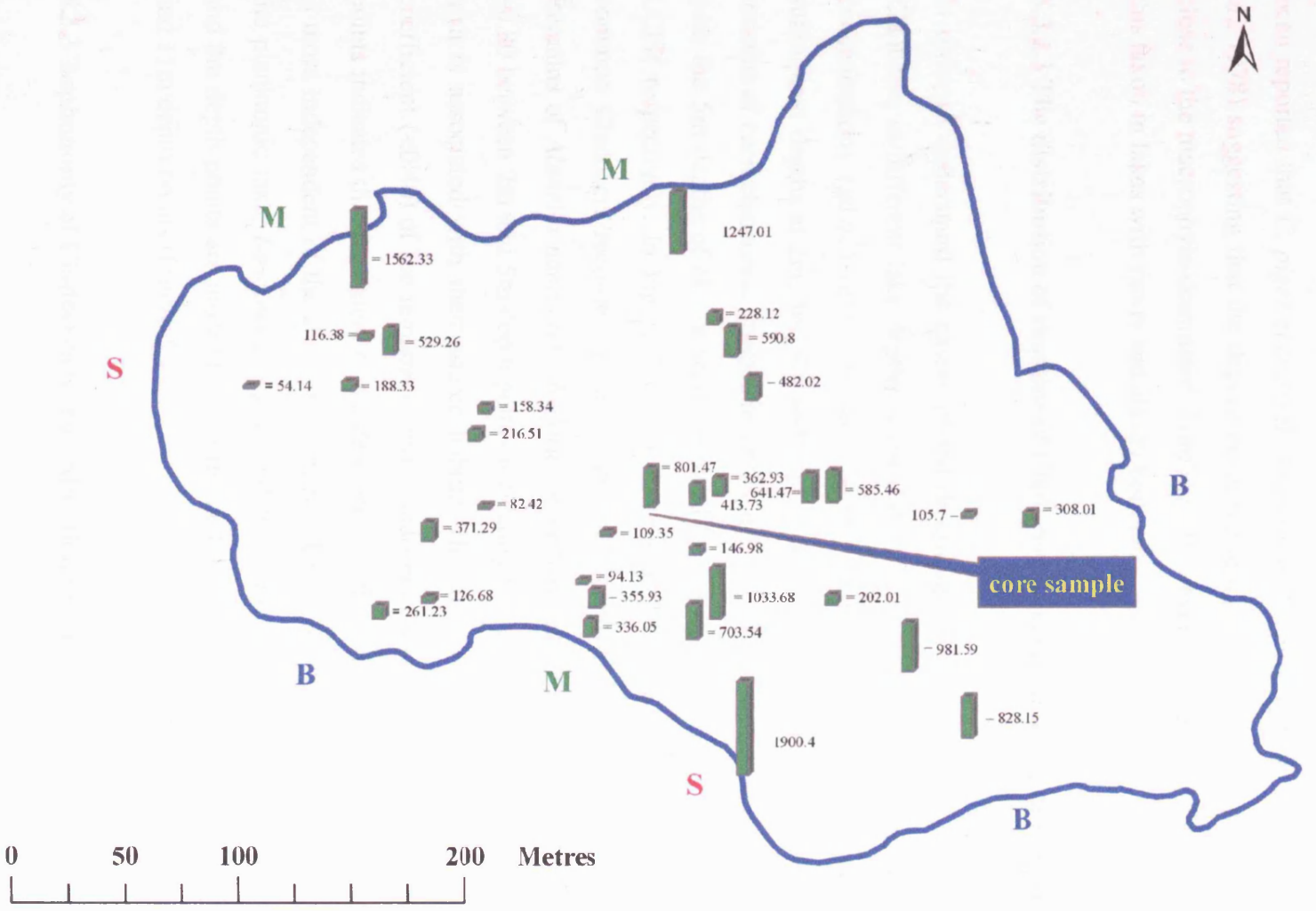


Figure 5.9: Deposition of the remains of *Monospilus dispar* In Loch Coire Fionnaraich, Scotland. The concentration of remains, number per gram of dry weight sediment (gdw^{-1}) in each sampling point is presented as bars. The sampling points are the GPS co-ordinates, which are described in detail in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran, are identified by M = Macrophyte, S = Sand and B = Boulder respectively.

C. piger

The distribution of the remains of *C. piger* shows a bias especially towards the northern part of the loch suggesting that proximity to shoreline habitats, particularly macrophytes, is significant (Figure 5.10). A relatively large number of remains are distributed across the northern and eastern sides of the loch compared to the west. It has been reported that *C. piger* exclusively lives in muddy macrophyte beds (Whiteside et al., 1978) suggesting that the deposition of the remains of this taxon should be highet close to the macrophyte-dominated shorelines. However, Fryer (1993) has also recorded this taxon in lakes with sandy and clayey bottoms.

5.3.2.3 The distribution of remains of Cladocera in relation to depth in LCFR

In order to understand the extent of the deposition of the remains of the individual Cladocera at different lake depths, a correlation analysis was carried out between the concentrations (gdw^{-1}) of the remains of the different taxa recorded between two subsequent depths at 2m, 5m, 8m and 11m. While doing this, the concentration of the remains of each cladoceran species recorded at 2m depths of all transects was correlated with the 5m depths of all transects followed by 5m vs 8m and 8m vs 11m depths in LCFR respectively. In Figure 5.11, the correlation between the remains of the most common Cladocera recorded in each subsequent depth points of LCFR is presented. Remains of *Alonella nana* and *Chydorus piger* had correlation coefficients as high as ~0.80 between 2m and 5m depth points indicating that the extent of deposition of these taxa is associated with their source habitat. However, the relatively low correlation coefficient (<0.40) of the remains of most cladoceran taxa between 2m and 5m depths points indicates that the extent of the deposition of the remains of these taxa in the loch is more independent of the shoreline habitats. Unexpectedly, however, the remains of the planktonic taxa, *Bosmina coregoni* and *Bosmina longispina* recorded between 5m and 8m depth points are more highly correlated than the remains recorded between 8m and 11m depth points (Figure 5.11).

5.3.3 Taphonomy of Cladocera using ordination of the surface sediment samples

In taphonomy, understanding how the assemblage structure of the remains of Cladocera is distributed across the lake bottom is essential, because this provides information on the relationships between the remains of the cladoceran species deposited at various

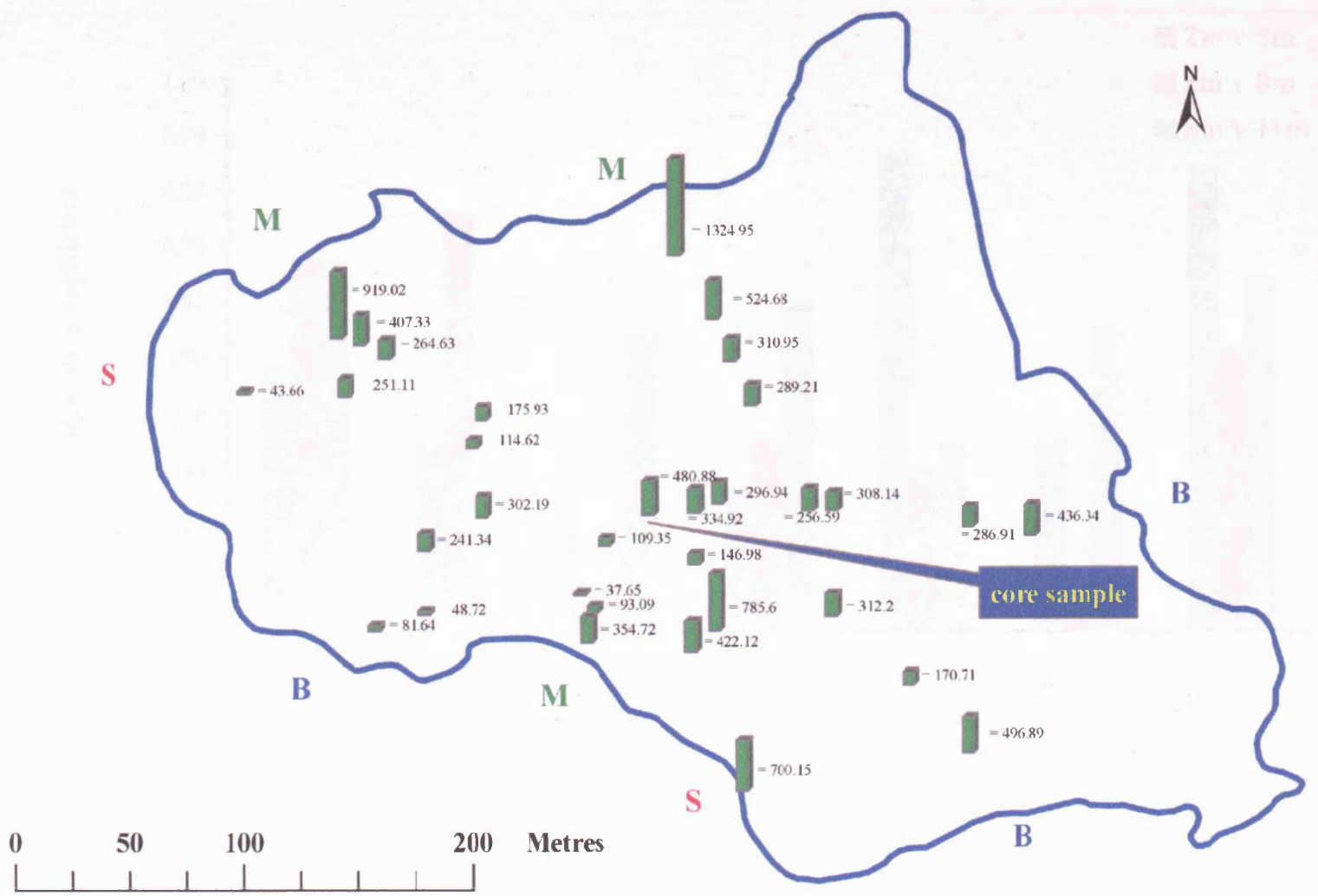


Figure 5.10: Deposition of the remains of *Chydorus piger* in Loch Coire Fionnaraich, Scotland. The concentration of remains, number per gram of dry weight sediment (gdw^{-1}) in each sampling point is presented as bars. The sampling points are the GPS co-ordinates, which are described in detail in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran, are identified by M = Macrophyte, S = Sand and B = Boulder respectively.

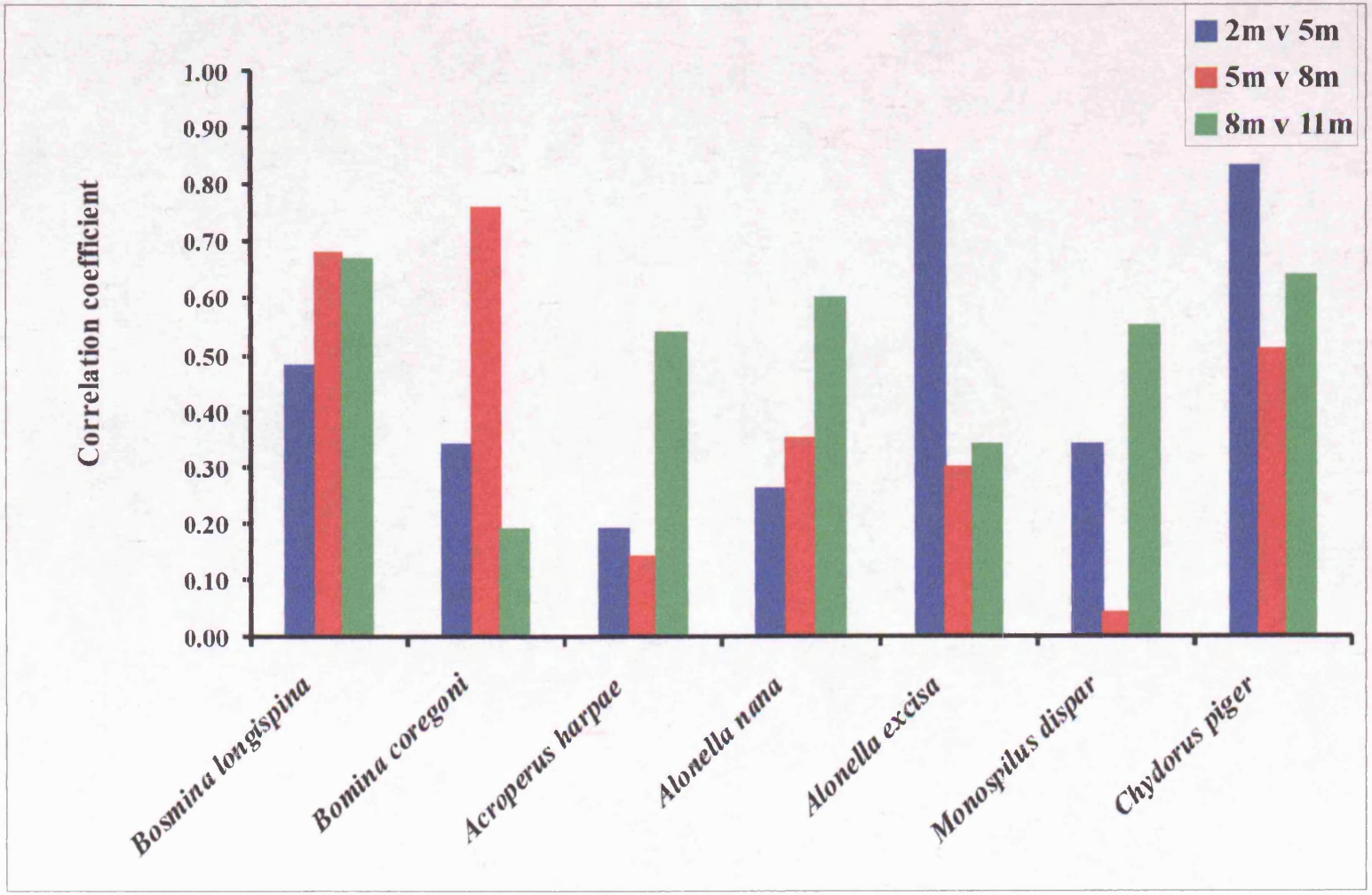


Figure 5.11: Correlation (N=8) between the concentration (gdw^{-1}) of the remains of the most common species of Cladocera deposited in the subsequent depths (2m v 5m, 5m v 8m and 8m v 11m) of Loch Coire Fionnaraich, Scotland. Correlation between 11m and 14m depth samples was not carried out due to a constant concentration (gdw^{-1}) of the remains for the core sample (14m).

lake depths. As a result, a comparison can be made on the species-specific deposition of the remains of Cladocera with respect to the source habitat, planktonic habitat and the lake centre. A variety of ordination techniques were used to identify such relationships.

Most of the remains recovered from the surface sediment samples were head-shields, carapaces, post-abdomens and post-abdominal claws. Cladoceran remains present in at least two of the samples with a relative proportion of more than 1% in at least one, were included for ordination analysis. This process reduced the number of species included in the analysis from 33 to 24.

5.3.3.1 Detrended correspondence analysis (DCA)

DCA with detrending by segments, down-weighting of rare taxa and non-linear rescaling of axes of 24 cladoceran species present in the 33 surface sediment samples showed a short gradient length (<1 SD) of axis 1 (Table 5.3) indicating linear ordination techniques such as principal components analysis (PCA) and redundancy analysis (RDA) were the appropriate methods to use.

Table 5.3: Summary of a DCA ordination of Cladocera assemblages in 33 spatial surface sediment samples, 32 samples along 8 transects and 1 core sample (N=33) in Loch Coire Fionnaraich, Scotland.

DCA axes	1	2	3	4
Eigenvalues (λ)	0.064	0.017	0.01	0.005
Lengths of gradient (standard deviation units)	0.875	0.515	0.38	0.806
Cumulative percentage (%) variance of species data	36.8	46.3	52.0	55.1
Sum of all unconstrained eigenvalues				**0.175**

5.3.3.2 Principal components analysis (PCA)

PCA was chosen to summarise the major patterns of variations of samples in the ordination diagram. The PCA axes showed that the maximum amount of variation in the species data was accounted for by the first two axes of the ordination, in which 59% and 10% of the variation respectively explained (Table 5.4). The faunistic assemblages of the species of cladocera fossils show that remains of three open water taxa, *B. coregoni*, *B. longispina* and *Daphnia* sp. and one littoral taxon, *A. quadrangularis* (not shown in figure) were closely associated with the sample recovered from the core sample (Figure 5.12). Assemblages of *B. coregoni* and *B. longispina* and *Daphnia* sp. in particular, were high in the deeper water samples, T4M11m and T5M11m, related to the transect

Table 5.4: Summary of a PCA ordination of Cladocera assemblages in 33 spatial surface sediment samples, 32 samples along 8 transects and 1 core-top sample (N=33) in LCFR.

PCA Axes	1	2	3	4
Eigenvalues (λ)	0.590	0.107	0.062	0.047
Cumulative % variance of species data	59.0	69.7	75.9	80.6

beginning from the macrophyte habitat (Figure 5.12). The fossil assemblages of littoral Chydorids, however, showed considerable variation along transects. Remains of some of the common Chydorids in the loch, such as *Monospilus dispar* and *Alonella nana*, were recovered in the samples, T3B5m, T8S5m, T8S2m and T3B2m associated especially with the boulder and sand-dominated habitats (Figure 5.12). The remains of *Rhynchotalana falcata*, *Alona affinis* and *Alona rustica* were associated with samples, T4M2m, T7B5m, T4M5m and T2S2m respectively (Figure 5.12). However, the remains of *R. falcata* in particular, were closely associated with the sandy habitat. The remains of *Chydorus piger* were associated with sample, T5M2m that was taken from a macrophyte-dominated substrate. *Alonella excisa*, *Graptoleberis testudinaria*, *Acroperus harpae* and *Eurycercus lamellatus* were associated with the samples related with all types of shoreline-habitats (Figure 5.12).

5.3.3.3 Redundancy analysis (RDA)

The RDA constrained with 6 'taphonomic' factors was performed to estimate the total explanatory power of the environmental variables overall. The result showed that the combination of all taphonomic factors together accounted for 71.1% of the total variance in which RDA axis 1 explained 66% of the total variation in the species data (Table 5.5). Both the first and all canonical axes involving 499 unrestricted Monte Carlo permutations tests in a reduced model were highly significant ($p<0.002$).

Table 5.5: Summary of a RDA ordination of Cladocera assemblages in 33 spatial surface sediment samples, 32 samples along 8 transects and 1 core sample (N=33) in LCFR, Scotland.

RDA Axes	1	2	3	4
Eigenvalues (λ)	0.662	0.038	0.009	0.003
Species-environment correlations	0.933	0.723	0.632	0.340
Cumulative percentage (%) variance -of species data	66.2	70.0	70.8	71.1
-of species-environment relationship	92.9	98.1	99.4	99.8
Sum of all canonical eigenvalues			=	**0.713**

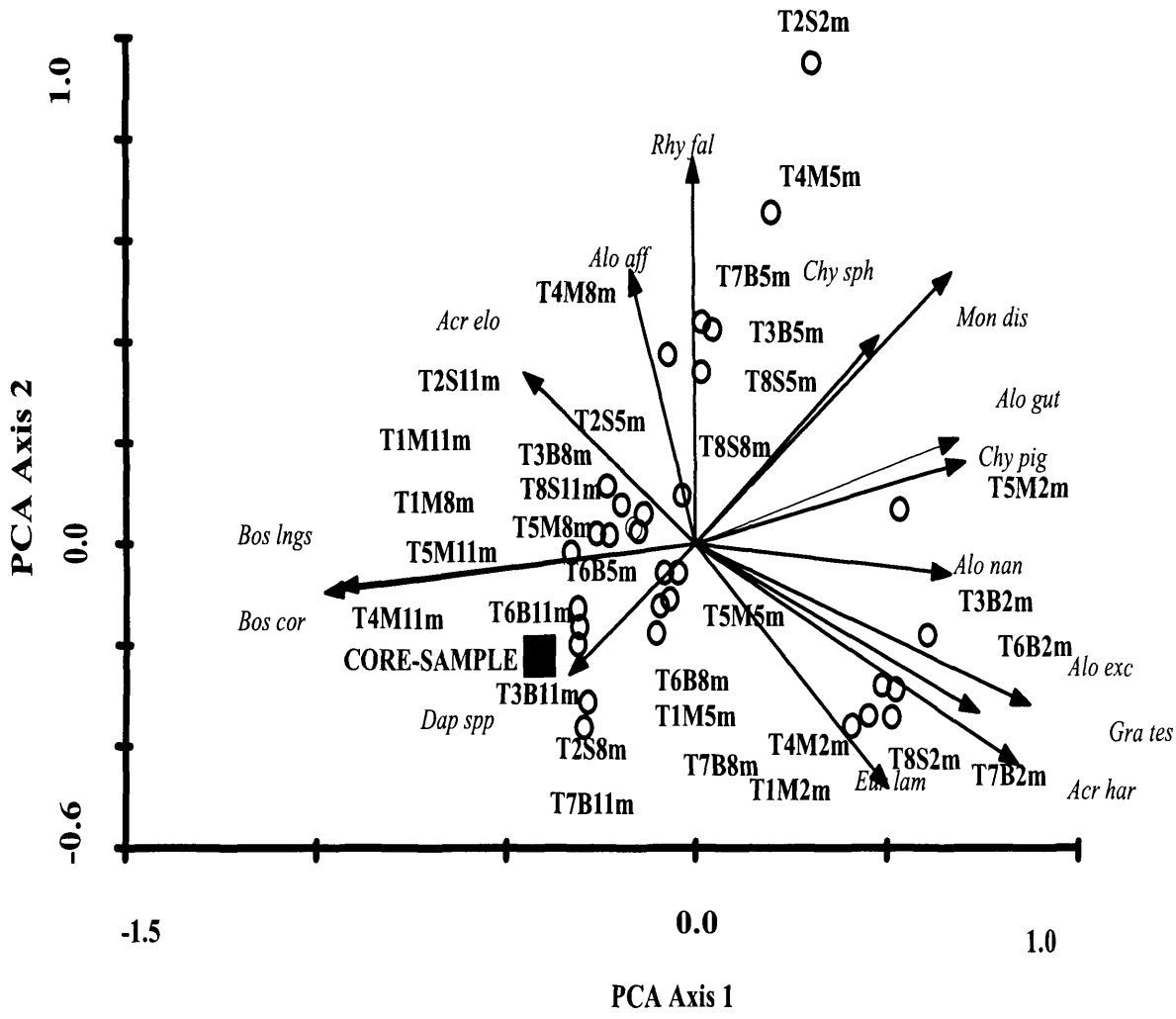


Figure 5:12: PCA biplot ordination of 33 (32+1) spatial surface sediments samples. The core sample is indicated by the symbol [■] in ordination diagram. Abbreviations for the samples are presented in Appendix 5.1. Abbreviations for major species shown in the diagram are: Eur lam (*Eurycercus lamellatus*), Acr har (*Acroperus harpae*), Gra tes (*Graptoleberis testudinaria*), Alo exc (*Alonella excisa*), Alo nan (*Alonella nana*), Alo gut (*Alona guttata*), Sid cry (*Sida crystallina*), Chy pig (*Chydorus piger*), Chy sph (*Chydorous sphaericus*) Mon dis (*Monospilus dispar*), Rhy fal (*Rhynchotalona falcata*), Alo aff (*Alona affinis*), Alo rus (*Alona rustica*), Alo elo (*Alonella elongatus*), Alo int (*Alona intermedia*), Bos lngs (*Bosmina longispina*), Bos cor (*Bosmina coregoni*), Dap spp (*Daphnia* sp.).

In RDA, the species composition was constrained to only one taphonomic variable at a time; the first eigenvalue (λ_1) was constrained, whereas the second eigenvalue (λ_2) was unconstrained. The λ_1: λ_2-ratio was then used to express the relative strength of each variable in explaining the variance (Lotter et al., 1997). The result showed that Depth had the maximum λ_1: λ_2-ratio in the species data (Table 5.6).

Table 5.6: Percentage variance explained by each taphonomic variable when RDA is constrained with a single explanatory variable and tested under Monte Carlo permutation tests involving 499 unrestricted random permutations. The variable with the highest variance and λ_1/λ_2 is highlighted as bold letters. P-values are given as, **p<0.01, *p<0.05.

Environmental variables	(λ_1)	(λ_2)	λ_1/λ_2	P- value	Variance explained (%)
Macrophyte	0.017	0.59	0.028	0.68	1.7
Sand	0.015	0.59	0.025	0.76	1.5
Boulder	0.018	0.58	0.031	0.64	1.8
Central	0.045	0.55	0.082	0.29	4.5
Depth	0.485	0.146	**3.32**	0.002	48.5**
LOI	0.144	0.509	**0.282**	0.008	14.4**

In order to achieve the best explanatory power of each taphonomic factor, a forward selection method involving 999 unrestricted Monte Carlo permutations tests were performed (ter Braak, 1990; ter Braak and Verdonschot, 1995). Depth was found to be the most highly significant variable with the highest extra fit in the species data followed by LOI (Table 5.7). None of the micro-habitats showed significant relationships with fossil assemblages of Cladocera. The summary statistics of two selected physico-chemical factors in relation to fossil assemblages of cladoceran remains in 33 surface sediment samples showed that the depth of the loch was the only significant factor in regulating the deposition of fossil remains of Cladocera in the lake basin (Table 5.8).

The result of a RDA biplot with 2 selected variables after forward selection is presented in Figure 5.13. The remains of two planktonic taxa *B. coregoni* and *B. longispina* were closely associated with the deepest water. Except for a few species (e.g. *Alona quadrangularis*), the fossil assemblages of most littoral taxa however, were restricted to the shallower water (<14m). Species-specific variations in the representation of fossil assemblages were observed in the 2m, 5m, 8m and 11m-depth samples (Figure 5.13). The remains of *Alona intermedia, Acroperus elongatus, Alona rectangula* had higher

representations at 11m-depth samples while the remains of *Rhynchotalona falcata* and *Alona rustica* were more highly represented in the sample recovered from 8m-depth (Figure 5.13). The remains of *Chydorus piger, Monospilus dispar* and *Alonella nana* were relatively high in the 2m and 5m-depth samples (Figure 5.13).

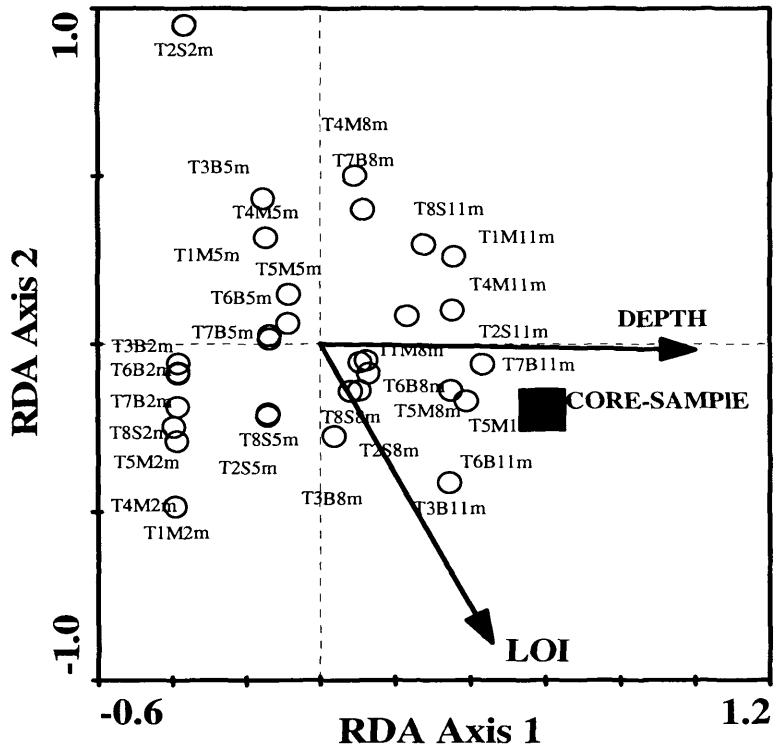
Table 5.7: Potential variance explained by each physico-chemical variable before forward selection and variance explained by those variables when added in forward selection in RDA. The p-values were obtained after Monte Carlo permutations tests, 999 unrestricted permutations in a reduced model. The p value for the overall model was obtained from 499 permutations and also was adjusted with Bonferroni type of corrections.

Taphonomic factors	**Variance explained before forward selection**	**Variance explained when added with forward selection**	**P-value**	**Remarks**
Depth (m)	0.485	**0.485**	**0.001**	First: Added
LOI (%)	0.144	**0.054**	**0.002**	Second: Added
Central	0.045			
Boulder	0.018			
Macrophyte	0.017			
Sand	0.015			
Sum of Variance		**0.539**		**Overall test p =0.01**

Table 5.8: Summary of RDA on relationships between cladoceran fossil assemblages in spatial surficial sediments of 33 samples in Loch Coire Fionnaraich and 2 selected physico-chemical variables, Depth and LOI, after forward selection.

Axes	**1**	**2**	**3**	**4**
Eigenvalues (λ)	0.485	0.054	0.130	0.073
Species-environment correlations	0.910	0.731	0.000	0.000
Cumulative percentage (%) variance				
-of species data	48.5	53.9	66.9	74.2
-of species-environment relation	90.0	100	-	-
Sum of all canonical eigenvalues				**= 0.539**

(a)



(b)

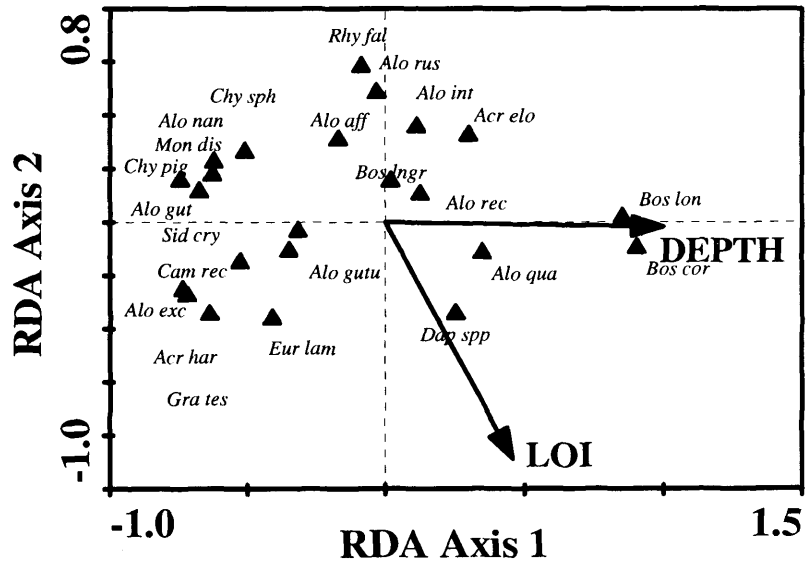


Figure 5.13: RDA biplots between axis 1 and 2 after forward selection, a. sample vs environment, b. species vs environment. Abbreviations for samples and species are presented in Appendix 5.1 and Appendix 5.2 respectively. The core sample is represented by a symbol (■).

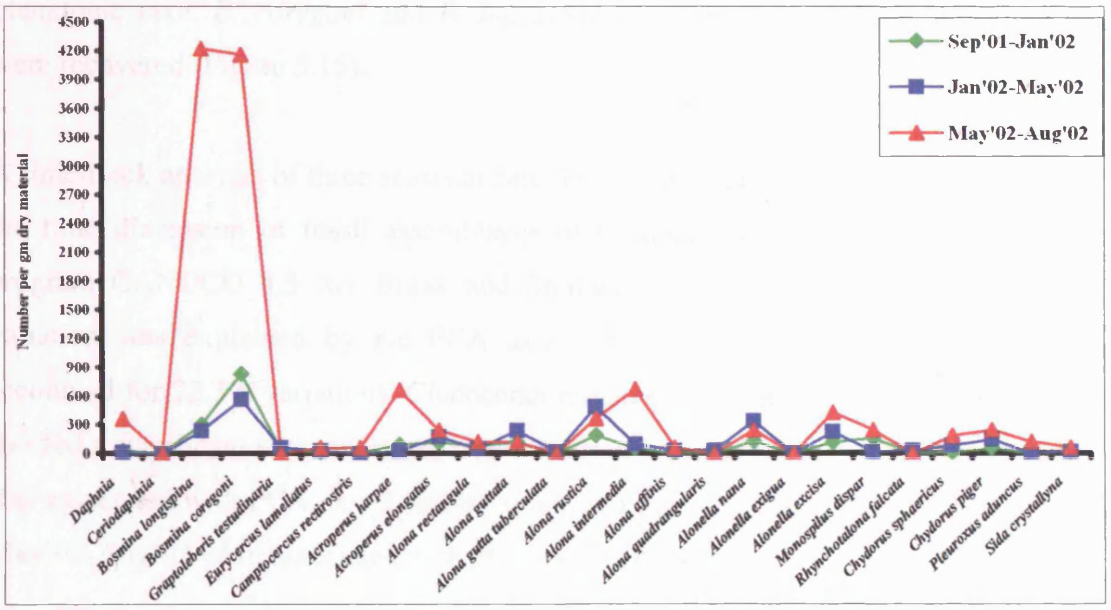
5.3.4 Sediment trap

Sediment traps act as a platform for sampling littoral and planktonic cladoceran remains before they are incorporated in lake sediments. Unlike the core sequence, sediment traps can be used to provide temporal environmental signals (e.g. seasonality), which are useful for monitoring the environmental health of a lake. Sediment traps are also a more efficient method for collecting modern cladoceran populations since the method for collecting contemporary cladoceran zooplankton requires a variety of plankton nets as well as significant amount of time and expense. In addition, due to their species-specific response to habitat type and seasonality, not all Cladocera can be collected in the contemporary samples while their remains are often retrieved in the sediment traps. Sediment traps also suffer from fewer mixing problems compared with surface sediments since the sediment in the surface is often influenced by the bottom dwelling animals (e.g. Cameron, 1995).

A total of 25 species of cladoceran zooplankton was recovered in the sediment trap, which was installed in the water column of Loch Coire Fionnaraich for a year in three different seasons, Sep'01-Jan'02, Jan'02-May'02 and May'02-Aug'02 respectively. The highest, 23 species, was recorded in Jan'02-May'02, followed by May'02-Aug'02 (n=20) and Sep'01-Jan'02 (n=19) respectively. Only 4 planktonic taxa were recorded, and the taxon *Ceriodaphnia* was present only in the sample recovered from Sep'01-Jan'02.

The number of remains recovered per gram dry matter (gdm^{-1}) and their relative abundance and composition (%) are presented in Figure 5.14. An exceptionally large number (>4200 gdm^{-1} dry material) of *Bosmina coregoni* remains was recovered from the sample of May'02-Aug'02 (Figure 5.14). Remains of a few species of Chydorids, *Acroperus harpae*, *Alona intermedia* and *Alonella excisa* were dominant in May'02-Aug'02, but the number of remains did not exceed 600 gdm^{-1} (Figure 5.14). The relative abundance and composition of cladoceran remains in the trap samples show that remains of *Bosmina coregoni* and *B. longispina* were the most abundant taxa in the loch. The percentage abundance of *B. coregoni* in Sep'01-Jan'02 and May'02-Aug'02 samples was about 30% of the total remains recovered from the loch. The abundance of *B. longispina* was 30% of the total remains recovered from May'02-Aug'02 (Figure 5.14b). The remains of most Chydorids, *Alona rustica*, *Alonella nana*, *Alonella excisa* and *Chydorus piger* had a relatively higher abundance (5-15%) in the sample of Jan02-

(a)



(b)

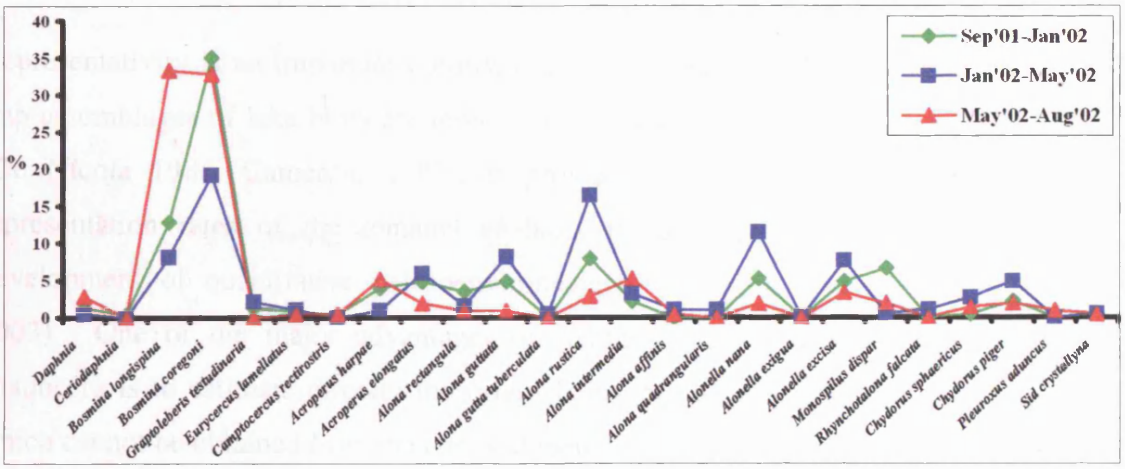


Figure 5.14: Composition (a) number per gram of dry matter in sediment trap (sedimented material-SM), (b) percentage, of cladoceran zooplankton present in sediment trap installed centrally over a year in Loch Coire Fionnaraich. The sediment trap was retrieved three times in January, May and August 2002.

May'02 (Figure 5.14b). A maximum 7 species with more than 5% of the total was recovered from the sample of Jan'02-May02, followed by Sep'01-Jan-02 (n=5) and May'02-Aug'02 (n=4) respectively (Figure 5.15). The average number of remains for the entire year show that only 3 taxa had more than 5% abundance, in which two planktonic taxa, *B. coregoni* and *B. longispina* and one littoral taxon, *Alona rustica* were recovered (Figure 5.15).

A time-track analysis of three seasonal samples was also carried out in PCA to identify the time dimension of fossil assemblages of Cladocera in sediment traps using the program CANOCO 4.5 (ter Braak and Šmilaeur, 2002). A total of 77.7% of total variation was explained by the PCA axis 1 followed by the PCA axis 2, which accounted for 22.3% variations. Cladoceran remains accumulated in the sediment traps showed a significant seasonal trend, where the trap installed between Sep'01 and Jan'02 was associated with PCA axis 2 and the other two traps installed in Jan'02-May'02 and May'02-Aug'02 were associated with PCA axis 1 (Figure 5.16).

5.3.5 Sediment trap vs the composition of remains in the core sample

Representativity is an important consideration in taphonomic studies in how sediment trap assemblages of lake biota are represented by fossil assemblages in core sediments (De Nicola 1986, Cameron, 1995). It provides an estimation of the differential representation rates of the remains of biota in lake sediments and supports the development of quantitative palaeoenvironmental reconstructions (e.g. Kato et al., 2003). One of the major advantages of sediment trap studies for taphonomy of Cladocera is to estimate directly the original flux of an individual fossil assemblage, which cannot be obtained from the core sediments (e.g. Takahashi et al., 1990).

After death, the remains of individual Cladocera sink through the water column. While sinking, a variety of factors influence the quality of the remains from its original properties, where depth is the foremost important factor. In shallower water, dissolution of remains appears to be minimal as compared to the deeper zones, since shallow depths require relatively less time for sinking than the deeper depths (e.g. Kato et al., 2003). However, sinking rates can vary between species depending on variations in the density, diameter and shape of the remains (e.g. Chumra et al., 1999). Presence of spines and other surface area appendages may affect the sinking velocity of the remains

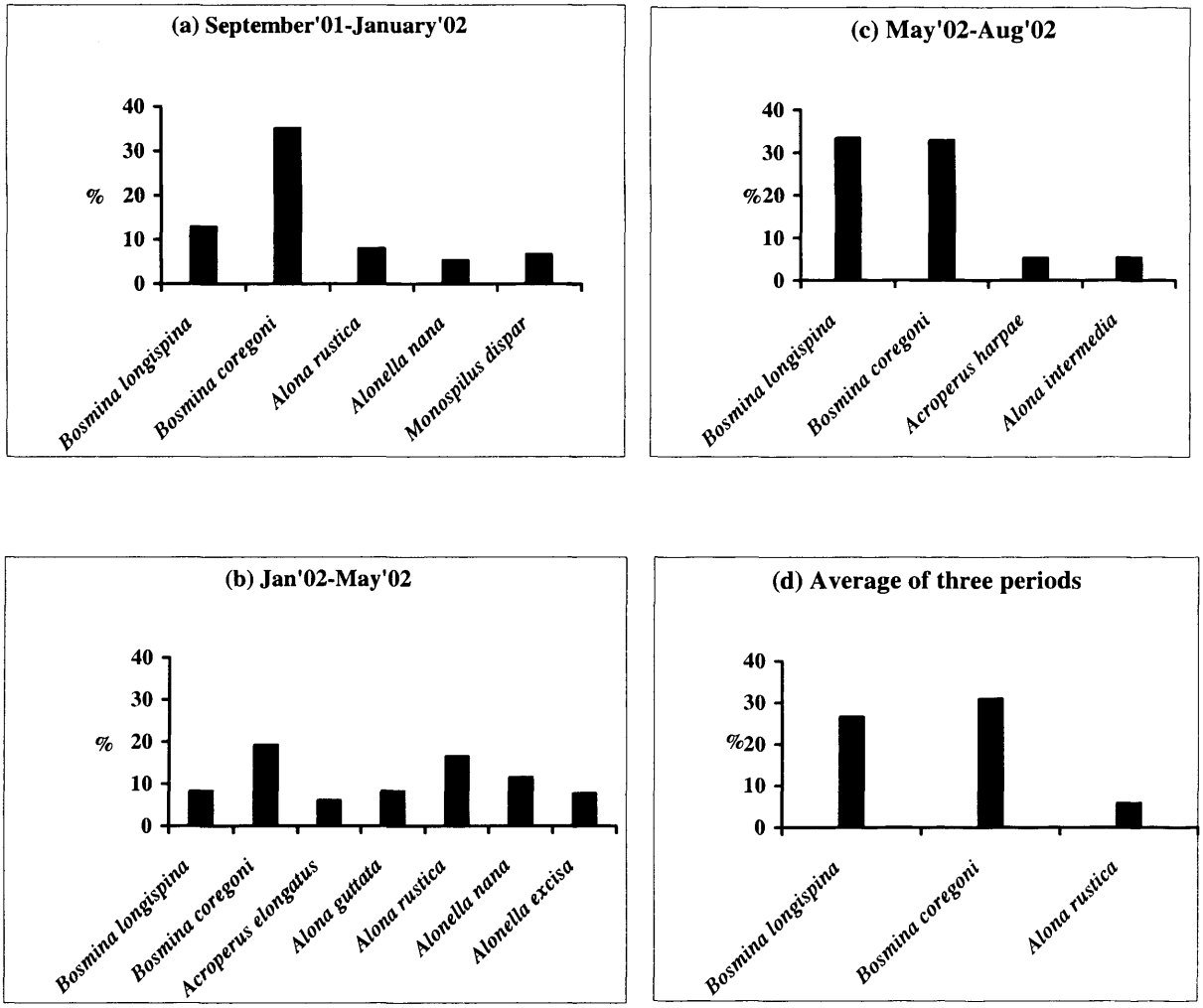


Figure 5.15: Common (>5%) cladoceran zooplankton taxa present in trap assemblages along three periods of trap exposure (a, b, c) and their average (d) over a year 2001/2002 in Loch Coire Fionnaraich, Scotland.

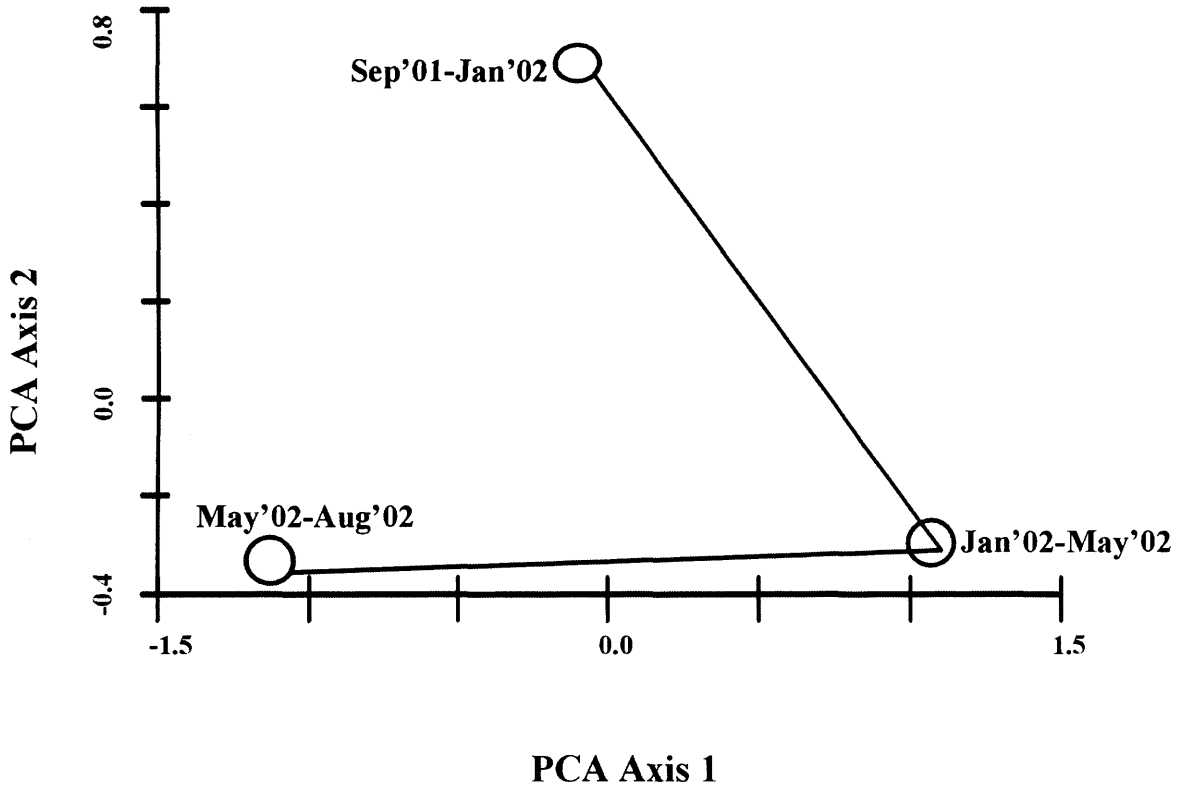


Figure 5.16: PCA time-series analysis of sediment trap materials of fossil Cladocera collected in three seasons (September 2001- January 2002, January 2002-May 2002 and May 2002-August 2002) between 2001 and 2002 in Loch Coire Fionnaraich, Scotland.

significantly. Cadée et al. (1992) carried out an experiment on the sinking velocity of krill (*Euphausia superba*) faecal strings in the Scotia Sea using sediment traps at various depths. They found that the smallest faecal strings were present only in the shallower traps. They further argued that krill feeding largely on diatoms produced faeces with a higher settling velocity than those feeding on other phytoplankton. Cladocera remains have differential sinking rates according to size similar to those reported for pollen (e.g. Chumra et al., 1999) and diatoms (Smayda, 1969). Remains of large (>1 mm length) Cladocera such as *Eurycercus lamellatus* and *Alona affinis* appear to sink much faster than other species. Fragmentation and dissolution of the remains of most aquatic biota take place at the sediment-water interface (cf. Chumra et al., 1999) through processes of decomposition, accelerated in many cases by bioturbation (Frey, 1988; Korhola and Rautio, 2001). The unequal tolerance of chitin to decomposition may also be an important factor affecting the differential representation of fossil Cladocera in lake sediments. However, no studies were found on biodegradation of chitin carried out for taphonomic purposes.

For Loch Coire Fionnaraich, an attempt has been made to estimate the representativity of Cladocera in the sediment. An approximate loss rate (%) and representation rate (%) of Cladocera remains in lake sediments can be estimated on the basis of the annual accumulation rate of the total Cladocera remains in the surface sediment sample recovered from the deepest basin of the lake, in relation to the annual sinking flux of the total Cladocera remains in the sediment trap as explained by Kato et al. (2003) for marine planktonic diatoms. The equations can be given as:

$$L = \frac{B - A}{B} * 100 \qquad \textit{Equation 5.1}$$

Where, L = Total loss rate during taphonomic processes

B = Annual sinking flux of the total cladoceran remains in the sediment trap ($cm^{-2}yr^{-1}$)

A = Annual flux of the total cladoceran remains in the core sample ($cm^{-2}yr^{-1}$)

The representation rate (P) of fossils will then be estimated as:

$$P = 100 - L \qquad \textit{Equation 5.2}$$

The representation of Cladocera in the core sample with respect to loss rates and representation rates during taphonomic processes in LCFR is presented in Table 5.9 and Figure 5.17. The annual sediment flux ($cm^{-2}yr^{-1}$) of remains in the trap was calculated by adding the total number of remains (gdm^{-1}) recovered in the three periods, Sepember'01-January'02, January'02-May'02 and May'02-August'02 respectively and then divided by the cross-section area of the sediment trap (i.e. $\pi r^2 = 22/7*5^2 = 78.57$ cm^2, where r is the radius of the trap). The annual accumulation rate of remains in the core sample was calculated on the basis of sediment accumulation rate with respect to ^{210}Pb dating (Table 7.2, Chapter 7) and the cross-section area of the sediment core used. The recent accumulation rate on the basis of ^{210}Pb dating in LCFR is 0.2 cm per year (Appleby, 2002, unpub. report). Since the thickness of the core surface sample was 0.5 cm, the section of the top sediment core represented 2.5 years. In order to estimate the sediment flux ($cm^{-2}yr^{-1}$) in the core sample, first the total number of remains (gdw^{-1} yr^{-1}) was calculated by dividing 2.5 years and then again divided by the cross-section area of the sediment core (i.e. $\pi r^2 = 22/7*3^2 = 28.28$ cm^2).

Assuming that the sediment trap and surface sediment receive the same initial flux in the loch, the result showed that the total sediment flux in the core sample was slightly higher than the total flux in the sediment trap (Table 5.9). However, the representation of remains varied considerably when the remains of individual Cladocera in the trap and the core sample were compared (Table 5.9, Figure 5.17).

Remains of a total of 12 species of Cladocera did not appear to be influenced significantly by taphonomic processes during sinking through the water column, and they were 'over-represented' in the sediment-water interface (Figure 5.17). These include two planktonic Cladocera, *Bosmina coregoni* and *B. longispina* and five littoral Cladocera, *Eurycercus lamellatus*, *Graptoleberis testudinaria*, *Alona affinis*, *Alona quadrangularis* and *Rhynchotalona falcata* respectively (Table 5.9). Remains of planktonic Cladocera, *Ceriodaphnia* spp. were not represented in the core sample, and remains of *Daphnia* were poorly represented (<40% representation rates). Littoral Cladocera, *Camptocercus rectirostris*, *Alona guttata tuberculata*, *Alonella exigua* and *Pleuroxus aduncus* were not represented in the fossil assemblages at the sediment-water interface since they were recovered only in the sediment traps (Figure 5.17). At least two taxa, *Acroperus elongatus* and *Alona rustica*, were found to be well represented with more than 70% of total remains preserved. However, *Acroperus harpae*, *Alona*

Table 5.9: Calculation of loss and representation rates of Cladocera using sediment flux in the trap and the core sample in Loch Core Fionnaraich, Scotland. Taxa with negative (-) loss rates and very high (>100%) representation rates indicate 'over represented', taxa with low loss rates (<30%) but with high representation rates (>70%) indicate 'highly represented', taxa with medium loss and representation rates (40-60%) indicate 'medium represented', taxa with very high loss rates (>70%) but with low representation rates (<40%) indicate 'low represented' and taxa which do not represent in the core sample but are recovered in the sediment trap indicate 'not represented'. Loss rates during taphonomic processes are presented in Figure 5.9 more clearly. The definitions of loss and representation rates and other details are presented in the text.

Species	Sediment flux in the trap number ($cm^{-2}yr^{-1}$)	Sediment flux in the core sample number ($cm^{-2}yr^{-1}$)	Loss rates (%)	Repres-entation rates (%)	Representation
Daphnia spp.	5.58	0.76	86.45	13.55	Low represented
Ceriodaphnia sp.	0.22	0.00	100.00	0.00	Not represented
Bosmina longispina	61.55	101.27	-64.53	164.53	Over represented
Bosmina coregoni	74.04	169.29	-128.63	228.63	Over represented
Graptoleberis testudinaria	1.61	3.78	-134.63	234.63	Over represented
Eurycercus lamellatus	1.47	4.53	-207.47	307.47	Over represented
Camptocercus rectirostris	1.00	0.00	100.00	0.00	Not represented
Acroperus harpae	11.67	6.80	41.74	58.26	Medium represented
Acroperus elongatus	6.09	5.29	13.10	86.90	Highly represented
Alona rectangula	4.04	2.27	43.85	56.15	Medium represented
Alona guttata	6.61	2.27	65.71	34.29	Low represented
Alona gutta tuberculata	0.47	0.00	100.00	0.00	Not represented
Alona rustica	14.15	10.58	25.25	74.75	Highly represented
Alona intermedia	10.43	5.29	49.26	50.74	Medium represented
Alona affinis	1.02	2.27	-122.95	222.95	Over represented
Alona quadrangularis	0.47	1.51	-218.89	318.89	Over represented
Alonella nana	9.83	10.58	-7.62	107.62	Over represented
Alonella exigua	0.24	0.00	100.00	0.00	Not represented
Alonella excisa	9.83	3.02	69.26	30.74	Low represented
Monospilus dispar	8.60	11.34	-31.85	131.85	Over represented
Rhynchotalona falcata	0.47	1.51	-218.90	318.90	Over represented
Chydorus sphaericus	3.51	3.78	-7.70	107.70	Over represented
Chydorus piger	6.14	6.80	-10.85	110.85	Over represented
Pleuroxus aduncus	1.56	0.00	100.00	0.00	Not represented
Sida crystallina	1.24	1.51	-22.11	122.11	Over represented
Total	**241.82**	**354.44**	-	-	-

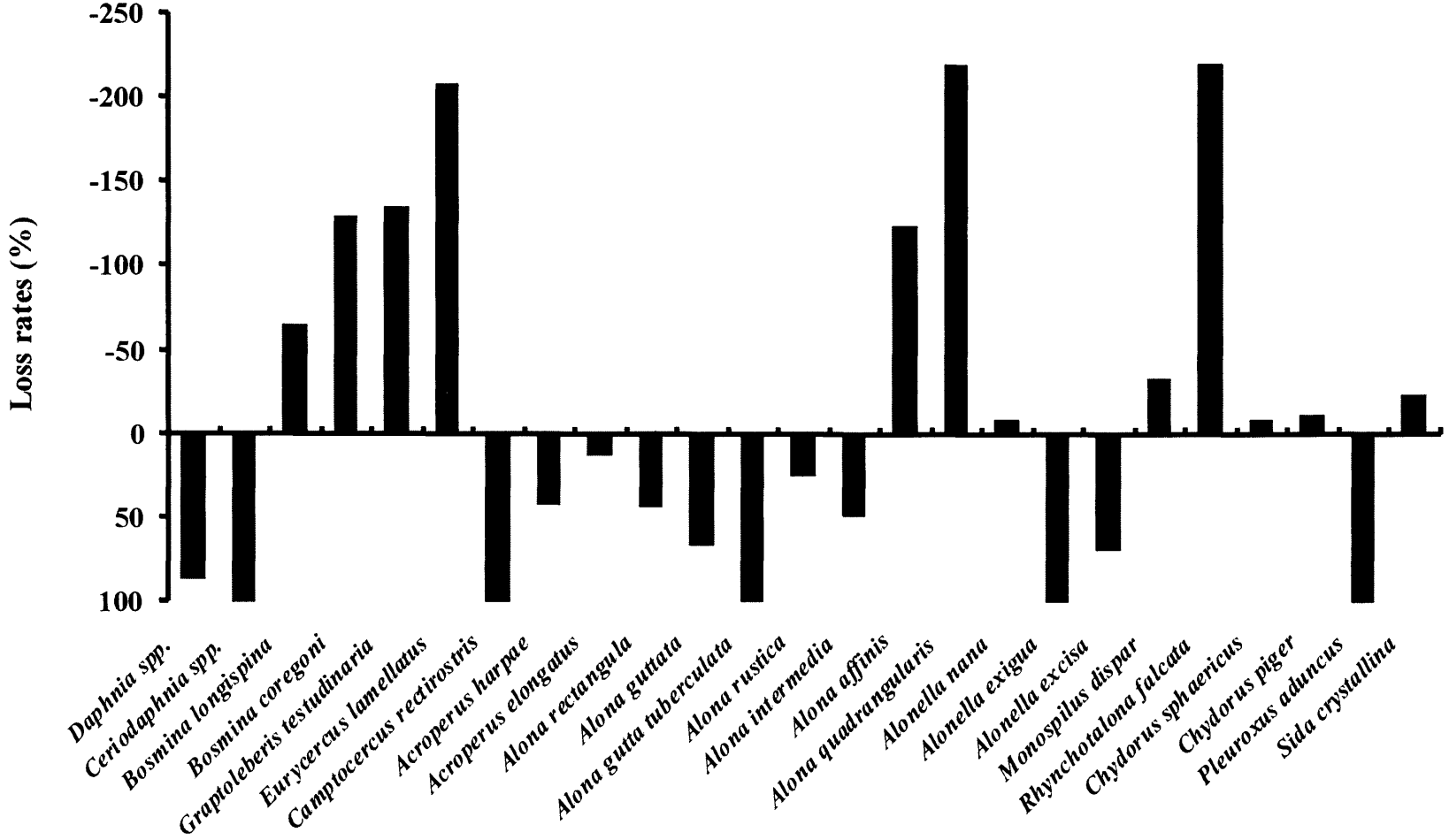


Figure 5.17: Total loss rates of fossil Cladocera during taponomic processes in Loch Coire Fionnaraich. Taxa with negative (-) loss rates are over-represented in the sediment. Taxa with positive (+) loss rates are under-represented (see table 5.9 for details).

rectangula and *Alona intermedia* were only moderately represented (40-60% representation rates) in the loch (Table 5.9, Figure 5.17). Two littoral taxa, *Alona guttata* and *Alonella excisa,* were found to be poorly represented showing only a small proportion (<40%) of their remains was preserved in the core sample (Table 5.9, Figure 5.17).

5.3.6 Source sample vs core sample assemblages

In the previous section the relationship between remains arriving in the deep water of the lake, represented by the sediment trap, and those preserved in the sediments were compared as an indicator of representation. However, the differences in the abundance of a cladoceran species in the source sample (original habitat) and their assemblages in the core sample are also an important indicator of the representativity since seasonal variations in ecological conditions and growing habits of Cladocera (e.g. littoral vs planktonic) are important factors affecting the representation of fossil Cladocera in lake sediments (Frey, 1988). In addition, the growth and development of Cladocera in relation to seasons also appear to be significant factors to contribute their fossil assemblages in the sedimentary assemblages (Frey, 1986). At the time when the Cladocera production is high, shedding of the exoskeleton in lake sediments is also assumed to be high. Moulting, in particular, contributes the significant number of remains to the sedimentary assemblages. However, moulting in Cladocera varies between species, as well as with seasonal temperature. The number of moulting in an individual animal is not known fully, though most *Daphnia,* for instance, moult 3-5 times during nauplier stages and have many moults during adult stage depending upon the temperature. Usually Cladocera lay eggs in the brood chamber just after moulting and those eggs hatch before the next moult. Depending upon species, one brood contains about 1-300 eggs and these eggs hatch in 2-5 days at 25 ^{0}C and in about 11 days at 10 ^{0}C. In a lifetime (2-4 months) there are roughly 20-25 broods resulting in hundreds of thousands of exoskeletons deposited in the sediments. What percentage of these exoskeletons during each moult is preserved, will vary strongly between sites.

One way of estimating the fossil representation in the lake sediments is by comparing species diversity and mean percentage composition (taxon rate) of live Cladocera in each habitat type with the percentage composition of remains deposited in the core sample. DeNicola (1986) proposed a 'community weighting approach' in order to

compare diatom communities with deep-water sedimentary assemblages. In the community weighting approach, the taxon rates in each community set are multiplied by an arbitrary numeric weight. For diatoms, De Nicola (1986) first measured the relative valve production rates of each taxon from three different communities of a lake followed by adding the three rates to make a single rate of production for all the taxa in the same lake. In Cladocera, the taxon rate (%) for the entire lake was produced after summing up the number of Cladocera filtered per litre of water in six seasonal visits (May'01, August'01, September'01, January'02, May'02 and August'02) from each micro-habitat, macrophyte, sand, boulder and planktonic and converted into a percentage count (Equation 5.3, Table 5.10). Methods for collecting and estimating the contemporary cladoceran zooplankton along micro-habitat types on a seasonal basis are described in detail in Chapters 3 and 5 respectively.

$$\% \text{ Mean/taxon rate of Cladocera} = \left\{ \sum_{i=1}^{n} Ai + \sum_{i=1}^{n} Bi + \sum_{i=1}^{n} Ci + \sum_{i=1}^{n} Di \right\} \Big/ 4 \qquad \textit{Equation 5.3}$$

Where, A, B, C and D are the percentage composition of a Cladocera in Macrophyte, Sand, Boulder and Planktonic habitats respectively; i is the season and n is the number of seasonal visits (i.e. 6).

In order to compare the taxon rates between the source and the core samples, the taxon rates of various species of *Daphnia* in the source sample presented in Table 5.10 was given as a single taxon rate value in Table 5.11. Similarly, the taxon rates of *Bosmina coregoni* and *Bosmina longispina* in the source sample presented in Table 5.10 were also given as a single taxon rate value for *Eubosmina* in Table 5.11. A total of 30 species of Cladocera were recorded in the source sample while only 19 species found in source sample were recovered from the core sample (Table 5.11). Two species of Chydorid Cladocera, *Alona rectangula* and *Alona quadrangularis* were not recorded in the source sample but recovered in the core sample (Table 5.11).

Of the five species of planktonic taxa, three, *Ceriodaphnia*, *B. longirostris* and *Diaphanosoma brachyurum* were recorded only in the source sample. Of the 27 littoral taxa, ten taxa, *Polyphemus pediculus*, *Alonella exigua*, *Camptocercus rectirostris*, *Oxyrella tenuicaudis*, *Pleuroxus truncatus*, *Lathonura rectirostris*, *Macrothrix* sp., *Leptodora kindtii*, *Bythotrephes longimanus* and *Streblocerus serricaudatus*, were

Table 5.10: Species richness and taxon rates (% mean) of living Cladocera in the source sample of Loch Coire Fionnaraich, Scotland.

Species	Macrophyte	Sand	Boulder	Planktonic	% Mean/Taxon rate
Daphnia galeata	0.00	0.00	0.05	3.12	0.79
Daphnia hyalina	0.00	0.00	0.00	3.47	0.87
Daphnia longispina	0.04	0.40	0.29	9.18	2.48
Daphnia magna	0.00	0.00	0.00	0.06	0.02
Daphnia culculata	0.00	0.00	0.00	0.13	0.03
Daphnia ambigua	0.00	0.00	0.00	0.10	0.03
Bosmina coregoni	2.57	1.92	1.19	47.77	13.36
Bosmina longispina	6.66	6.86	1.00	33.77	12.07
Alona rectangula	0.00	0.00	0.00	0.00	0.00
Acroperus elongatus	54.82	40.90	72.11	0.00	41.96
Monospilus dispar	0.16	0.24	0.05	0.19	0.16
Chydorus piger	0.33	0.41	0.10	0.05	0.22
Chydorus sphaericus	0.06	0.30	0.15	0.00	0.13
Alonella excisa	0.00	0.32	1.91	0.00	0.56
Alonella nana	1.32	0.42	0.67	0.15	0.64
Acroperus harpae	4.97	4.41	12.32	0.00	5.43
Alona guttata	0.94	0.51	0.64	0.00	0.53
Alona intermedia	0.00	0.00	0.46	0.00	0.11
Alona rustica	0.99	0.88	1.52	0.05	0.86
Eurycercus lamellatus	0.33	0.04	0.00	0.20	0.14
Alona affinis	0.03	0.00	0.00	0.00	0.01
Alona quadrangularis	0.00	0.00	0.00	0.00	0.00
Rhynchotalona falcata	0.11	8.54	0.15	0.00	2.20
Sida crystallina	1.90	0.00	0.00	0.00	0.47
Graptoleberis testudinaria	0.72	0.26	0.00	0.00	0.24
Ceriodaphnia dubia	0.01	0.00	0.00	0.86	0.22
Bosmina longirostris	0.39	0.00	0.00	0.48	0.22
Diaphanosoma brachyurum	0.00	0.07	0.00	0.05	0.03
Polyphemus pediculus	23.37	33.52	6.38	0.05	15.83
Alonella exigua	0.00	0.00	0.15	0.03	0.04
Oxyurella tenuicaudis	0.00	0.00	0.05	0.00	0.01
Camptocercus rectirostris	0.00	0.00	0.10	0.00	0.02
Pleuroxus truncatus	0.00	0.00	0.47	0.00	0.12
Lathonura rectirostris	0.00	0.00	0.05	0.00	0.01
Macrothrix sp.	0.12	0.00	0.05	0.15	0.08
Leptodora kindtii	0.12	0.00	0.00	0.00	0.03
Bythotrephes longimanus	0.00	0.00	0.00	0.12	0.03
Streblocerus serricaudatus	0.03	0.00	0.15	0.00	0.05
Species richness	**19**	**17**	**23**	**20**	**36**

Table 5.11: Taxon rates and differences in taxon rates (%) of Cladocera between source sample and the core sample in Loch Coire Fionnaraich, Scotland. Representation of Cladocera with respect to differences in taxon rates are calculated here and demonstrated in Figure 5.10. Taxa with zero taxon rates in the core sample (i.e. b) do not show a meaningful analysis to calculate the differences in taxon rates (i.e. b-a), thus these taxa are given as 'n/a or not applicable' for taphonomy of Cladocera through this approach. The taxon rates for *Daphnia* and *Eubosmina* were the average from the species of these taxa in the source sample (also see Table 5.10).

Species	Taxon rate or % Cladocera recovered in the source sample (a)	Taxon rate or % remains recovered in the core sample (b)	Differences in taxon rates (b-a)
Daphnia	4.22	0.21	-4.01
Eubosmina (coregoni+longispina)	25.46	76.33	+50.87
Alona rectangula	0.00	0.64	+0.64
Acroperus elongatus	41.96	1.49	-40.47
Monospilus dispar	0.16	3.20	+3.04
Chydorus piger	0.22	1.92	+1.70
Chydorus sphaericus	0.13	1.07	+0.94
Alonella excisa	0.56	0.85	+0.29
Alonella nana	0.64	2.99	+2.35
Acroperus harpae	5.43	1.92	-3.51
Alona guttata	0.53	0.64	+0.11
Alona intermedia	0.11	1.49	+1.38
Alona rustica	0.86	2.99	+2.13
Eurycercus lamellatus	0.14	1.28	+1.14
Alona affinis	0.01	0.64	+0.63
Alona quadrangularis	0.00	0.43	+0.43
Rhynchotalona falcata	2.20	0.43	-1.77
Sida crystallina	0.47	0.43	-0.04
Graptoleberis testudinaria	0.24	1.07	+0.83
Ceriodaphnia (n/a)	0.22	0.00	-0.22
Bosmina longirostris (n/a)	0.22	0.00	-0.22
Diaphanosoma brachyurum (n/a)	0.03	0.00	-0.03
Polyphemus pediculus (n/a)	15.83	0.00	-15.83
Alonella exigua (n/a)	0.04	0.00	-0.04
Oxyrella tenuicaudis (n/a)	0.01	0.00	-0.01
Camptocercus rectirostris (n/a)	0.02	0.00	-0.02
Pleuroxus truncatus (n/a)	0.12	0.00	-0.12
Lathonura rectirostris (n/a)	0.01	0.00	-0.01
Macrothrix (n/a)	0.08	0.00	-0.08
Leptodora kindtii (n/a)	0.03	0.00	-0.03
Bythotrephes longimanus (n/a)	0.03	0.00	-0.03
Streblocerus serricaudatus (n/a)	0.05	0.00	-0.05
Species richness	**30**	**19**	**-**

recorded only in the source sample (Table 5.11). The taxon rate of *Daphnia* in the core sample was found to be significantly lower than its taxon rate in the source sample. However, the taxon rate of *Bosmina coregoni* and *Bosmina longispina* together (*Eubosmina* sp.) were three times higher in the core sample than in the source sample (Table 5.11). Exceptionally, a high taxon rate (42%) was found for *Acroperus elongatus* in the source sample compared to the core sample (1.49%). The second highest taxon rate (16%) was found in *Polyphemus pediculus* in the source sample (Table 5.11). Except for three Chydorid taxa, *Acroperus elongatus*, *Acroperus harpae* and *Rhynchotalona falcata*, all other Chydorid taxa had higher taxon rates in the core sample than in the source sample (Table 5.11).

Representation of Cladocera in the core sample with respect to the differences in taxon rates between source and core samples suggests that *Eubosmina* is the only taxon that has exceptionally large positive values (Figure 5.18). Other taxa such as *Monospilus dispar*, *Alonella nana* and *Eurycerus lamellatus* also have low but positive taxon rates indicating their representation in the core sample (Figure 5.18). However, negative taxon rates in *Daphnia* as well as other littoral species such as *A. elongatus*, *P. pediculus* and *A. harpae* show that they were poorly represented in the sedimentary assemblages (Figure 5.18).

5.3.7 Integration of the surface sediment samples, the trap sample, the source sample and the core sample

Differences of Cladoceran remains may be expected due to non-uniform mixing, differential transport efficiency from littoral to deep water and decomposition of remains close to the source community. Thus the representation of Cladocera in lake sediments can also be examined by comparing percentage composition of contemporary Cladocera with the composition of remains in surface sediment samples along transects, core sample and trap assemblages using two approaches such as ordination (e.g. DCA and PCA) and a simple 'integration by the percentage composition' approaches.

5.3.7.1 Ordination

A total of 35 samples was used for an indirect gradient analysis in which 32 spatial surface sediment samples, one core sample, assumed to be a representative sample for palaeolimnological purposes, one sediment trap sample, and one contemporary sample

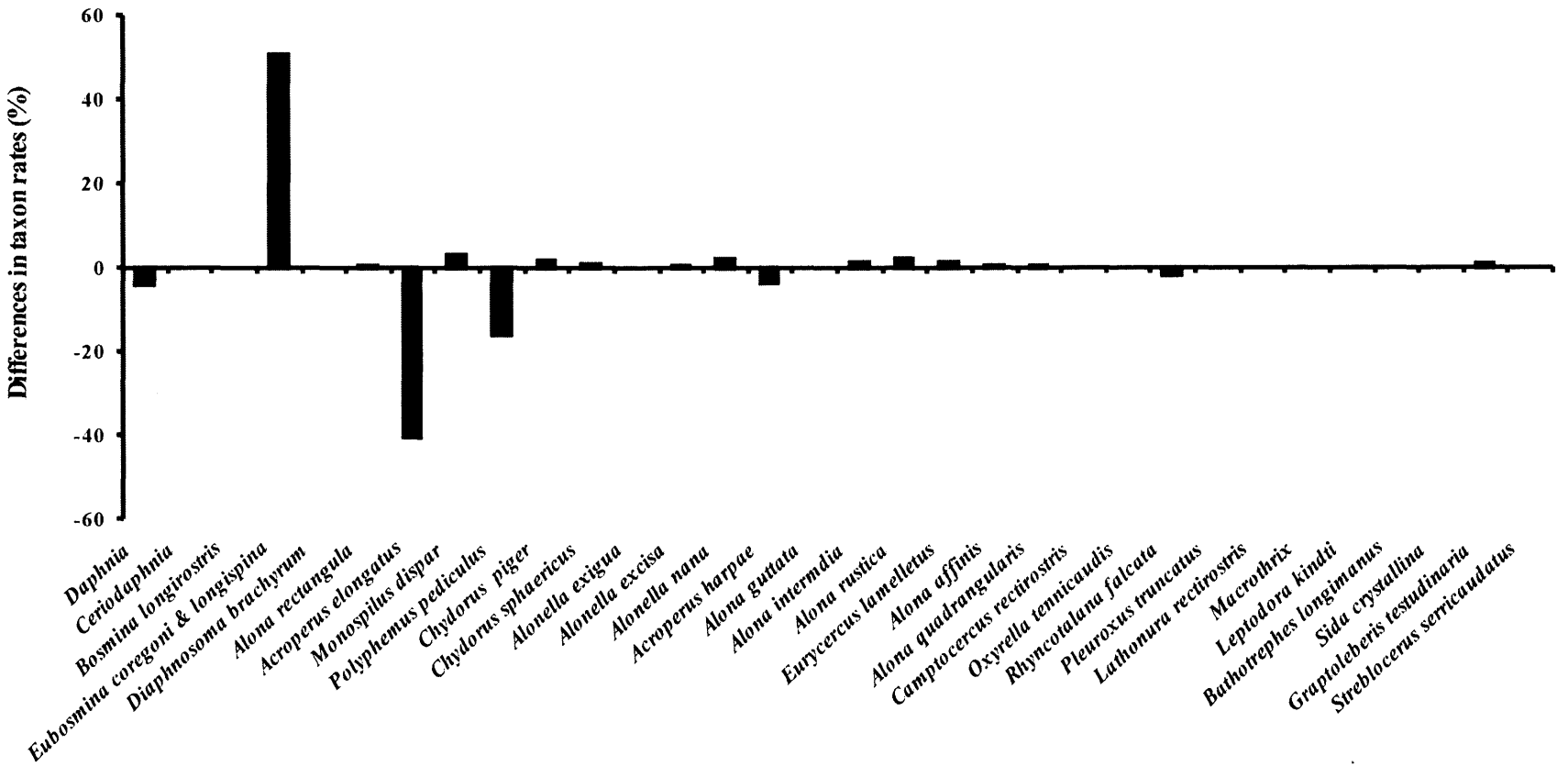


Figure 5.18: Representation of Cladocera in Loch Coire Fionnaraich with respect to differences in taxon rates (%). Differences in taxon rates are calculated on the basis of percentage abundance of Cladocera in the source sample and in the core sample. Negative taxon rates indicate that taxa recovered in the source sample were higher than the taxa recovered in the core sample. Positive taxon rates indicate that taxa recovered in the core sample were higher than the taxa recovered in the source sample. Numerical calculation of taxon rates is presented in Table 5.11.

derived from Chapter 4 were included for the analysis. Cladocera present in at least two of the total samples with a relative proportion of more than 1% in at least one of these samples were included for the ordination. A total of 22 species met the criteria. DCA with detrending by segments, down-weighting of the rare taxa and non-linear rescaling of axes of 22 cladoceran species present in 35 samples showed a linear distribution of species data with 1.12 SD gradient length of DCA axis 1. Since the gradient length of species data was less than 2, therefore PCA was chosen for the patterns of variations in species data among samples. Summary of PCA ordination and the sample scores are presented in Table 5.12a & b. The PCA axes show that the maximum amount of variation in the species data is about 58% (Table 5.12a).

The variations explained by samples, has been expressed by PCA sample scores. Sample T3B2m had the highest sample score in axis 1 followed by T5M2m (Table 5.12b). The sample score for the core sample was as high as the other highest sample scores along axis 1 (Table 5.12b). The PCA sample score along axis 2 was, however, significantly higher in the contemporary sample compared to the other samples (Table 5.12b).

A graphical representation of the relationship between samples and species in PCA ordination is summarised in Figure 5.19. The contemporary sample appeared to be an 'outlier' in the ordination diagram in which the littoral Chydorid, *Acroperus elongatus* had an exceptionally high representation. Most other Chydorids such as *Acroperus harpae*, *Alonella excisa*, *Graptoleberis testudinaria*, *Alonella nana*, *Alona guttata*, *Chydorus piger* and *Monospilus dispar* were however, associated with the spatial surface sediment samples recovered at 2m depth (Figure 5.19). The planktonic *Eubosmina* was dominant in the core sample as well as in the spatial surface sediment samples recovered from 8m and 11m depths. *Daphnia* had a higher representation in the sediment trap and the contemporary sample compared to spatial sediment samples (Figure 5.19).

Table 5.12: (a) Summary of PCA and (b) PCA sample scores of core sample, spatial surface sediments, sediment trap and contemporary samples of Cladocera in Loch Coire Fionnaraich.

PCA Axes	1	2	3	4
Eigenvalues (λ)	0.547	0.133	0.094	0.045
Cumulative % variance of species data	54.7	68.0	77.4	81.9

Figure 5.12: (b)

SAMPLES	Axis 1	Axis 2	Axis 3	Axis 4
CORE-TOP (CORE SAMPLE)	-1.32	-0.27	-0.76	-1.00
T1M2m	1.40	0.20	-1.20	-0.99
T1M5m	-0.22	-0.11	-0.43	2.26
T1M8m	-0.71	-0.60	-0.06	-0.74
T1M11m	-0.48	-0.53	0.01	0.54
T2S2m	1.03	0.30	3.45	2.04
T2S5m	-0.59	-0.26	0.25	0.44
T2S8m	-0.90	-0.07	-1.03	-0.18
T2S11m	-0.73	0.00	0.50	-0.42
T3B2m	**2.21**	0.90	-0.26	-1.32
T3B5m	0.23	-1.05	1.20	-0.32
T3B8m	-0.41	-0.14	0.24	0.14
T3B11m	-1.02	0.89	-0.31	0.85
T4M2m	1.53	0.49	-1.06	0.55
T4M5m	0.73	-1.03	2.02	-1.91
T4M8m	-0.17	-0.60	1.21	-0.15
T4M11m	-1.07	-0.11	-0.35	0.09
T5M2m	1.85	-0.79	-0.06	0.43
T5M5m	-0.12	-0.33	-0.32	1.97
T5M8m	-0.80	-0.40	0.03	-0.68
T5M11m	-1.04	-0.29	-0.07	-0.54
T6B2m	1.62	0.64	-0.84	0.33
T6B5m	-0.22	-0.14	-0.23	1.95
T6B8m	-0.26	0.06	-0.34	-0.70
T6B11m	-0.98	-0.19	-0.39	-1.27
T7B2m	1.75	0.08	-1.23	-0.44
T7B5m	0.12	-0.63	1.42	-1.76
T7B8m	-0.30	-0.17	-0.63	0.57
T7B11m	-0.92	-0.30	-1.28	-0.52
T8S2m	1.78	0.35	-0.98	-0.03
T8S5m	0.12	-0.63	1.05	-0.03
T8S8m	-0.05	-0.47	0.21	0.80
T8S11m	-0.46	-0.24	0.04	0.22
TRAP	-0.76	0.25	-0.96	0.43
CONTEMPORARY	-0.83	**5.18**	1.18	-0.60

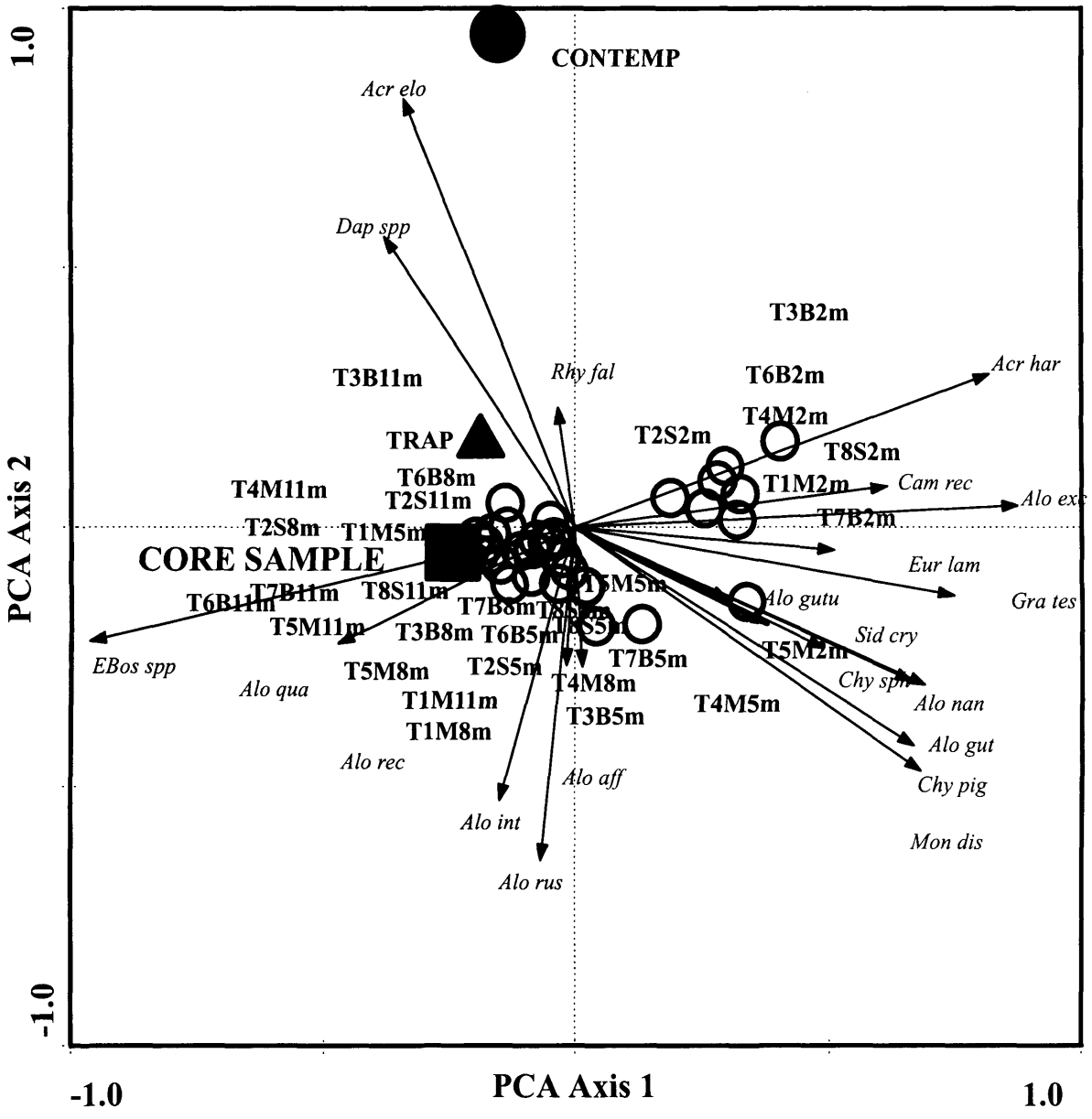


Figure 5.19: PCA biplot ordination of 35 samples comprising from four different types of samples, spatial surface sediment samples (n=32), core sample (n=1), sediment trap sample (n=1) and contemporary sample (n=1) in Loch Coire Fionnaraich, Scotland. The symbols for the core sample, trap and contemporary samples are given as (■), (▲), (●) respectively. Abbreviation for samples and taxa is given in Appendices 5.1 and 5.2.

5.3.7.2 Integration by the percentage compositions of Cladocera in the surface sediment samples, the core sample, the source sample and the trap sample

An integration of the percentage compositions of the remains of Cladocera in the spatial surface sediment samples, the core sample, the trap sample and the source sample shows that *Eubosmina* sp. (*B. coregoni* plus *B. longispina*) and *M. dispar* are the two most represented taxa in the core sample (Figure 5.20). However, *Eubosmina* sp. is the only taxon, which has a very high representation (>50%) when comparisons were made between the source sample and the core sample, and the trap sample and the core sample separately (Figure 5.20). When the source sample was compared with the core sample, a very small number (n=5) of littoral taxa with a low representation (1-5%), represent the core sample (Figure 5.20). When the trap sample was compared with the core sample, however, large number (n=10) of littoral taxa were found to be over-represented (>100%) in the core sample, but among them the remains of *R. falcata*, *A. qudrangualris*, *E. lamellatus* and *G. testudinaria* had a very low abundance (<4%) in the core sample and in the trap sample, as shown by the contemporary study in Chapter 4 (Table 4.2) and the spatial surface sediments and the sediment trap studies in this chapter (see Table 5.2 and Table 5.9). At least 5 taxa, which have zero representation (Figure 5.20) in the core sample, are the rare taxa for this loch. Except *Eubosmina* sp., none of the dominant taxa in the source sample were found to represent the trap assemblages. More interestingly, the most dominant taxon in the source sample, *A. elongatus*, was not represented as highly (>100%) as the other littoral taxa in the core sample (Figure 5.20).

5.4 Discussion

Cladocera fossil assemblages in lacustrine sediments are increasingly important for reconstructing past climate change (Lotter et al., 2000a; Ammann et al., 2000). However, understanding the representation of such microfossils is essential since the reliable reconstructions depend largely on understanding the relationship between living and fossil assemblages (Frey, 1986; Korhola, 1990; Korhola and Rautio, 2001). Palaeolimnologists often make an assumption that the remains of both littoral and planktonic groups of Cladocera are homogenised in the lake centre before being deposited in sediments (Frey, 1986) and they use these remains as a representative sample for palaeoenvironmental reconstructions (Mueller, 1964; Frey, 1988; Korhola

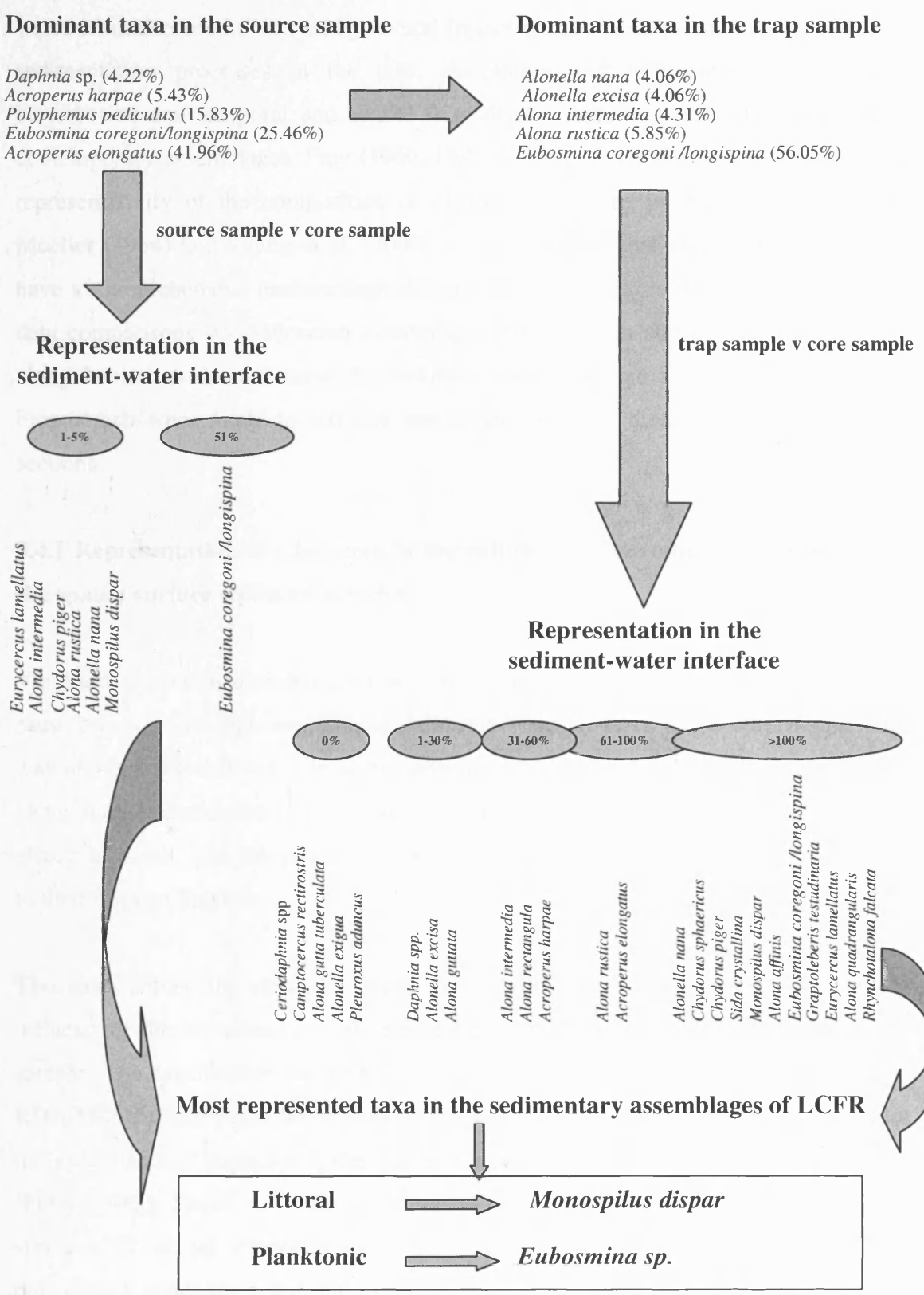


Figure 5.20: Schematic diagram for the representation of Cladocera in the sedimentary assemblages in LCFR using the integration percentage composition approach of the spatial surface sediment samples, source sample, the trap sample and the core sample. Taxa are arranged in order from the lowest (left) to the highest representation (right). Representation in the sediment-water interface is based on Table 5.9, Table 5.10 and Table 5.11.

and Rautio, 2001). However, the composition of fossil Cladocera assemblages in deep-water sediments are influenced by several factors such as basin morphometry; transport-sedimentation processes in the lake, dissolution and fragmentation of remains, bioturbation and temporal and spatial (e.g. depth, micro-habitat types) variations in contemporary assemblages. Frey (1960, 1986, 1988) highlighted the assumption of the representativity of the composition of cladoceran remains in deep-water sediments. Mueller (1964) and Rautio et al. (2000) attempted to test this assumption, but did not have a comprehensive methodological approach. Therefore, in this study a variety of data comparisons on cladoceran assemblages derived from surface sediment samples along habitat associated transects, sediment traps and core samples of Loch Coire Fionnaraich were made to test this assumption, and are discussed in the following sections.

5.4.1 Representation of Cladocera in the sedimentary assemblages compared with the spatial surface sediment samples

Variations in the spatial distribution of remains of Cladocera in lake sediments can cause biases in the representation of sedimentary assemblages in the core sample. One way of assessing such bias can be by comparing the surface sediment samples collected along habitat-associated transects with the core surface sample taking account the effects of depth, lake morphometry, sediment type, and the proximity of samples taken to their original habitats.

This study shows that increasing depth appears to be one of the most important factors influencing the representation of sedimentary assemblages of Cladocera in the core sample. The quantitative analyses of the assemblages using ordination techniques in RDA Monte Carlo permutation tests suggests that depth was the most important factor in explaining the variation in the spatial assemblages of fossil Cladocera in the loch (Figure 5.13). Depth is important in many ways, either by influencing the habitat structure of living Cladocera, as described in Chapter 4, or by structuring the taphonomic zones for fossil deposition. Taphonomic zones (where remains are in the process of deposition and preservation) vary from shallow shoreline areas to deep offshore regions (e.g. Alhonen, 1970).

However, the concentration of remains in the habitat-associated transects towards the lake centre, shows that after death or exoskeleton discard, the highest number of littoral taxa, particularly the Chydorid remains, are deposited close to their original habitat, while the highest number of planktonic remains is deposited in the deepest water and decline gradually towards the lakeshore (Table 5.2). This indicates that the source habitat where the Cladocera first die appears to be the most important factor to begin the taphonomic processes and fossil representations. Efremov (1940) presented this hypothesis long ago, while describing the taphonomy of vertebrate animals. Mueller (1964) carried out a study of Cladocera deposition along various transects in a North American lake, and reported that most littoral taxa, mainly Chydorids, discard their exoskeletons in the source habitat and are then transported towards the lake centre most probably by wind-induced water currents. He argued that during transportation, their abundances should decline with increasing depth and distance. Whiteside and Harmsworth (1967) also argued that the remains of littoral Cladocera are assumed to be deposited in higher numbers in lake basins nearest to their original habitat than in the offshore locations. A similar result for variations in the diatom composition of the surface sediment along transects in Lake Sallie, Minnesota was described by Bradbury and Winter (1976). The diatom valves in this lake were preferentially deposited close to their living habitats (Bradbury and Winter, 1976).

As for diatoms, the Cladocera, particularly Chydorids, have diverse preferences for micro-habitat types such as macrophytes, sandy and stony shoreline habitats (Whiteside and Harmsworth, 1967; Whiteside, 1974; Whiteside et al., 1978), and this should be reflected by the composition of the surface sediment assemblages (e.g. Whiteside and Harmsworth, 1967; Frey, 1988). Variations in shoreline micro-habitat types play a significant role in fossil deposition (e.g. Whiteside and Swindoll, 1988). In Loch Coire Fionnaraich, the highest and lowest concentration of littoral Chydorid remains in the 2m-depth of T1 (Macrophyte) and T2 (Sand) respectively were possibly because they are the most and least preferred habitat types for different species of Chydorid Cladocera (e.g. Whiteside and Harmsworth, 1967; Whiteside, 1970; 1974). Particularly, the result in the PCA (Figure 5.12) shows that the remains of two species of Cladocera, *Rhynchotalona falcata* and *Monospilus dispar* have a clear association with their source habitats mainly sand and boulders (e.g. Frey, 1988, 1986; Korhola, 1999. The TWINSPAN classification in Figure 4.4 in Chapter 4 also shows the association between *M. dispar* and the sandy habitat.

The influence of micro-habitat sources and lake morphometry on the deposition of the remains of Cladocera, as well as an insight into their pathways of transportation in the lake basin, can be best illustrated by bar diagrams in Arc-GIS (Figures 5.4-Figure 5.10). Planktonic taxa such as *Bosmina coregoni* and *Bosmina longispina* are predominantly pelagic in habitat. They occurred in greatest abundances in the core sample (Figure 5.4, Figure 5.5) while the most littoral taxa (e.g. *A. harpae, A. nana, M. dispar, C. piger*) were mostly deposited in greatest quantity close to their original habitat (Figure 5.6, Figure 5.7, Figure 5.9, Figure 5.10). However, spatial variations in the concentration of littoral taxa such as *A. excisa* (Figure 5.8) suggest there are species-specific variations in transportation, deposition and representation of sedimentary assemblages in the loch. Alhonen (1970) highlighted the significance of basin morphometry on the deposition of cladoceran remains and proposed that the effects of basin morphometry and the shoreline habitat types on spatial distribution of fossil assemblages in the loch are quantified effectively by the ratio between littoral and planktonic Cladocera. Mueller (1964) argued that the littoral:planktonic ratio of fossil Cladocera has a direct relationship with the relative area and volume of the littoral and planktonic zones, and could be a useful indicator of changing basin morphometry. Variations in the L:P ratio of samples along the transects in Loch Coire Fionnaraich demonstrate clear patterns of assemblage composition related to lake morphometry and increasing depth as expected. In most transects, the L:P ratios decrease with increasing depth (Table 5.2). However, variations in L:P ratios of Cladocera at the similar depths of the different transects indicates the influence of differences in bathymetry (Figure 5.3) as well as transect-associated shoreline habitat types (Figure 5.1). For example, the L:P ratios in 2m depth of T1, associated with macrophytes, are significantly lower than the other transects of the same depth suggesting that unlike other transects, the 2m depth of T1 coincides with the habitat for both littoral and planktonic Cladocera and the deposition of their exoskeletons (Table 5.2). However, the 2m depths of most transects have high L:P ratios indicating that shallow marginal habitats are ideal sites for littoral Cladocera (e.g. Whiteside and Swindoll, 1988) and the taphonomic processes of most littoral remains begin from here.

In general, the remains at the 5m-depth of most transects are relatively low for both planktonic and littoral taxa suggesting that, probably due to the bathymetric effects, this location is neither a preferred habitat for either group of Cladocera nor the best point for

fossil accumulation and representation. The remains of Cladocera are likely to be loosely and temporarily settled on the basin-slope. For example, while sampling at the 5m depth of T4, the macrophyte associated transect, a narrow and steep slope was found (Figure 5.3). De Nicola (1986) also described differences in sedimentary assemblages of diatoms in the North American lakes due to variations in their basin slopes. The variations in L:P ratios of remains in 8m and 11m depths of most transects are not so large indicating that most planktonic remains are deposited in offshore zones and their sedimentary assemblages are likely to be representing the core sample derived from near the lake centre.

The remains of planktonic taxa *Bosmina* and *Daphnia* in this study were also deposited in highest abundance in the lake centre though they were often also found in the marginal areas (Figure 5.4, Figure 5.5, Appendix 5.5). Even though the abundance of littoral taxa declined towards the lake centre, the number of littoral species present in the offshore samples (Table 5.2) did not vary significantly with samples retrieved from nearer to the shoreline zones indicating that the core sample represents the Cladocera with respect to species diversity in the loch. Absence of two species of Chydorids such as *Camptocercus rectirostris* and *Alona guttata tuberculata* in the core sample reflects their low abundance in the contemporary samples (Chapter 4, also see section 5.4.3).

The correlation between the concentrations of remains in two subsequent depth points in Loch Coire Fionnaraich an insight into the deposition pattern of the remains of individual Cladocera in lake sediments. Taxa such as *Chydorus piger*, *Sida crystallina* and *Alonella nana* are truly phytophylus species (Whiteside et al., 1978). The positively high correlation between the concentration of the remains of these taxa deposited in 2m and 5m depths of LCFR suggests that the deposition of the remains of these taxa is concentrated close to their source habitats. However, the remains of the littoral taxa found in different shoreline habitats (e.g. rock, sand) suggest these taxa are transported further offshore more easily. This is revealed by the high positive correlation between the remains of the Cladocera deposited in 8m and 11m depths. The remains of the littoral taxon, *Rhynchotalona falcata* shows a negative correlation between 2m and 5m depths indicating that the remains of this taxon appear to be deposited exclusively in sandy substrata (e.g. Frey, 1986). The depositional environments of the loch could also influence the taphonomy of Cladocera as shown by the negative correlation between the concentrations of remains deposited in 8m and 11m depths for *Alona intermedia* and

Sida crystallina. For example, remains are lower where the rock beds are predominant. Remains associated with rocks and boulders are loosely attached and scoured off more easily than remains attached to organic materials.

LOI was the second most important explanatory variable in the RDA suggesting that the organic content of sediment also affect the composition of fossil Cladocera. This is probably an effect of organic rich sediments being associated with plankton, and the focusing of organic rich sediments in deeper water. Remains of species with a larger body size such as *Eurycercus lamellatus*, *Alona affinis*, *Alona quadrangularis* are well represented in the core sample (Table 5.2) suggesting that the size and shape of remains may also play a role in fossil representation (Frey, 1988; Korhola and Rautio, 2001). However, the relatively high number of remains of most of the smaller Chydorids, *Acroperus harpae, Acroperus elongatus, Alona rustica, Alona intermedia* and *Chydorus sphaericus* in the core sample suggest that all littoral taxa are effectively transported to the lake centre by mechanisms such as sediment focusing (Blais and Kalff, 1995). These effects are further explored in the sediment trap approach in sections 5.4.2 and 5.4.3.

5.4.2 Representation of Cladocera in the trap sample

Sediment traps have become increasingly important in environmental reconstruction research in recent years (e.g. Takahashi et al., 1990). This approach enables the flux of microfossils to the sediment, as well as temporal changes in species diversity and composition of biota in the lake to be assessed. Traps also integrate the remains of littoral and contemporary cladoceran communities before being deposited in lake sediments (e.g. Kato et al., 2003). However, representation of fossils using trap assemblages can also be influenced by several factors such as the seasonality, time resolution, and resuspension of sediments.

In Loch Coire Fionnaraich, the relatively small variations in the species richness in the sediment traps recovered over three seasons suggest that the remains of planktonic and littoral Cladocera are well integrated before being incorporated into lake sediments. However, the large number of remains of *Bosmina coregoni* and *B. longispina* recovered between spring and summer 2002 reflect the dominant production of these taxa during the warmer seasons. There were relatively few Chydorid remains in the trap suggesting that only a small proportion of the littoral remains reach the centre.

Interestingly though, the remains of some species of Chydorids such as *Alona rustica, Alonella nana, Alonella excisa* and *Alona guttata* retrieved from the trap installed between winter and spring 2002 were similar in abundance to the remains of *Bosmina coregoni* retrieved in the same season. This suggests that the littoral Chydorids do not vary temporally as strongly as planktonic taxa, but may be related to other mechanisms such as time resolution and resuspension of sediments and are described in the next paragraphs. A very small proportion of the remains of other planktonic taxa such as *Daphnia* and *Ceriodaphnia* in the sediment traps in most seasons indicates that these animals are either less associated with seasonality or their remains are destroyed shortly after their death. Frey (1960) reported that the remains of *Daphnia* and *Ceriodaphnia* are less capable of being preserved in sediments compared to other planktonic taxa such as *Bosmina*. Krause (1959) hypothesised that the remains of *Daphnia* may be influenced markedly by chemical, bacterial and fungal processes. Compared to *B. coregoni* and *B. longispina* the abundances of *Daphnia* and *Ceriodaphnia* were also rather low in the planktonic community (see Table 4.1 in Chapter 4).

Using the traps to assess seasonal changes in littoral cladoceran remains is difficult as the trap contents also reflect the amount of time to reach the traps as well as seasonality. In the PCA time-track result, the Jan'02-May'02 is strongly associated with PCA axis 1 (Figure 5.15) indicating this is the time for most littoral taxa to reach the lake centre (see also Figure 5.14). This may include remains that were produced in previous seasons (e.g. Frey, 1988, Korhola and Rautio, 2001). Increased numbers of remains in Jan'02-May'02 sample also indicates the increased resuspension of sediments during winter.

The trap records show that most of the dead Cladocera are disarticulated before being accumulated in the trap probably due to movement and transportation of remains and the effects of the resuspension of sediments. Resuspension is controlled by the pattern of water circulation and probably it is also associated with seasonality when wind-induced wave action is most intense (e.g Cameron, 1995). The depth of water may also have played a role on resuspension since turbulence often increase in lakes with shallow water (De Nicola, 1986). Some fragmentation might also have occurred during KOH treatment and slide preparations in the laboratory (e.g. Flower, 1993; Charles et al., 1994). A direct examination of trap materials under a microscope before laboratory treatment would help to identify the true proportion of unfragmented remains in the

trap. The trap sample of Loch Coire Fionnaraich was, however, rather poor since it contained many spines and unwanted particles, which required a KOH treatment.

5.4.3 Representation of Cladocera in the sedimentary assemblages when compared with the composition in the sediment trap sample

In Loch Coire Fionnaraich, the composition of remains in the trap assemblages was compared with the composition of remains in the core sample to evaluate the representation of fossil sedimentary assemblages in the loch. However, a number of factors, such as shape and size of remains, sinking velocities, water-depth, resuspension and bioturbation are found to play significant roles in determining the composition of remains and on the loss and representation rates of Cladocera due to the taphonomic processes at the mud-water interface.

The composition of Cladocera in the sedimentary assemblages in Loch Coire Fionnaraich as shown by loss and representation rates in Table 5.9 and Figure 5.17 indicates that the core sample appears to contain a mixed assemblage of fossils representing the dominant taxa in the loch. However, the zero representation of the rare taxa in the core sample (Figure 5.17, Figure 5.20) indicates that there are biases in the representation and such biases may have an influence on reconstructions especially in cases concerning taxa that are highly sensitive to the environmental variable to be reconstructed.

In a total of 25 taxa recorded in the trap, 14 taxa had very good representation, and 3 had medium-representation rates. Some taxa are more abundant in the core than the trap, this is interesting as the annual flux of aquatic remains to the sediment traps should be higher than the flux in the core surface sample since most remains undergo subsequent taphonomic changes in the sediment-water interface (e.g. Kato et al., 2003). The reasons for this "over-representation" are not known and may simply be related to random factors associated with sampling either related to the trap or the sediment core.

For the remains of eight other cladoceran taxa, *Daphnia*, *Alona guttata*, *Alonella excisa*, *Ceriodaphnia*, *Camptocercus rectirostris*, *Alona guttata tuberculata*, *Alonella exigua* and *Pleuroxus aduncus* trap fluxes are higher than the sediment (Table 5.9, Figure 5.17). The annual flux of the remains of the first three of these taxa in the trap was

found to be significantly higher than in the core sample, and the annual flux of the remains of remaining five taxa was only recorded in the sediment trap (Table 5.9) suggesting that the remains of these taxa are destroyed at the sediment surface once they are deposited due to bioturbation and chemical and microbial decomposition (Frey, 1960, 1986,1988; Korhola and Rautio, 2001).

5.4.4 Representation of Cladocera in the sedimentary assemblages in comparison with the source sample

There are significant differences between the composition of the fossil assemblages in the core sample and the cladoceran communities in the lake. Firstly, not all Cladocera in the source community were recovered in the lake sediments (Table 5.11). Secondly, some Cladocera were recorded in the core sample but not recorded in the source samples. Thirdly the overall composition of the core sample does not match the composition of any source sample. Whilst these results are expected, accounting for these differences quantitatively is difficult, as the seasonal production rate of individual Cladocera is virtually unknown due to temperature specific variations in the moulting rates (e.g. Allan, 1976). The specific area of littoral and planktonic habitats available for Cladocera, needed to estimate the total production of the community, is also unknown. However, the estimated taxon rates for individual taxa appear to be a useful index for this comparison. For example, the high taxon rate of *Eubosmina* in the fossil assemblages indicates a high representation rate, while the low taxon rates for *Daphnia* indicates a low representation rate (Table 5.11, Figure 5. 20). A relatively high taxon rate for *Polyphemus pediculus* for the source community, but a zero rate for the fossils assemblages indicates that this taxon could not be taken into account in the comparison (Table 5.11). A high taxon rate for the Chydorid species, *Acroperus elongatus* in the source community but a significantly low rate in the fossil assemblages also indicates its poor representation in the fossil assemblages. The taxon rate described here is an assumption made to compare the mean percentage of live Cladocera in each micro-habitat type with the percentage composition of remains deposited in the core sample. However, this taxon rate is very limited because a true comparison needs the numbers to be weighted according to the size of the habitats being compared.

When using an integrated approach in PCA, the core sample, which is assumed to be the representative of the lake community, showed strong similarities with surface sediment

samples and the sediment trap sample but the contemporary sample in the ordination diagram was an 'outlier' (Figure 5.19). There are two main reasons for this: (a) the contemporary sample is less integrated than the sub-fossil samples being limited in time and space (b) the sub-fossil samples are biased by under-representation of some, mainly littoral taxa, and over-representation of others (especially well-preserved planktonic taxa) (Figure 5.17 and Figure 5.20). Separating these factors requires a more detailed and sustained study, especially of cladoceran production rates.

5.5 Conclusions

Taphonomy is an important component of palaeolimnological science. It provides insights into fossil transportation, deposition and preservation in sediments and into the processes of accumulation in the sediment record. In the absence of such understanding, environmental reconstruction using subfossil assemblages of aquatic organisms can be biased since not all material is transported to the coring site or is preserved there.

In LCFR, patterns of accumulation are influenced by the distribution of littoral and planktonic habitats. Most littoral Cladocera are deposited close to their original habitat while remains of planktonic Cladocera are deposited maximally in deepwater locations. However, the remains of littoral taxa in the offshore locations are not always associated with the nearest shoreline microhabitat type, but are influenced also by a variety of factors, especially spatial variations in basin depth and by wind-induced movement of the water currents as indicated by the LOI of the sediments and the correlation between the concentration of remains deposited in two subsequent depths of the loch. The Arc-GIS approach is also useful in providing the concentration of the remains of the individual Cladocera deposited at exact depth point of the loch, and this approach can be utilised for other aquatic organisms.

Finally, taphonomy is an important area of investigation for consideration in the future in order to improve the use of Cladocera and to avoid bias in environmental reconstruction. A more quantitative solution in taphonomy of Cladocera could be developed if methods of collecting samples in the source community, especially the littoral zone, and the trap samples in the lake offshore, were improved.

Chapter 6

Fossil Cladocera as an indicator of climate change in mountain lakes: development of a surface water temperature transfer function

6.1. Introduction

This chapter focuses on the development of a summer lake surface-water temperature (LSWT) transfer function using the modern assemblage structure of fossil Cladocera across the Scottish and Norwegian mountain lakes training set. The study sites cover wide altitudinal and latitudinal gradients, so have potential to reflect climate change through changes in biological communities (Battarbee, 2000). The cladoceran is selected as potentially one of the most useful biological proxies following previous demonstrations of the value of fossil Cladocera for past environmental reconstruction in mountain lakes (Lotter et al., 1997; Korhola, 1999). In this study, a variety of powerful multivariate techniques, such as direct and indirect gradient analyses in ordinations, significance tests involving Monte Carlo permutations and robust statistical procedures for cross validation and error estimations have been employed on the calibration data-set before the development of the transfer function model on summer LSWT (e.g. ter Braak et al., 1993; Birks, 1995; Lotter et al., 1997; Korhola, 1999).

6.2. Materials and methods

6.2.1 Laboratory methods

Modern cladoceran remains from 72 training-set sites from Scotland and Norway were analysed. A detailed procedure for data screening from the original sites and analysis of Cladocera has been presented in Chapters 2 and 3. At least 200 remains were counted from surface sediment samples from 68 sites. Four sites were recorded with low numbers of remains (<200) and these were excluded from the list. All Cladocera remains found (e.g. carapaces, head-shields, post-abdomen, post-abdominal claws, and ephippia) were tabulated separately, but only the most frequent body parts for each

taxon were used for calculating the species abundance. If the two halves of the bilateral carapace had come apart, as is often the case with some of the larger species (e.g. *Eurycercus*), one half was counted as half an individual. Badly fragmented remains were counted if they contained a clear diagnostic feature as described in Goulden (1969). The total number of remains was calculated on per gram dry sediment basis and later converted into percentages of individual taxa for numerical analysis.

A total of 42 cladoceran species were recorded from the 68 samples (Appendix 6.1). However, only cladoceran species present in at least two of the sites with a relative proportion of more than 1 % in at least one of these lakes were included for analysis (Korhola, 1999). A total of 28 cladoceran taxa met these criteria. Identification of Cladocera was based on procedures given by Frey (1959, 1960, 1986), Lotter et al. (1997), Korhola (1999), Duigan and Birks (2000), Korhola et al. (2000) and Korhola and Rautio (2001). Uncertainty over the identification of *Bosmina coregoni* and *Bosmina longispina* still exists, related to problems on headpore features and size and shape of the mucros (ventral tip of the carapace). *B. coregoni* was identified on the basis of oval and reticulated headpores with relatively short and thick mucros while *B. longispina* was identified as rectangular and non-reticulated headpores with relatively long and thin mucros (Appendices 3.1.2.1 and 3.1.2.2). Carapaces of small *Alona* spp. are also difficult to identify accurately. The most difficult species encountered were the shells of *A. intermedia* and *A. rectangula*. *Daphnia* was not identified to species level due to taxonomic difficulties. However, the post abdominal claws of most species counted were likely to be *D. longispina*. This taxon is also common in European mountain lakes and its post-abdominal claws are well preserved in lake sediments (Frey, 1986).

The percentage dry weight (DW) and loss on ignition (LOI) values were also calculated from each training-set site in order to calculate the number of cladoceran remains per gram of dry sediment and per gram total organic content in the sediment.

6.2.2 Numerical analyses

6.2.2.1 Ordination

A detail description on introduction and methods to the numerical analyses for ordination used in this Chapter is presented in Chapter 3. Principal components analysis

(PCA) of environmental data was carried out for explanatory variables of Scotland and Norway separately and then together. All available 21 explanatory variables in 72 samples, after excluding the non-limnological variables, latitude, longitude and altitude, were included in the data-set in order to evaluate the major patterns of variations of the environmental variables in the ordination. In all cases, the PCA was performed focusing the scaling on inter-species correlations, and with the species scores divided by the standard deviation (ter Braak & Šmilauer, 2002). Environmental data (untransformed) were also centered by species while running the PCA in each case (ter Braak & Šmilauer, 2002).

The gradient length, or standard deviation of cladoceran species present in Scotland (N =14) and Norway (N =54), as well as in the combined (N = 68) training-set sites was assessed using detrended correspondence analysis (DCA) with down-weighting of the rare taxa, squared-root transformation and non-linear rescaling of axes (ter Braak & Šmilauer, 2002). In DCA, the standard deviation of species data was less than 2SD in all cases indicating that linear approaches of indirect (e.g. PCA) and direct (e.g. RDA) gradient analyses were the appropriate forms of analysis to be used. Direct gradient analysis (RDA) was, however, carried out only for the combined Scottish and Norwegian data-set.

In PCA of the cladoceran species data, the scaling of the species data was focused on inter-species correlations, and the species scores were divided by the standard deviation (ter Braak & Šmilauer, 2002). The species data were square-root transformed and centered by species to explore the cladoceran species data in the calibration data-set. The response of the assemblage structure of Cladocera to environmental variables was analysed using multiple linear regressions and ordinations such as RDA and partial RDAs in CANOCO version 4.5 (ter Braak and Šmilauer, 2002). Detailed applications of these analyses are described below (section 6.3).

Multiple regression methods were also used to explore the niche species response in the calibration data-set (McCullagh and Nelder, 1989). Two Gaussian type models, weighted averaging (WA) and Huisman-Olff-Fresco (HOF) models (Huisman et al., 1993) based on generalized linear regressions (ter Braak & Prentice, 1988) were used to define the optima and tolerance ranges of Cladocera, and their statistically significant response curve to a particular environmental gradient.

6.2.2.2 Weighted-averaging (WA) regression

WA regression was used to estimate the species' optima and tolerances with respect to known environmental variables in the programme CALIBRATE version 0.81 (Juggins and ter Braak unpublished).

In WA regression species show a unimodal relationship to environmental variables, in which the species' presences are concentrated around the peak of the Gaussian curve (ter Braak and van Dam, 1989). For instance, in a lake with a certain surface water temperature, Cladocera with their LSWT optima close to the lake water temperature will tend to be the most abundant taxa present. The weighted averaging taxon response optima for an environmental variable is, therefore, calculated by averaging the values of the given environmental variable of samples, in which the taxon occurs, weighted by the taxon's relative abundance (e.g. Birks et al., 1990). The WA estimate of taxon's optima ($\hat{u}_k$) is:

$$\hat{u}_k = \sum_{i=1}^{n} y_{ik}x_i / \sum_{i=1}^{n} y_{ik} \qquad \textit{Equation 6.1}$$

Where, x denotes the variable of interest, x_i the value of x in sample i and y_{ik} the abundance of taxon k in sample i (y_{ik}).

The effective number of occurrences of taxa influences the WA-optima of a taxon (Birks, 1995). Hill (1979) suggested an adequate measure of occurrences of the taxon using *N2*. *N2* lies between 1 and the actual number of occurrences, WA tolerances ($\hat{tk}$), weighted standard deviation can be corrected for bias by dividing $\hat{tk}$ by $(1\text{-}1/N2)^{1/2}$ (Line et al., 1994).

$$\hat{tk} = \left[\sum_{i=1}^{n} y_{ik}(xi - \hat{u}_k)^2 / \sum_{i=1}^{n} y_{ik} \right]^{1/2} \qquad \textit{Equation 6.2}$$

It has been argued that the estimates of optima and tolerances of taxa with high *N2* (e.g. >3) values are often regarded as ecologically reliable measures than the optima and tolerances of taxa with low *N2* (e.g. <3) values (Reed, 1998).

6.2.2.3 HOF models

The niche species response to the environment was carried out by using HOF (Huisman et al., 1993) models (Oksanen, unpublished program) and the estimated optima and tolerances of each taxon to the environmental variable were performed using a

Weighted Averaging (WA) regression in CALIBRATE version 0.61 (Juggins & ter Braak, unpublished program). HOF models are effective statistical tools for evaluating response curves such as skewed or non-unimodal distribution that most other generalized linear regression models do not perform (Oksanen & Minchin, 2002). HOF models were originally proposed by Huisman et al. (1993) with a set of five hierarchic models (skewed unimodal, symmetric unimodal, monotonic sigmoidal increasing, monotonic sigmoidal decreasing and null or flat), in which the species response curves find the simplest possible response model that adequately describes the patterns of occurrence and abundance of species data. In HOF, the most complex model defines a skewed response function followed by symmetrical, monotonic and null or flat responses (Equation 6.3).

$$\mu(a, b, c, d; x, m) = M\frac{1}{1+\exp(a+bx)}\ \frac{1}{1+\exp(c-dx)} \qquad \textit{Equation 6.3}$$

Where, m is the expected value which is dependent on the known values of the gradient (x) and maximum value (M), and the four estimated parameters (a, b, c, d) of the function. The maximum likelihood function used in the HOF model is non-linear in parameters, and so the parameters must be estimated using iterative methods (J. Oksanen, unpublished model software programme).

While doing this, the simplest statistically significant response model for each taxon was achieved by fitting the most complex model first, and progressively removing the parameters from the regression model. This was done until the model was simplified without a significant change $p<0.05$) in the deviance. Deviance is a goodness-of-fit statistic based on a likelihood ratio that can be used in F-ratio tests (Crawley, 1993; Lotter et al., 1997).

6.2.2.4 Development of a summer LSWT transfer function, and reconstruction of past summer LSWT of Loch Coire Fionnaraich

The reconstruction of past summer LSWT from the cladoceran subfossils in the sediment core involved two important steps: regression and calibration.

Step 1 (Regression): Estimation of modern calibration function or regression coefficients ($\hat{U}_m$).

$Y_m = \hat{U}_m (X_m)$ *Equation 6.4*

Y_m = modern surface sample data

X_m = associated environmental data

or,

Inverse regression:

$X_m = \hat{U}^{-1}_m (Y_m)$ *Equation 6.5*

Step 2 (Calibration): Estimation of the transfer function equation, X_f, or to reconstruct past lake surface water temperature from fossil core data

$\hat{X}_f = \hat{U}^{-1}_m (Y_f)$ *Equation 6.6*

$\hat{X}_f$ = past lake surface water temperature

Y_f = fossil core data or fossil set

The Cladocera-inferred summer LSWT transfer function models were developed using WA, PLS and WA-PLS regression and calibration methods in the program CALIBRATE (version 0.81, Juggins and ter Braak, unpublished), and the are described in the results (section 6.3). The best transfer function model obtained in Chapter 6 was then used to reconstruct the past summer LSWT of Loch Coire Fionnaraich inferred by the sub-fossil assemblages of Cladocera in LCFR2 using the program CALIBRATE (version 0.81, Juggins and ter Braak, unpublished program) in Chapter 7.

The WA method is widely used for inferring past limnological changes including physical variables related to climate (Lotter et al. 1997). It has many advantages such as niche space partitioning and empirical predictive powers. ter Braak & Juggins (1993) reported that WA performs well with noisy, species rich, compositional data, with species that may be absent in many samples, and with long ecological gradients (>3 SD). However, this method does not assume linearity and is less sensitive to outliers (Birks 1995).

The partial-least squares (PLS) regression was primarily developed as a partial component regression (PCR) in chemometrics (Geladi and Kowalski, 1986). In PLS, components are selected to maximize the co-variance with the response variables. PLS usually requires fewer components and gives a lower prediction error (RMSEP) than PCR. But PLS regression can be biased since some data are discarded while selecting

uncorrelated orthogonal components. Though PLS performs very well by combining desirable properties of inverse regression (high correlation) into one technique and it always gives a better fit (r^2) value than PCR with the same number of components (Eriksson et al., 1995).

One important limitation of WA is that it ignores residual correlations among biological data, namely correlations that remain after fitting the environmental variable of interest, *x*. Such correlation may result from environmental variables that are not taken into account in WA (ter Braak and Juggins, 1993). However, WA-PLS uses the residual correlation structure in the data to improve the fit between the biological data and *x* in the modern training set (ter Braak and Juggins, 1993) resulting in a simpler 'minimal adequate model' as described in Crawley (1993). Thus, usually, WA-PLS can be regarded as the unimodal-based equivalent of the linear based PLS. It has become a popular model for developing transfer functions in palaeolimnology (Brooks and Birks, 2000). The performance of the minimal adequate WA-PLS model is based on a combination of low root-mean-square-error of prediction (RMSEP), a low maximum bias (ter Braak & Juggins, 1993), and a high coefficient of determination (r^2) between the observed and predicted values, usually estimated by leave-one-out cross validation techniques (e.g. jack-knifing) (Birks et al., 1990; ter Braak and Juggins, 1993; Birks, 1995; Olander et al., 1999).

The central aim of this study was to develop a Cladocera-based summer LSWT inference model. The DCCA for summer LSWT was performed with detrending-by-segments, non-linear rescaling and squared-root transformation of percentage data and down-weighting of the rare taxa. The length of gradient for the first and second axes of DCCA was less than 2 SD units, suggesting that the partial least squares (PLS) regression and calibration is the best approach for the development of a Cladocera-based summer LSWT inference model (Birks, 1998). The PLS model was then evaluated on the basis of the lowest root mean squared error of prediction (RMSEP) obtained by leave one-out cross validation (jack-knifing), the highest coefficient of determination (r^2) between observed and Cladocera-inferred values, and the low maximum bias along the temperature gradient (ter Braak and Juggins 1993). The PLS transfer function model was also compared with weighted averaging (WA), weighted averaging-partial least squares (WA-PLS) models in CALIBRATE (version 0.81,

Juggins & ter Braak, unpublished program). In all methods (WA, PLS and WA-PLS), the species data were square-root transformed before analysis.

6.3 Results

6.3.1 Exploratory data analysis (EDA)

6.3.1.1. Explanatory variables

In a total of 24 explanatory variables, 3 variables (latitude, longitude and altitude) were spatial or geographical variables, and the remaining 21 variables were environmental variables comprising both physical and chemical variables. However, the three spatial variables were excluded from the data-set before analysis due to their non-limnological characteristics and likely to have the overriding effects on the chemical variables in ordination.

Scotland and Norway have many similarities in mountain lake ecosystems (see Chapter 2 for details). In Chapter 2, it was aimed that using a constant alkalinity against altitude approach in the selection of sites in the training set was maximizing the climate gradients in the data-set. However, Scottish and Norwegian sites have significant differences in altitudinal and latitudinal variables as well as in the characteristics of the catchments. In the following sections, the Scottish and Norwegian data-sets are described and analysed using the ordinations, and the results of these ordinations are then compared with the combined data-set of both regions.

Principal components analysis (PCA)

(i) Scottish data-set

PCA was used to summarise the patterns of variations within the 21 environmental variables of the 14 Scottish samples by selecting the options by focusing scaling on inter-species correlation and dividing by standard deviation, and centering by species in CANOCO 4.5 ordination (ter Braak and Šmilauer, 2002). PCA axis 1 explained 95% of the total variations in the data-set followed by PCA axis 2, which explained only 4.3% variations of the data-set in ordination (Table 6.1). The mean annual precipitation was the most significant variable explaining the highest variations in the ordination by the PCA

Table 6.1: Summary of PCA of a total of 21 environmental variables in 14 sites of Scotland.

PCA Axes	1	2	3	4
Eigenvalues (λ)	0.950	0.043	0.003	0.002
Variance explained (cumulative %) in the environmental data	95.0	99.3	99.6	99.8

axis 1 (Figure 6.1a). NO_3 concentration is, however, negatively correlated with the mean annual precipitation in PCA axis 1 (Figure 6.1a). All temperature related variables, mean July air temperature, mean summer lake surface water temperature (LSWT) and the mean January air temperature are associated with PCA axis 2, where the major chemical variables such as, Na, Cl, Mg and conductivity are also positively correlated. Other variables, alkalinity and pH are negatively correlated with Na, Cl, Mg and conductivity in PCA axis 2 (Figure 6.1a). A number of sites in Scotland are low altitude sites. The main study site is very closely associated with the mean annual precipitation in as shown by PCA axis 1 (Figure 6.1a).

(ii) Norwegian data-set

PCA was also used to summarise the patterns of variations in 21 environmental variables in 58 Norwegian samples by focusing the scaling on inter-species correlations and dividing by standard deviation, and centering by species in CANOCO 4.5 ordination (ter Braak and Šmilauer, 2002). PCA axis 1 explained 95.7% variations of the total variations in the environmental data followed by PCA axis 2, which explained only the small (3.7%) fraction of the variations of the total variations in the data-set (Table 6.2).

Table 6.2: Summary of PCA of a total of 21 environmental variables in 58 sites of Norway.

PCA Axes	1	2	3	4
Eigenvalues (λ)	0.957	0.037	0.003	0.002
Variance explained (cumulative %) in the environmental data	95.7	99.4	99.7	99.9

The mean annual precipitation was again the most significant variable explaining the highest variations by the PCA axis 1 (Figure 6.1b). Unlike Scotland, other climate related variables such as, mean July air temperature, mean January air temperature and the mean summer lake surface water temperature (LSWT) in Norwegian sites were associated with PCA axis 1 (Figure 6.1b). However, after precipitation, the mean

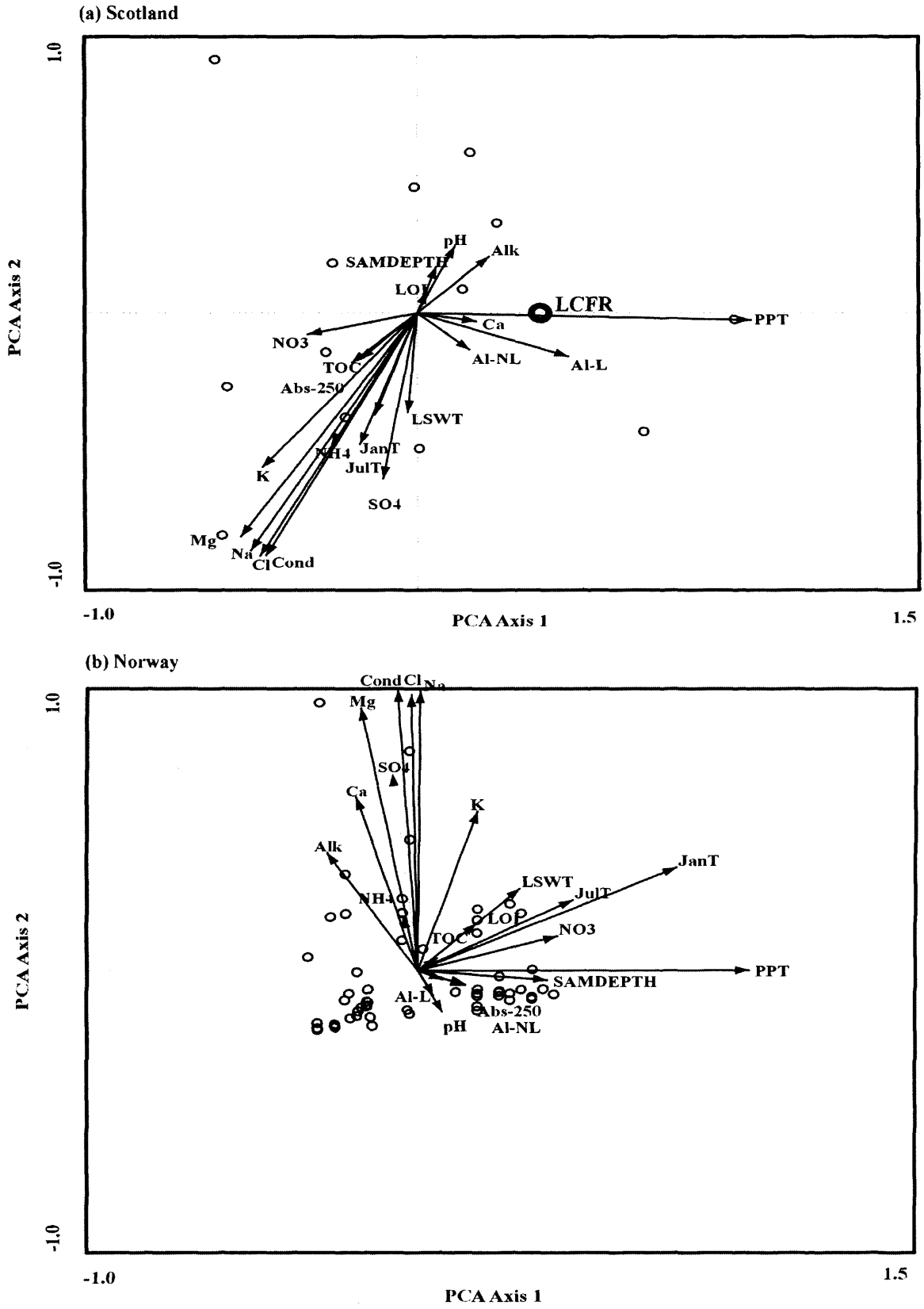


Figure 6.1: PCA biplot ordinations of a total of 21 environmental variables for sites in (a) Scotland and (b) Norway. Circles represent sites (samples). In Scotland, the site, Loch Coire Fionnaraich (LCFR), where the comprehensive study for contemporary and fossil Cladocera was carried out, is identified by a large bold circle. Abbreviations for samples are presented details in Appendix 2.1.

January temperature was the major climatic variable in the ordination of the Norwegian data-set (Figure 6.1b). Unlike in Scotland, NO_3 concentration in Norway was positively correlated with mean annual precipitation along PCA axis 1 (Figure 6.1b). A large number of sites, which receive the higher amount of mean annual precipitation in Norway as shown by the ordination, also have relatively high maximum depth (Figure 6.1b). Major chemical variables such as Na, Cl, Mg, conductivity, SO_4 were positively correlated in PCA axis 2 (Figure 6.1b). A group of sites is also associated with high altitude in PCA axis 2. Compared to altitude, the latitudinal variations are not that significant in the PCA ordination (Figure 6.1a & b).

(iii) Justification for the merger of the Scottish and Norwegian data-sets

It is very difficult to observe the real patterns of the environmental variables in the ordination of the Scottish data-set due to their smaller size (N = 14), however, the PCA ordinations in Figure 6.1 a & b show that both Scottish and Norwegian data-sets appear to have some similarities in the patterns of environmental variables that explain variation between sites. The PCA axis 1 of both data-sets explained the maximum variation of all environmental variables, where mean annual precipitation is the most important climatic variable to influence the data-sets. Except Ca, other major physico-chemical variables, such as, Na, Cl, Mg and conductivity are also positively correlated with PCA axis 2 of the ordinations of both data-sets (Figure 6.1 a & b). Originally, it was thought that the high latitudinal (Arctic) sites of Norway, which fitted into the criteria of constant alkalinity against altitude, might become 'outliers' in the ordination. However, no such significant influence in the high latitudinal sites in the ordination was observed in the Norwegian data-set (Figure 6.1b).The only differences in the two data-sets in the ordinations were temperature values. All temperatures (mean July, January and summer LSWT) in the Scottish data-set are associated with PCA axis 2, however, temperature in the Norwegian data-set are associated with PCA axis 1 (Figure 6.1 a & b). The highly significant influence of temperature on the ordination of the Norwegian data-set was possibly due to the increased temperature gradients across Norway compared to the Scotland.

(iv) Merger of the Scottish and Norwegian data-sets

In order to understand the patterns of the variations in the environmental variables, a PCA ordination was carried out on a combined Scottish and Norwegian data-set. The patterns of variation explained by the ordination in the combined data-set was as high as

the patterns of variations explained by the Norwegian data-set. A total of 95.6% of the variation was explained by PCA axis 1 only (Table 6.3). The climatic variable such as mean annual precipitation and mean January air temperatures are associated with PCA axis 1 while most chemical variables such as Ca, Mg, Na and conductivity are associated with PCA axis 2 (Table 6.4).

Table 6.3. Summary of PCA of a total of 21 environmental variables in 72 sites of combined Scottish and Norwegian training set.

PCA Axes	1	2	3	4
Eigenvalues (λ)	0.956	0.038	0.003	0.002
Variance explained (cumulative %) in the	95.6	99.4	99.7	99.8

Table 6.4: Summary of PCA scores of 21 environmental variables in 72 sites of Scotland and Norway. Bold numbers represents the highest species score among four axes.

Variables	Axis 1	Axis 2	Axis 3	Axis 4
pH	0.16	-0.0695	-0.4304	**0.3303**
Alkalinity (μeql^{-1})	-0.2317	0.2724	-0.0519	**0.3662**
Conductivity (μScm^{-1})	0.0205	**0.9635**	0.1179	0.1802
Na (μeql^{-1})	0.1044	**0.9875**	0.0064	-0.0828
NH_4 (μeql^{-1})	-0.0879	0.1557	**0.4513**	0.3437
K (μeql^{-1})	0.0809	**0.4465**	0.2478	0.4433
Mg (μeql^{-1})	-0.1007	**0.9435**	0.0673	-0.1255
Ca (μeql^{-1})	-0.2473	0.4394	0.3813	**0.7651**
Cl (μeql^{-1})	0.0454	**0.9967**	-0.0216	0.0062
NO_3 (μeql^{-1})	**0.3418**	0.0379	-0.0712	0.2785
SO_4 (μeql^{-1})	-0.1433	**0.5604**	0.2159	0.5242
Al-NL (μgl^{-1})	0.0937	-0.0976	**0.9437**	-0.2885
Al-L (μgl^{-1})	-0.0253	-0.1582	**0.7556**	-0.1371
Abs –250	0.0414	-0.0387	**0.8908**	-0.2829
TOC (mgl^{-1})	0.0143	0.017	0.9067	-0.2228
Mean Sampling (Coring) Depth (m)	**0.316**	-0.075	0.2374	0.0858
Mean July Air Temperature (July T) (^0C)	0.3831	0.1263	**0.5631**	0.2758
Mean January Air Temperature (Jan T) (^0C)	**0.7856**	0.3857	0.0078	-0.0864
Mean Lake Surface Water Temperature (LSWT) (^0C)	0.2187	0.1774	**0.5268**	0.3326
Mean Annual Precipitation (PPT) (mm)	**1.0000**	-0.0021	-0.0001	0.0007
LOI (%)	0.2789	0.1853	**0.4442**	0.0748

The combined ordination between the Scottish and Norwegian data-set shows that the Scottish sites have rather high winter temperatures compared to Norwegian sites (Figure 6.2). The other measured temperature values, mean July and summer lake surface water tempratures (LSWT), are also positively associated with Scottish sites (Figure 6.2).

The UKAWMN, EMERGE Scottish and Norwegian sites are also classified in PCA ordination. No such variation is observed between the UKAWMN and EMERGE Scottish sites (Figure 6.3). However, the Norwegian sites are found to be slightly different from Scottish sites as shown by Figure 6.3. At least one site (L190MED) in Norway along PCA axis 2 appears to have a relatively higher influence on the ordination (Figure 6.3). Larger variations in the Norwegian sites are mainly caused by variables such as Mg, conductivity, Cl and Na along PCA axis 2 (Figure 6.3)

6.3.1.2. Species data

A total of 28 cladoceran taxa was included for ordination analysis for the joint Scottish and Norwegian data-set, where 3 species, *Bosmina longispina*, *Bosmina coregoni* and *Daphnia* spp. were open-water taxa, while the remaining 25 were littoral species. Among the littoral taxa, 24 were from the family Chydoridae and one was from the family Sididae (*Sida crystallina*). The ephippia of *Daphnia* and chydorids were recorded in the samples though they were not abundant enough to be included for analysis. Before running the ordination of the combined data-set, the DCA and PCA of Scottish and Norwegian data-sets were also analysed separately.

Detrended correspondence analysis (DCA)

A DCA of 26 species of Cladocera present in 14 Scottish samples was carried out by detrending by segments, square root transformation and down-weighting of rare taxa. A total of 35% variation was explained by the first two DCA axes (Table 6.5). The gradient length of species data show that species are linearly distributed (Table 6.5).

Table 6.5: Summary of a DCA of the 26 species of Cladocera in 14 sites in Scotland.

DCA axes	**1**	**2**	**3**	**4**
Eigenvalues (λ)	0.057	0.046	0.022	0.00
Length of gradient	0.931	0.819	0.679	0.47
Cumulative percentage variance of species data	0.473	34.8	42.3	44.5
Sum of all unconstrained eigenvalues =				**0.294**

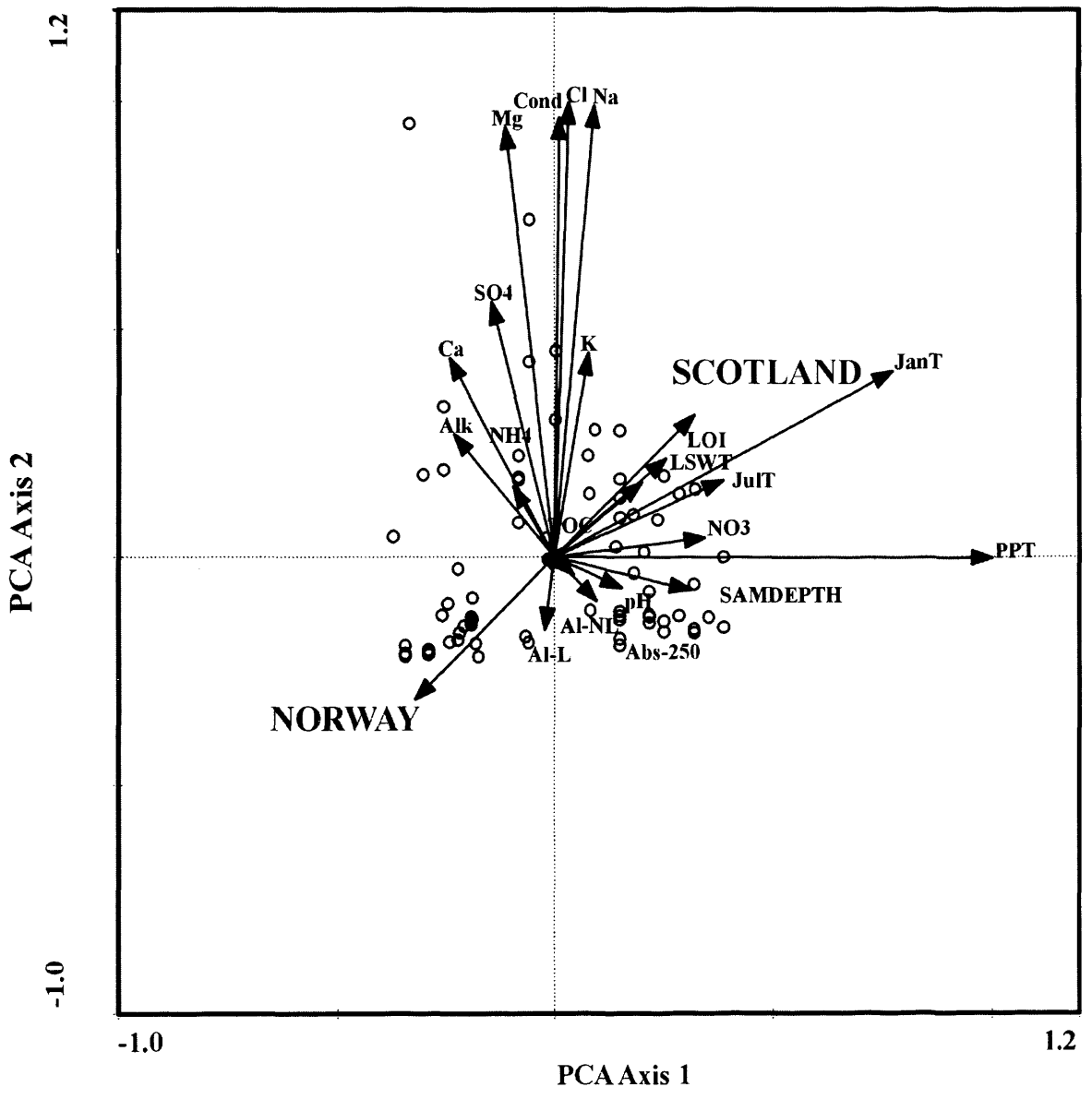


Figure 6.2: PCA biplot ordinations of a total of 21 spatial and environmental variables in 72 sites for Scotland and Norway. Circles represent sites (symbols). Abbreviations for samples are presented in Appendix 2.1.

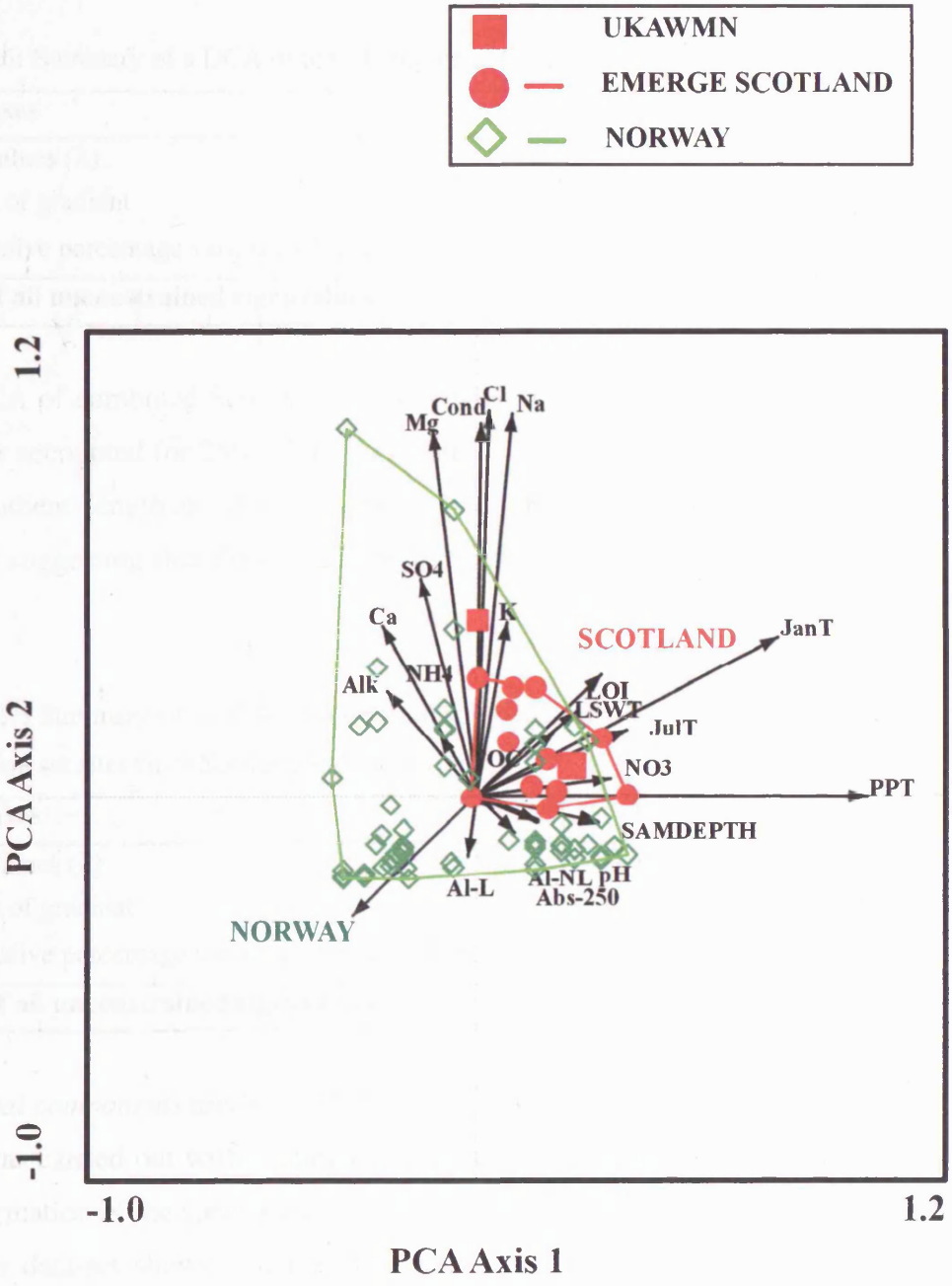


Figure 6.3: PCA bipolot ordination of 21 environmental variables in 72 sites of Scotland and Norway. EMERGE and UKAWMN Scottish and Norwegian sites are classified in the ordination. Abbreviations for environmental variables are presented in Table 6.4.

A DCA of 24 species of Cladocera present in 54 Norwegian samples was carried out by detrending by segments, squared-root transformation and down-weighting of rare taxa. A total of 26% of the variation was explained by the first two DCA axes (Table 6.6), which was less than the variation explained by the first two DCA axes of the Scottish data-set. The gradient length of the species data shows that the species in the Norwegian data-set are also linearly distributed (Table 6.6).

Table 6.6: Summary of a DCA of the 24 species of Cladocera in 54 sites in Norway.

DCA axes	**1**	**2**	**3**	**4**
Eigenvalues (λ)	0.084	0.070	0.048	0.03
Length of gradient	1.301	1.151	1.604	0.92
Cumulative percentage variance of species data	14.1	25.9	34.1	39.2
Sum of all unconstrained eigenvalues =				**0.593**

The DCA of combined Scottish and Norwegian data-set showed that the first two axes together accounted for 25% of the cumulative variation of the species data (Table 6.7). The gradient length or standard deviation of the species data after DCA was 1.37 (<2SD) suggesting that the overall species data had a linear distribution (e.g. Korhola, 1999).

Table 6.7: Summary of a DCA with detrending-by-segments of the 28 species of Cladocera of 68 training set sites from Scotland and Norway.

DCA axes	**1**	**2**	**3**	**4**
Eigenvalues (λ)	0.075	0.063	0.042	0.03
Length of gradient	1.378	1.593	1.235	1.02
Cumulative percentage variance of species data	13.50	25.00	33.5	38.0
Sum of all unconstrained eigenvalues =				**0.555**

Principal components analysis (PCA)

PCA was carried out with scaling on the inter-species correlation and the squared-root transformation of the species data in CANOCO 4.5. A PCA of cladoceran species in the Scottish data-set shows that the PCA axis 1 and 2 together explained 57.5% of the variation of the total variation in the data-set (Table 6.8). However, the first two PCA axes of the Norwegian data-set together explained 50% of the total variation in the cladoceran data-set (Table 6.9). The results suggest that the cladoceran community present in the Scottish data-set has a stronger response in the ordination than the cladoceran community present in the Norwegian data set.

Table 6.8: Summary of a PCA of the 26 species of Cladocera of 14 Scottish sites.

PCA Axes	1	2	3	4
Eigenvalues (λ)	0.362	0.213	0.101	0.096
Variance explained (cumulative %) in the species data	36.2	57.5	67.6	77.2

Table 6.9: Summary of a PCA of the 24 species of Cladocera of 54 Norwegian sites.

PCA Axes	1	2	3	4
Eigenvalues (λ)	0.279	0.223	0.115	0.095
Variance explained (cumulative %) in the species data	27.9	50.2	61.7	71.2

PCA biplot ordinations of Cladocera species present in the Scottish and Norwegian data-sets are presented separately in Figure 6.4. Two species of planktonic Cladocera, *Bosmina coregoni* and *Bosmina longispina* were dominant species in both data-sets. The abundance of *B. coregoni* in the Scottish data-set is explained significantly by PCA axis 1, while the abundance of *B. longispina* is explained by PCA axis 2 (Figure 6.4a). Abundance of *B. coregoni* and *B. longispina* is closely associated with the site, Loch Coire Fionnaraich (LCFR), where the comprehensive study for contemporary and fossil Cladoceran was carried out (Figure 6.4a). The littoral cladoceran taxa in the Scottish data-set have also played a significant role in the ordination as most of these taxa are associated with PCA axis 1 (Figure 6.4a). PCA ordination of the Norwegian data-set shows that at least three species of Cladocera dominate the community, which include: two planktonic Cladocera, *B. coregoni* and *B. longispina* and one littoral taxon, *Alonella nana* (Figure 6.4b). However, the majority of littoral taxa is associated with PCA axis 1 (Figure 6.4b).

PCA of the combined data-sets of Scotland and Norway shows that the PCA axis 1 and 2 explained the maximum variation in the species data where these two axes together explained a total of 48.9% of total variation in the biological data-set (Table 6.10a). However, the total variance explained only by PCA axis 1 and 2 of the littoral taxa is slightly lower (40.4%) than for the overall taxa (Table 6.10b). In general, no such obvious clustering in the assemblage structure of the overall cladoceran species was observed along the training-set (Figure 6.5). The faunistic assemblages of the Cladocera showed that the two open-water taxa *Bosmina longispina* and *B. coregoni* have played a dominant role in influencing the overall cladoceran assemblages in the ordination diagram (Figure 6.5). However, a relatively large number of littoral taxa are associated

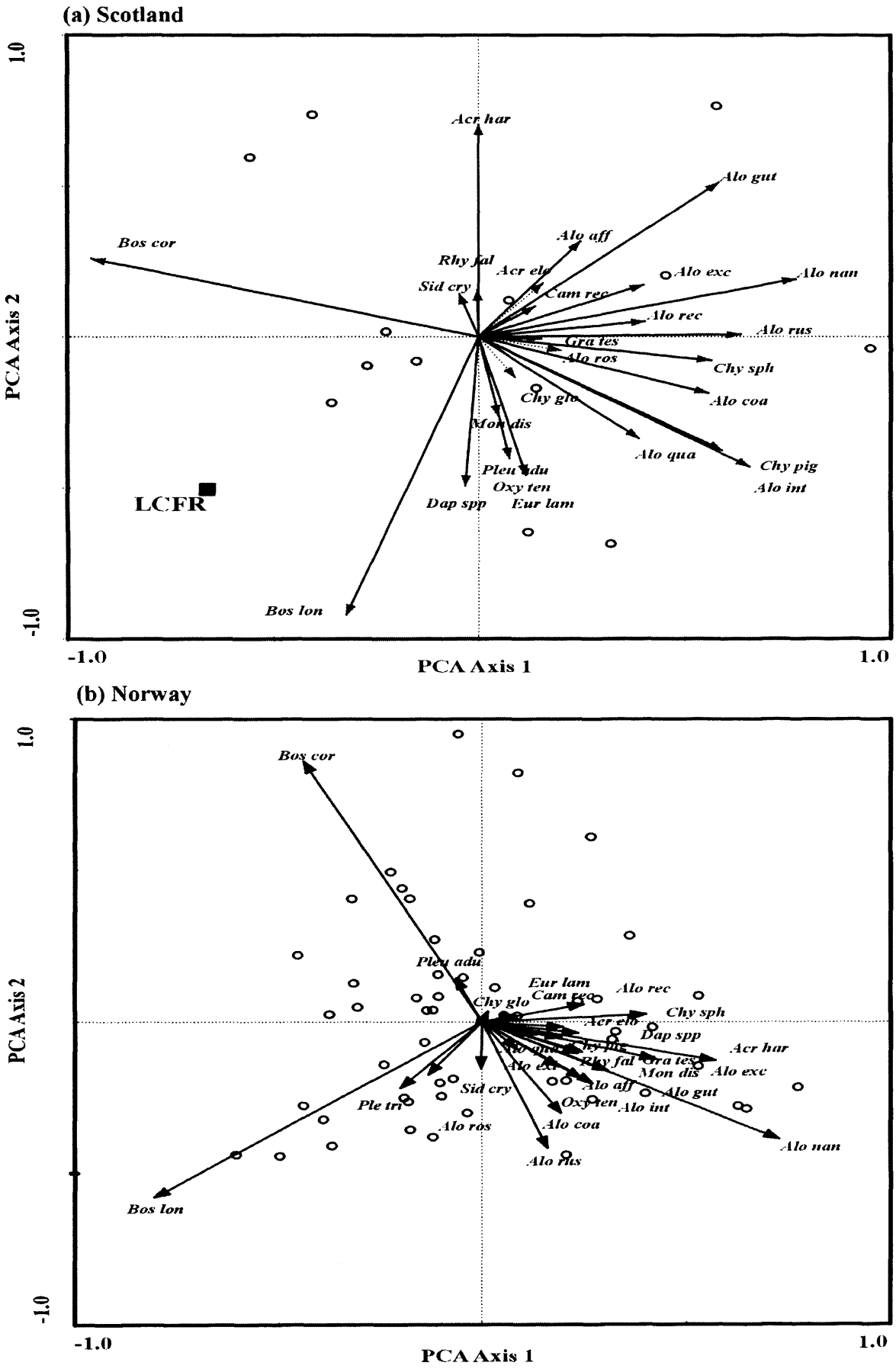


Figure 6.4: PCA biplot ordination of (a) 26 modern cladoceran remains present in 14 surface sediment samples from Scotland and (b) the remains of 24 cladoceran species present in 54 samples from Norway. Sampling codes and abbreviations for species data are presented in Appendix 2.1 and Appendix 6.2 respectively. LCFR stands for Loch Coire Fionnaraich.

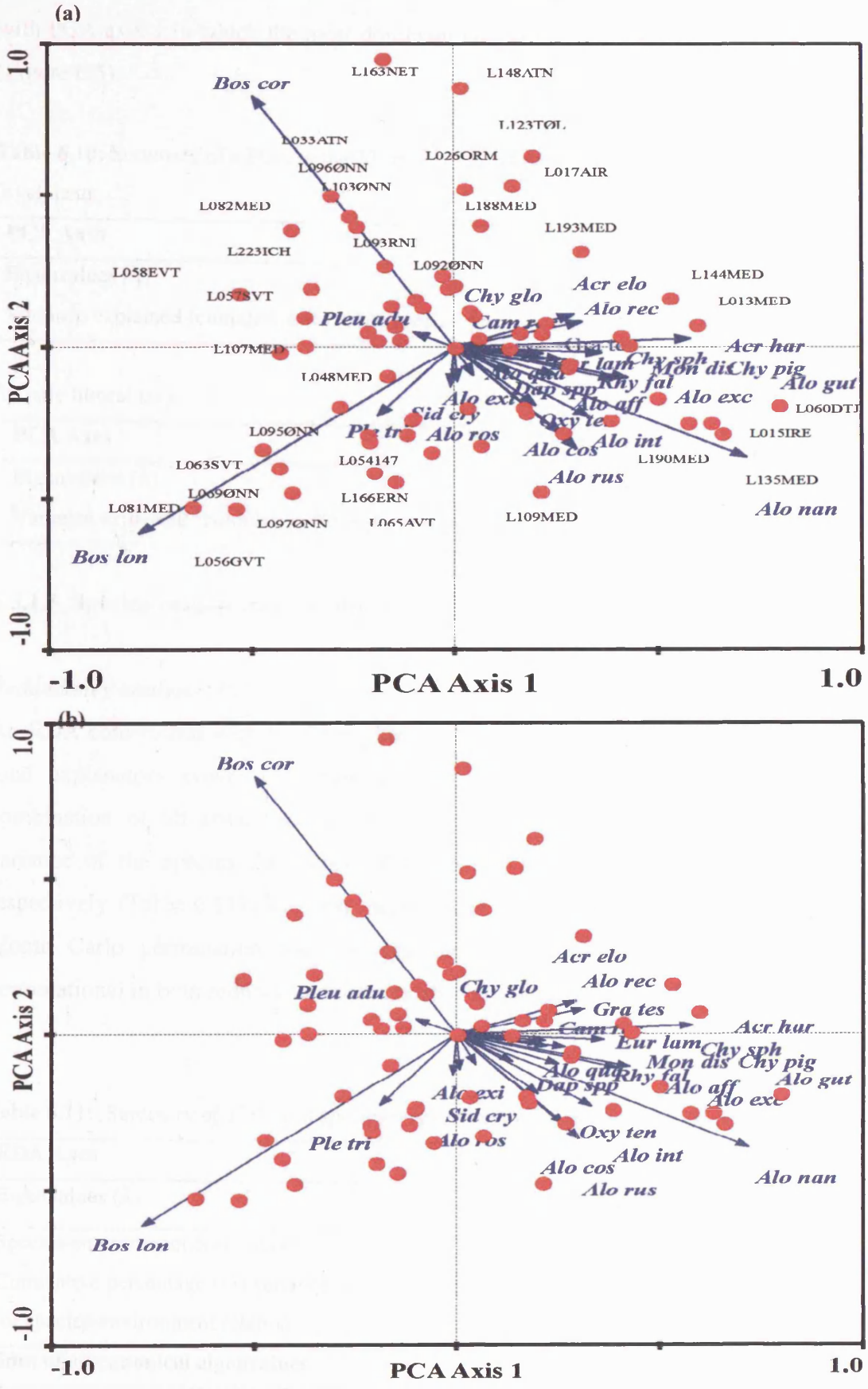


Figure 6.5: PCA biplot ordination of 28 modern cladoceran remains present in 68 surface sediment samples from Scotland and Norway: (a) all taxa showing sample labels; (b) all taxa without showing sample labels. Sampling codes and abbreviations for species data are presented in Appendix 2.1 and Appendix 6.2 respectively.

with PCA axis 1 in which the most dominant taxa are *A. nana*, *A. excisa* and *A. harpae* (Figure 6.5).

Table 6.10: Summary of a PCA of the 28 species data of 68 training set sites from training set.

(a) all taxa

PCA Axes	1	2	3	4
Eigenvalues (λ)	0.275	0.214	0.104	0.089
Variance explained (cumulative %) in the species data	27.5	48.9	59.3	68.1

(b) only littoral taxa

PCA Axes	1	2	3	4
Eigenvalues (λ)	0.242	0.161	0.139	0.083
Variance explained (cumulative %) in the species data	24.2	40.4	54.2	62.6

6.3.1.3. Species-environment relationships

Redundancy analysis (RDA)

An RDA constrained with the 21 explanatory variables was performed to estimate the total explanatory power of environmental variables. The result showed that the combination of all environmental variables together explained 50.3% of the total variance of the species data where RDA axis 1 and 2 explain 18.3% and 10.5% respectively (Table 6.11). The first canonical as well as all canonical axes under the Monte Carlo permutation tests (unrestricted permutations involving 999 random permutations) in both reduced and full models were significant (p = 0.001).

Table 6.11: Summary of a RDA of species-environment relationships in of 68 training set sites.

RDA Axes	1	2	3	4
Eigenvalues (λ)	0.183	0.105	0.064	0.045
Species-environment correlations	0.822	0.790	0.741	0.680
Cumulative percentage (%) variance -of species data	18.3	28.8	35.2	39.7
-of species-environment relation	36.4	57.2	67.0	79.0
Sum of all canonical eigenvalues				**= 0.503**

The variance inflation factor (VIF) is an important measure used to identify the multi-collinearity (MC) of the explanatory variables. A high VIF often has a greater chance of

finding an insignificant regression coefficient, which means that severe multi-collinearity effects are present in the data-set (e.g. Wooldridge, 2000). Since the training set also had MC effects, its improvement was considered essential in order to obtain the best model for the species-environment relationships, which could explain the maximum variance in the overall species data (ter Braak, 1994). However, there is no theoretical rule to predict the threshold value for the 'high' VIF, neither is there a theory which explains that MC is found in the data-set (Wooldridge, 2000). However, in palaeolimnological data-sets, the presence of MC is considered when the VIF is 20 or more (e.g. Korhola, 1999). While running the RDA, multi-collinearity (i.e. VIF >20) was also found in the training set. Thus each time, a variable with a high (>20) VIF was deleted objectively to reduce the effects of MC on the ordination. The process was repeated until the all environmental variables in the data-set were under VIF <20 (Table 6.12).

The environmental variables with >20 VIF were Cl, conductivity, TOC and Na (Table 6.12). An unrestricted permutation test involving 199 and 999 random permutations of the Monte Carlo permutations showed a relatively high p value ($p<0.001$) after deletion of the environmental variables with high VIFs. When those environmental variables with high VIFs were excluded and ran RDA, the combination of 17 environmental variables together explained 44% of the total variance of the species data where RDA axis 1 and 2 explained 16.2% and 10.1% respectively (Table 6.13). The first canonical as well as all canonical axes under the Monte Carlo permutation tests (unrestricted permutations involving 999 random permutations) in both reduced and full models were significant ($p = 0.001$).

Figure 6.6 shows the reduced RDA biplot ordination of 17 environmental and fossil assemblages of Cladocera in 68 training set sites. The ordination diagram shows that the sampling depth, Mg and SO_4 are explained by RDA axis 1, while the summer LSWT, July temperature and LOI are explained by RDA axis 2 (Figure 6.6a & b). Many species of chydorids are associated with Mg and SO_4, while the open-water species mainly *Bosmina longispina* is associated with sampling depth (Figure 6.6b). A planktonic taxa, *Daphnia*, and a few number of littoral taxa such as *Alona rustica*, *Alona guttata* and *Sida crystallina* are associated with warmer water temperatures (Figure 6.6b). In order to minimise the environmental variables which best explain the maximum variation in the species data, a forward selection statistical method (ter Braak, 1990; ter Braak and

Table 6.12: Variance inflation factors of 21 environmental variables. Those with high VIF were deleted until each variable was retained to <20 in each analysis in order to minimise the highly correlated environmental variables in the data-set. Abbreviations for environmental variables are presented in Table 6.4.

Variables	Weighted Mean	Stand-ard Devia-tion	VIFs of all enviro-nmental variables	VIFs after the highest VIF of previous column deleted	VIFs after the highest VIF of previous column deleted	VIFs after the highest VIF of previous column deleted	VIFs after the highest VIF of previous column deleted
pH	6.14	0.28	6.26	5.45	5.28	4.71	4.54
Alk (μeql^{-1})	33.28	9.95	6.95	3.53	3.53	3.27	3.19
Cond ((μScm^{-1})	24.35	13.89	89.68	87.91	**deleted**	-	-
Na ((μeql^{-1})	108.24	80.60	241.18	57.84	26.06	26.03	**deleted**
NH_4 (μeql^{-1})	0.86	1.83	2.40	2.06	2.03	1.97	1.97
K (μeql^{-1})	8.13	4.33	4.39	3.56	3.09	3.03	2.85
Mg (μeql^{-1})	38.39	23.71	49.60	27.75	23.22	23.16	4.17
Ca (μeql^{-1})	71.43	32.58	31.51	10.26	6.09	6.09	5.72
Cl (μeql^{-1})	103.65	100.32	361.05	**deleted**	-	-	-
NO_3 (μeql^{-1})	2.75	6.94	3.54	1.60	1.56	1.56	1.53
SO_4 (μeql^{-1})	39.60	19.62	19.73	5.84	5.26	5.26	5.12
A l-NL (μgl^{-1})	26.40	35.59	15.64	15.16	15.14	13.62	13.58
Al-L (μgl^{-1})	6.69	10.77	3.37	3.34	3.30	3.30	3.07
Abs –250	0.15	0.17	42.15	37.89	37.76	14.14	14.13
TOC (mgl^{-1})	4.33	3.28	49.96	49.34	49.07	**deleted**	-
SAMDEPTH (m)	9.36	5.78	1.70	1.70	1.64	1.64	1.63
JulT (^{0}C)	11.65	1.96	4.71	4.69	4.46	4.36	4.35
JanT (^{0}C)	-3.50	3.76	9.79	9.79	9.71	9.71	7.39
LSWT (^{0}C)	14.15	3.54	5.50	4.69	4.58	3.49	3.40
PPT (mm)	1598.06	652.69	5.82	5.63	5.20	5.07	4.93
LOI (%)	37.27	15.98	2.65	2.65	2.63	1.90	1.90

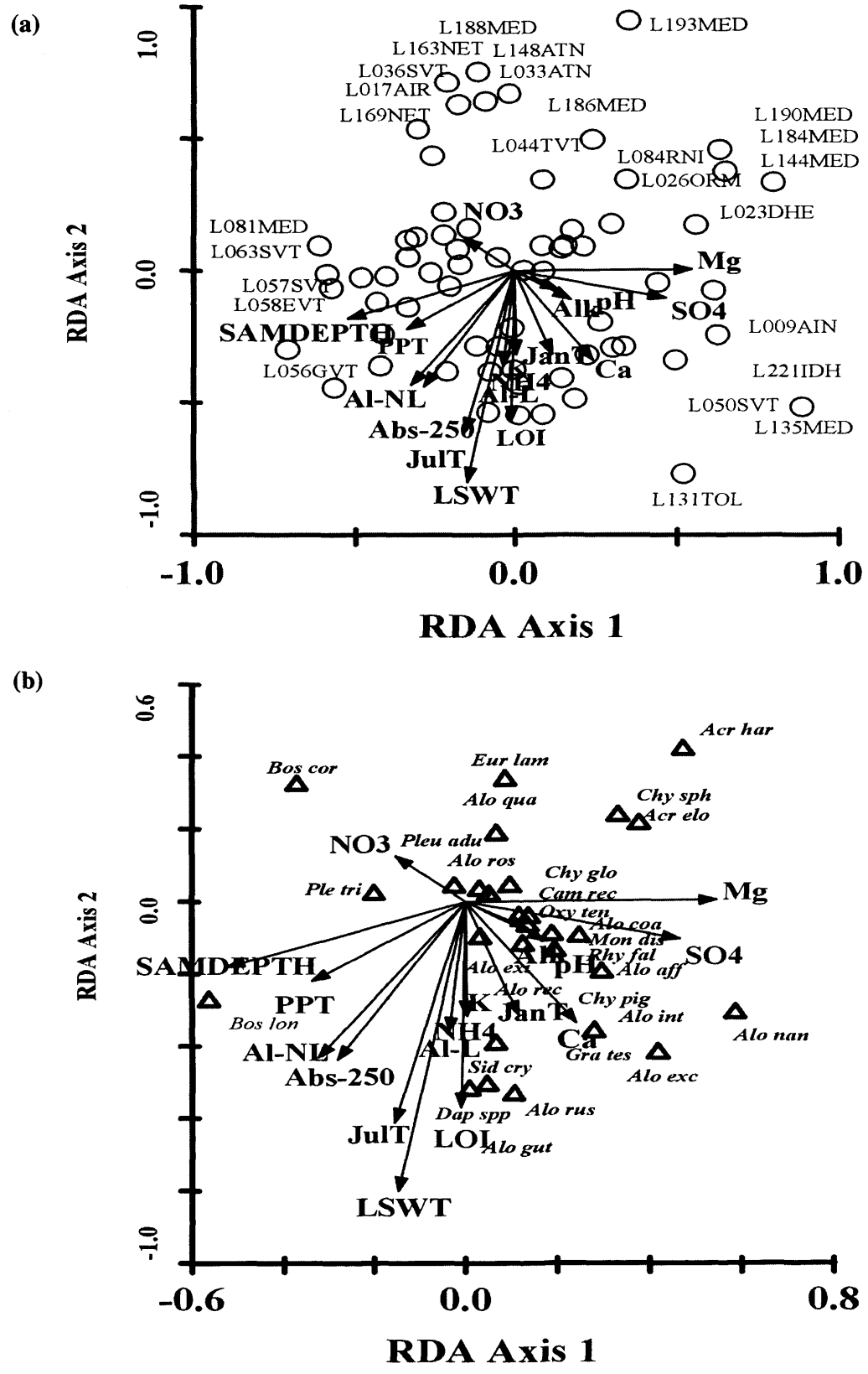


Figure 6.6: RDA biplots between axis 1 and axis 2 after the deletion of four environmental variables with high VIF values. (a) samples v environment, (b) species v environment. Abbreviations for samples, environment and species data are presented in Appendix 2.1, Table 6.4 and Appendix 6.2 respectively.

Verdonschot, 1995) under associated Monte Carlo permutation test (unrestricted permutations involving 999 random permutations in the reduced model) was performed (e.g. Manly, 1991) only with environmental variables with low VIFs (<20).

In the first step of the forward selection, the mean summer lake surface-water temperature (LSWT) was included in the model since the summer LSWT was the variable with the highest extra fit (Table 6.14). It also had significant marginal effects ($p<0.001$) and the highest λ_1: λ_2-ratio when the species composition was constrained by this variable only (see Table 6.17). In the second step, SO_4, a variable highly collinear with Mg and Ca, was the variable with the highest extra fit with significant marginal effects, and so was added into the model (Table 6.14). It was also highly significant with a high λ_1:λ_2-ratio when the species data were constrained to this variable (see Table 6.14).

Table 6.13: Summary of a RDA of species-environment relationships in of 68 training set sites from Scotland and Norway after deleting the environmental variables with high VIFs.

RDA Axes	**1**	**2**	**3**	**4**
Eigenvalues (λ)	0.162	0.101	0.057	0.036
Species-environment correlations	0.776	0.805	0.757	0.538
Cumulative percentage (%) variance				
-of species data	16.2	26.3	32.0	35.5
-of species-environment relation	36.9	59.9	72.8	81.0
Sum of all canonical eigenvalues				**= 0.439**

In the third step, sampling (coring/maximum) depth was the variable with the highest extra fit and was added into the model.

Of the various climatic variables (summer LSWT, mean July and January air temperatures and precipitation) considered to influence the community structure of Cladocera in the training set, summer LSWT was selected to develop the inference model because summer LSWT is highly correlated with the duration of the ice-free seasons and with atmospheric air temperature during summer (e.g. Livingstone and Lotter, 1998). Even though the next variable with the highest extra fit after maximum depth was mean January air temperature, it was not added into the model. It was considered that the mean January air temperature was not as influencing as summer

Table 6.14: Potential variance explained by each environmental variable (VIF<20) before forward selection and variance explained by those environmental variables when added in forward selection in RDA. The p-values were obtained after Monte Carlo permutations tests, 999 unrestricted permutations in the reduced model. P-values were adjusted in Bonferoni-type adjustment. The p value for the overall model is obtained from 99 permutations. Abbreviations for environmental variables are presented in Table 6.4.

Environmental variables only with low (<20) VIF	**Variance explained before forward selection**	**Variance explained when added with forward selection**	**P-value**	**Remarks**
LSWT (^{0}C)	0.080	**0.080**	**0.001**	First: Added
Mg (μeql^{-1})	0.055			
SAMDEPTH (m)	0.055	**0.044**	**0.007**	Third: Added
SO_4 (μeql^{-1})	0.050	**0.063**	**0.002**	Second: Added
JulT (^{0}C)	0.049			
PPT (mm)	0.047			
A l-NL (μgl^{-1})	0.043			
JanT (^{0}C)	0.042			
Abs –250	0.038			
LOI (%)	0.039			
Ca (μeql^{-1})	0.038			
K (μeql^{-1})	0.023			
pH	0.023			
Al-L (μeql^{-1})	0.016			
NO_3 (μeql^{-1})	0.013			
Alk (μeql^{-1})	0.013			
NH_4 (μeql^{-1})	0.013			
Sum of Variance	-	**0.187**		**Overall test P =0.05**

LSWT in driving the cladoceran community in the data-set since the λ_1:λ_2- ratio for mean January air temperature was significantly lower than the λ_1:λ_2- ratio for summer LSWT in the data-set (Table 6.17). The variables with the highest extra fit after mean January air temperature were pH followed by K^+. However, neither of these variables was added into the model since they had low λ_1:λ_2- ratio and also had non-significant marginal effects (Table 6.17). Each marginal effect under forward selection was adjusted under Bonferoni-type adjustment (Lotter et al., 1997) since the significance test in forward selection is often too liberal (ter Braak and Šmilauer, 2002). The Bonferoni adjustment is more powerful since the procedure involves a test of statistical significance, by dividing the alpha level of the significance test into n(n-1)/2 categories, where n represents the number of samples being compared (ter Braak and Šmilauer, 2002).

The summary statistics for 3 selected environmental variables in 68 Scottish and Norwegian training set sites shows that the first two RDA axes explained 11.3% and 6.9% of the total variation in the species data (Table 6.15). The cumulative variance for species data indicates that 3 selected environmental variables in forward selection are good representatives of overall ecological patterns within the data-set (Table 6.15). The overall model including axis 1 and 2 was found to be significant ($p < 0.001$) in Monte Carlo permutation tests involving 999 unrestricted random permutations in the reduced model.

Table 6.15: Summary of RDA ordination of species-environment relationship in surficial sediments of 68 sites with 3 selected environmental variables after forward selection.

Axes	**1**	**2**	**3**	**4**
Eigenvalues (λ)	0.11	0.06	0.0004	-
Species-environment correlations	0.71	0.69	0.460	-
Cumulative percentage (%) variance -of species data	11.3	18.2	18.60	-
Sum of all canonical eigenvalues =				**0.186**

The RDA axes can also be interpreted by regression or canonical coefficients as well as correlation coefficients (Table 6.15). The t-values of the regression coefficient can be compared with the critical value of student t distribution with n-q-1 degrees of freedom (where, n = number of samples, q = number of environmental variables). The variable is shown to contribute significantly to the regression if its t-value in absolute value exceeds the critical value (the critical value for t-test at the 5% level of significance is

ca. 2.1, if n-q-1 > 18) (ter Braak and Šmilauer, 2002). In Table 6.16, all three variables in forward selection, SO_4, sampling depth and mean lake surface water temperature, are significant variables contributing to axis 1 and 2 (Table 6.16).

Table 6.16: Regression/canonical coefficients, t-values of regression coefficients and inter-set correlations of three selected environmental variables (* indicates t-test significant at: ($p< 0.05$, N = 68, df = 68-3-1 = 64)

Environmental variables	Regression/canonical coefficients		t-values of regression coefficients		Inter-set correlations	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
SO_4 (μeql^{-1})	0.6892	0.3101	5.287*	2.216*	0.3319	0.4166
SAMDEPTH (m)	-0.52	-0.4285	-4.1858*	-3.2145*	-0.4667	-0.1941
Summer LSWT (^0C)	-0.6622	0.8179	-4.9917*	5.7456*	-0.3703	0.586

The result of a RDA biplot with 3 environmental variables selected after forward selection is presented in Figure 6.7. The sampling sites with respect to the three selected variables are evenly distributed throughout the ordination diagram. However, a relatively large number of sites is associated with lower water temperature values and the sites in this group are distributed towards the opposite direction of the vector related to higher mean lake surface water temperature (Figure 6.7a). A relatively large number of littoral cladoceran taxa such as *A. harpae*, *A. elongatus*, *E. lamellatus* and *A. quadrangularis* are associated with this group (Figure 6.7b). Particularly low altitude Norwegian sites are associated with warmer water values and the sites within this group are distributed towards the vector of the mean lake surface water temperature (Figure 6.7a). Some sites in Norway are also associated with high SO_4. However, sites with low SO_4 are positively correlated with sampling depth in the data-set (Figure 6.7a).

In an attempt to estimate the explanatory power of each of the 21 environmental variables individually (marginal effects) for each biological data-set, a series of RDAs was performed. The percentage of the variance in the biological data-set explained by each variable was calculated and the statistical significance of each model was assessed by an unrestricted Monte Carlo permutation test involving 999 random permutations (Table 6.17) (Lotter et al., 1997). While doing this, the species composition was constrained to only one explanatory variable at a time; the first eigenvalue (λ_1) is constrained, whereas the second eigenvalue (λ_2) is unconstrained. Therefore, the λ_1: λ_2-ratio can be used to express the relative strength of each variable in explaining the

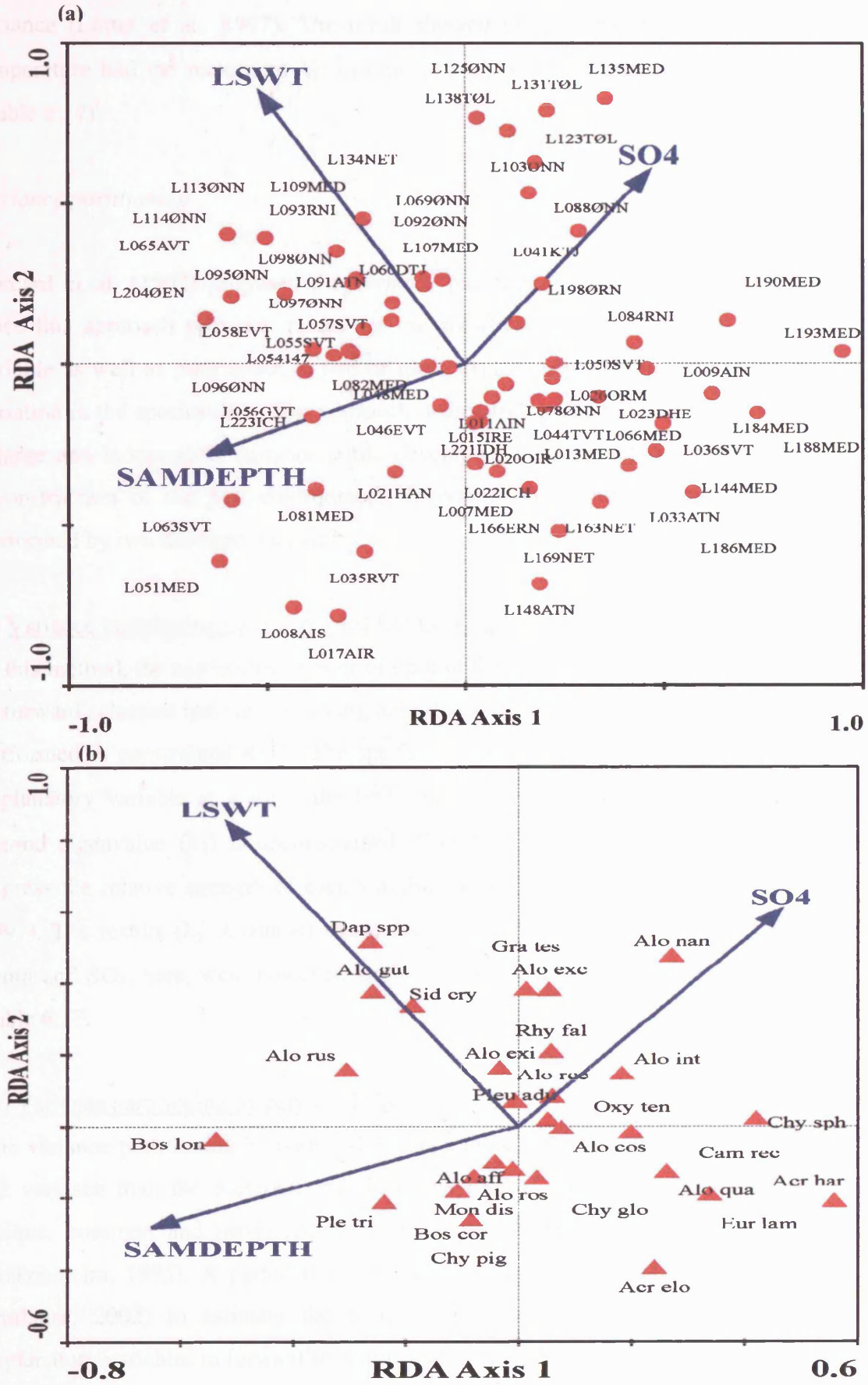


Figure 6.7: RDA biplot between axis 1 and axis 2 after forward selection. (a) samples v environment, (b) species v environment. Abbreviations for samples, environment and species data are presented in Appendix 2.1, Table 6.4 and Appendix 6.2 respectively.

variance (Lotter et al., 1997). The result showed that the mean lake surface water temperature had the maximum λ_1: λ_2-ratio as well as the highest variation explained (Table 6.17).

Variance partitioning

Borcard et al. (1992) proposed the variance partitioning approach in palaeoecology since this approach provides values for the significant strength of each explanatory variable as well as joint effect of two or more explanatory variables in explaining the variation in the species data. This approach is therefore particularly useful in extracting a large and independent variance while developing a robust inference model for the reconstruction of the past environment. In ordination, variance partitioning can be performed by two different methods.

(i) Variance partitioning by constrained RDAs of significant variables

In this method, the explanatory power of each of the 3 environmental variables selected in forward selection individually (marginal effects) for each biological data set has been performed in constrained RDA. The species composition was constrained to only one explanatory variable at a time; the first eigenvalue (λ_1) is constrained, whereas the second eigenvalue (λ_2) is unconstrained. Therefore, the λ_1: λ_2-ratio can be used to express the relative strength of each variable in explaining the variance (Lotter et al., 1997). The results (λ_1: λ_2-ratios) shown by three variables, summer LSWT, sampling depth and SO_4, here, were however, similar to the results shown by these variables in Table 6.17.

(ii) Variance partitioning by partial RDAs

The variance partitioning by partial RDAs is a more powerful approach to decompose the variance than the previous one since this method can be useful to estimate the unique, common and partial common variances, in the species data (Qinghong & Bråkenhielm, 1995). A partial RDA was employed in CANOCO 4.5 (ter Braak and Šmilauer, 2002) to estimate the total variation explained by the three selected explanatory variables in forward selection, and to separate the pure climatic effects from the others. The procedure was carried out in two steps (Table 6.18): (a) running RDA without co-variables; and (b) running partial RDAs using one of the three explanatory variables as the 'main variable' and the other two remaining variables as 'co-variables'.

Table 6.17: Percentage variance explained by each environmental variable when RDA is constrained with a single explanatory variable and tested under Monte Carlo permutation tests involving 999 unrestricted random permutations. The variable with the highest variance and λ_1/λ_2 is highlighted. P-values are given as, ***p<0.001, **p<0.01, *p<0.05.

Environmental variables	(λ_1)	(λ_2)	λ_1/λ_2	**P-value**	**Variance explained (%)**
pH	0.023	0.271	0.08	0.125	2.3
Alkalinity (μeql^{-1})	0.013	0.273	0.05	0.541	1.3
Conductivity (μScm^{-1})	0.049	0.238	0.21	0.003	4.9**
Na (μeql^{-1})	0.053	0.232	0.23	0.001	5.3***
NH_4 (μeql^{-1})	0.013	0.275	0.05	0.533	1.3
K (μeql^{-1})	0.032	0.275	0.12	0.030	3.2*
Mg ((μeql^{-1})	0.055	0.231	0.24	0.001	5.5***
Ca (μeql^{-1})	0.038	0.266	0.14	0.014	3.8*
Cl (μeql^{-1})	0.055	0.229	0.24	0.001	5.5***
NO_3 (μeql^{-1})	0.016	0.271	0.06	0.364	1.6
SO_4 (μeql^{-1})	0.051	0.242	0.21	0.003	5.1**
Al-NL (μgl^{-1})	0.046	0.264	0.17	0.005	4.6**
Al-L (μgl^{-1})	0.023	0.275	0.08	0.123	2.3
Abs-250	0.04	0.266	0.15	0.01	4.0**
TOC (mgl^{-1})	0.051	0.266	0.19	0.003	5.1**
SAMDEPTH (m)	0.055	0.238	0.23	0.03	5.5**
JulT (^{0}C)	0.049	0.274	0.18	0.002	4.9**
JanT (^{0}C)	0.042	0.273	0.16	0.011	4.2**
Summer LSWT (^{0}C)	**0.08**	**0.274**	**0.29**	**0.001**	**8.0*** **
PPT (mm)	0.047	0.261	0.18	0.005	4.7*
LOI (%)	0.039	0.275	0.14	0.015	3.9*

By this way, all variables and combinations of variables were performed at least once as 'main' and 'co-variables'. In total, the RDA was run for 12 times for the three combinations of the explanatory variables (Table 6.18).

Table 6.18: Variance partitioning by Partial-RDA of Cladocera. LSWT and SAMDEPTH represent the summer lake surface water temperature and sampling depth.

		FIRST RUN			
Environmental variables				**Co-variable**	**Total Eigenvalue**
LSWT + SO_4 + SAMDEPTH				None	0.186
		COMBINATION 1			
Run	**Environmental variable**	**Co-variable**	**Eigen-value**		
[1]	LSWT	SO_4 + SAMDEPTH	0.081		0.186
[2]	SO_4 + SAMDEPTH	None	0.105		
[3]	SO_4 + SAMDEPTH	LSWT	0.106		0.186
[4]	LSWT	None	0.080		
Joint effect: LSWT ⟷ SO_4+SAMDEPTH = 0.105 - 0.106 = 0.080 - 0.081 = - 0.001					
		COMBINATION 2			
Run	**Environmental variable**	**Co-variable**	**Eigen value**		
[1]	SO_4	LSWT + SAMDEPTH	0.055		0.187
[2]	LSWT + SAMDEPTH	None	0.132		
[3]	LSWT + SAMDEPTH	SO_4	0.135		0.186
[4]	SO_4	None	0.051		
Joint effect SO_4 ⟷ LSWT + SAMDEPTH = 0.132 – 0.135 = 0.051 – 0.055 = -0.003					
		COMBINATION 3			
Run	**Environmental variable**	**Co-variable**	**Eigen-value**		
[1]	SAMDEPTH	LSWT + SO_4	0.044		0.186
[2]	LSWT + SO_4	None	0.142		
[3]	LSWT + SO_4	SAMDEPTH	0.131		0.186
[4]	SAMDEPTH	None	0.055		
Joint effect: SAMDEPTH ⟷ LSWT + SO_4 = 0.142- 0.131 = 0.055 – 0.044 = 0.110					

The total explained variation was decomposed into seven parts: (a) pure LSWT (b) pure SO_4, (c) pure SAMDEPTH, (d) joint LSWT+SO_4, (e) joint LSWT+SAMDEPTH, (f)

joint SO_4 + SAMDEPTH and (g) joint LSWT+SO_4+SAMDEPTH (Figure 6.8). In the first run, the bulk variation of the species data explained by three explanatory variables was 18.6% (Table 6.18). In partial RDAs, the pure influence of mean lake surface water temperature, SO_4 and sampling depth were 8.1%, 5.5% and 4.4% respectively (Table 6.17, Figure 6.8). The joint influence or the common variation of all three explanatory variables (LSWT + SO_4 + SAMDEPTH) played the major role in explaining the total variance (9.2% of 0.186) in the species data (Figure 6.8 & 6.9). However, the joint influences or partial common variation of the explanatory gradient did not influence the species data (Figure 6.9). The effect of the summer LSWT was highest among the unique variation explained by the pure effect of three explanatory variables. The summer LSWT was also highly significant ($p<0.001$) in Monte Carlo permutation tests involving 999 permutation test for explaining the species data suggesting that the mean lake surface water temperature appears to be an important gradient in driving the assemblage structure of the fossil Cladocera in Scottish and Norwegian mountain lakes indicating its potential for developing an inference model.

The relative abundance of fossil Cladocera is shown against the mean summer lake surface-water temperature in the training set (Figure 6.10). In general, the low lake surface water temperatures (e.g. 7.5-9 ^{0}C) are related to sites situated in higher altitudes (e.g. L148ATN, L163NET) and latitudes (e.g. L186MED, L169NET, L188MED) of Norway. Interestingly some high latitude sites, for example, L184MED (71.02 ^{0}N) and L190MED (70.32 ^{0}N) in the Norwegian Arctic showed higher temperature values (>11 ^{0}C) than the sites of EMERGE Scotland (e.g. L017OIR, L022ICH, L008AIS) indicating that the variation in the abundance of Cladocera was not influenced by significant latitudinal variations in the data-set (Figure 6.10). However, the altitudinal variation, as it was hypothesised, was considered to be an important factor in regulating the surface water temperature gradient and the cladoceran community structure in the training set. The low altitude UKAWMN site of Scotland, Loch Coire Fionnaraich (LCFR), where the comprehensive study for contemporary and fossil Cladocera was carried out, is located at about midway between the lowest and the highest surface water temperature gradients and is comparable to the summer LSWT of most low altitude-latitude sites of Norway.

Two sites in Scotland and a large number of low altitude sites (<400m) in Norway have rather high summer LSWT values (≥13 ^{0}C), where the percentage abundance of

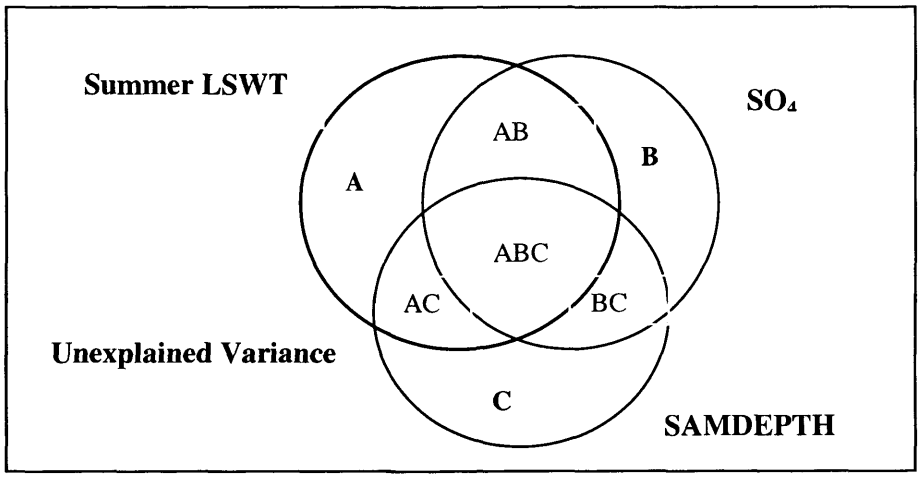


Figure 6.8: Variance partitioning of species data in RDA. In the diagram, A = Pure LSWT; B = Pure SO_4; C = Pure SAMDEPTH; and interactions are, AB = LSWT ΩSO_4; AC = LSWT ΩSAMDEPTH; BC = SO_4ΩSAMDEPTH; ABC = LSWT ΩSO_4ΩSAMDEPTH respectively. Abbreviations for environmental variables are presented in Table 6.4.

Equation A :

From the Table 6.15:

AB + AC + ABC = - 0.001

AB + BC + ABC = - 0.003

AC + BC + ABC = 0.11

Equation B

A + B + AB = 0.081 + 0.055 + AB = 0.142 - 0.110 = 0.032

B + C + BC = 0.055 + 0.044 + BC = 0.105 - (-0.001) = 0.106

A + C + AC = 0.081 + 0.044 + AC = 0.132 - (-0.003) = 0.135

By solving equation A&B

AB = 0.032 - 0.081 - 0.055 = 0.032 - 0.136 = -0.104

BC = 0.106 – 0.055 - 0.044 = 0.106 – 0.099 = 0.007

AC = 0.135 – 0.081 – 0.044 = 0.135 - 0.125 = 0.010

and

ABC = -0.001 – (-0.104) – (0.010) = -0.001+ 0.104 - 0.010 = 0.104-0.011 = 0.092

ABC = -0.003 – (-0.104) – (0.007)= -0.003 + 0.104 – 0.007 = 0.104 - 0.010 = 0.092

ABC = 0.11 – 0.011– 0.007 = 0.110 – 0.018 = 0.092

Unique variation = A + B + C = 0.081 + 0.055 + 0.044 = 0.180

Common variation = ABC = 0.092

Total explained variance = (0.092) + (-0.104 + 0.007 + 0.010) + (0.081 + 0.055 + 0.044) = 0.186

Partial common variation = AB + BC + AC = -0.104 + 0.007 + 0.010 = -0.104 + 0.017 = -0.087 (non-existent)

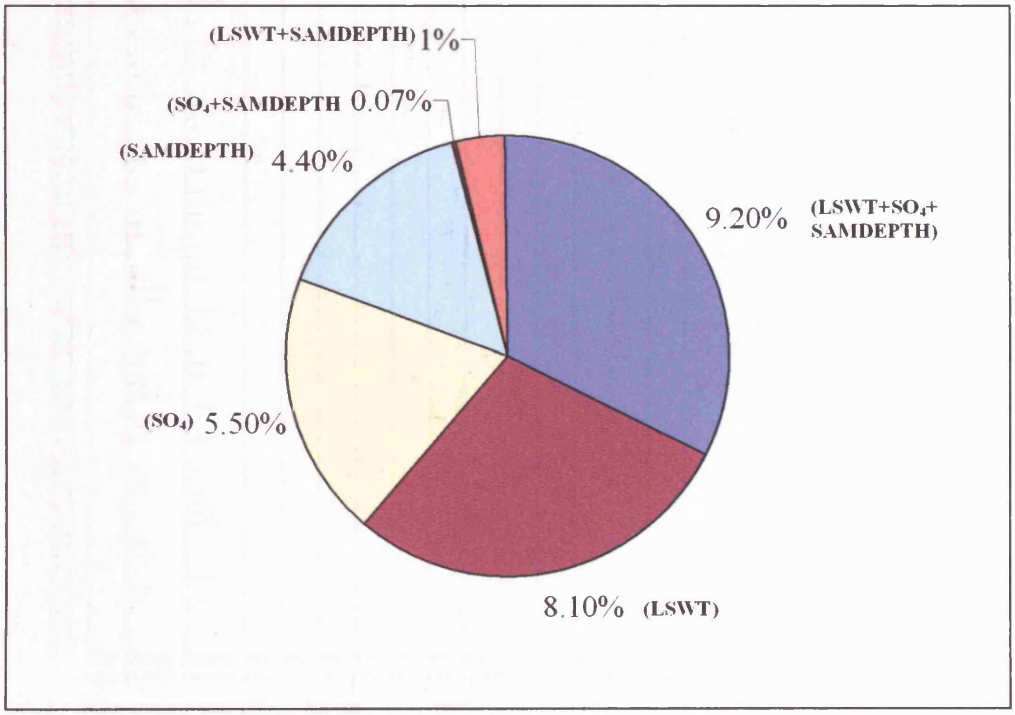


Figure 6.9: The sources of variation for the Cladocera. Total variation explained by three environmental variables is 18.6% (eigenvalue 0.186) for Cladocera.

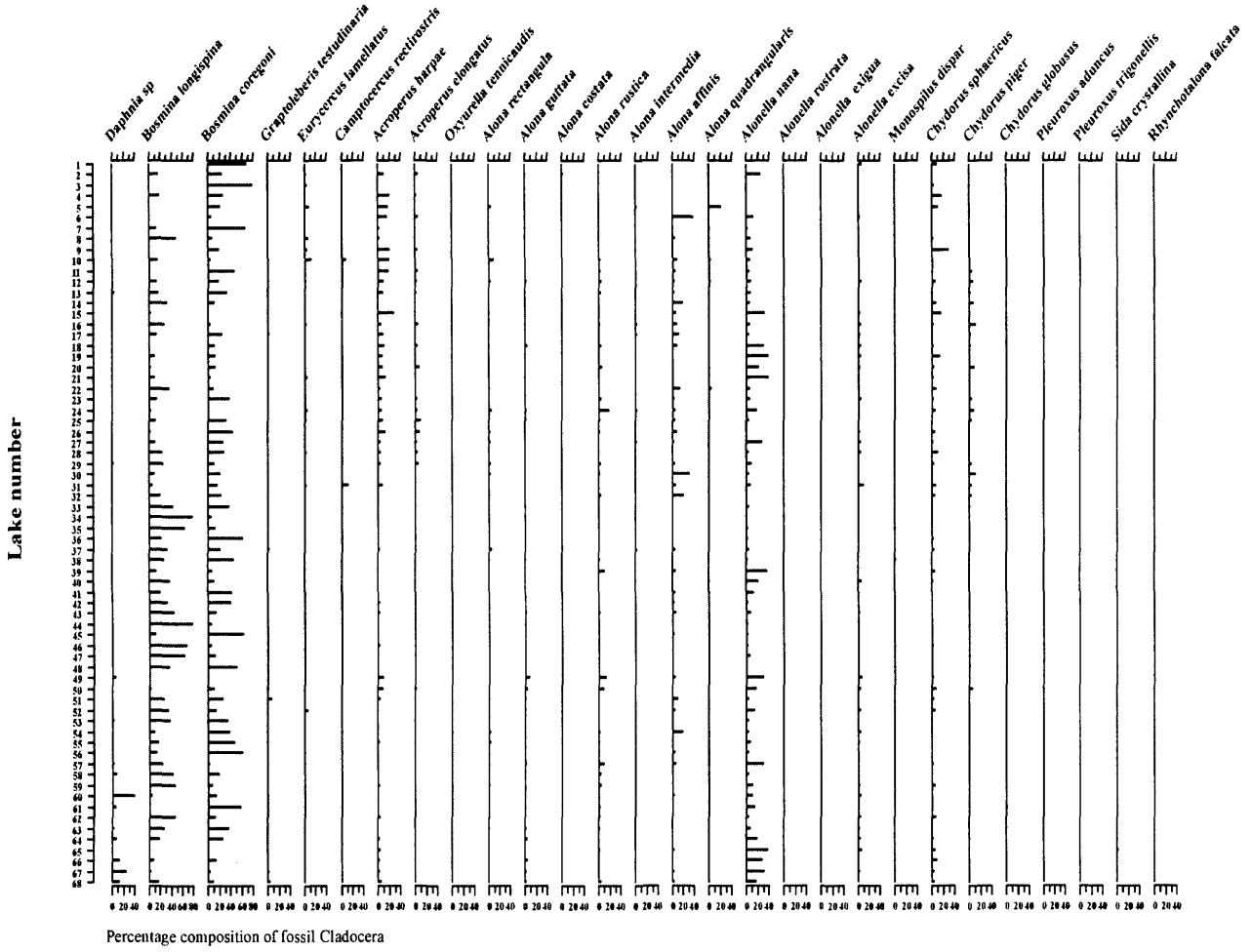


Figure 6.10: Composition (%) of Cladocera along summer LSWT gradients. Lakes arranged from the lowest temperature (top) and the highest temperature (bottom) are given in brackets: (1) L148ATN (7.50 ^{0}C) (2) L186MED (7.5 ^{0}C), (3) L163NET (8.5 ^{0}C), (4) L169NET (9 ^{0}C), (5) L188MED (9 ^{0}C), (6) L144MED (9.2 ^{0}C), (7) L033ATN (9.5 ^{0}C), (8) L166ERN (9.8 ^{0}C), (9) L193MED (9.8 ^{0}C), (10) L036SVT (10 ^{0}C), (11) L017AIR (10 ^{0}C), (12) L022ICH (10.8 ^{0}C), (13) L008AIS (10.99 ^{0}C), (14) L035RVT (11 ^{0}C), (15) L184MED (11 ^{0}C), (16) L007MED (11.2 ^{0}C), (17) L023DHE (11.2 ^{0}C), (18) L013MED (11.5 ^{0}C), (19) L044TVT (11.5 ^{0}C), (20) L009AIN (11.64 ^{0}C), (21) L190MED (11.8 ^{0}C), (22) L066MED (12 ^{0}C), (23) L020OIR (12.2 ^{0}C), (24) L015IRE (12.3 ^{0}C), (25) L021HAN (12.3 ^{0}C), (26) L026ORM (12.3 ^{0}C), (27) L011AIN (12.4 ^{0}C), (28) L084RNI (12.6 ^{0}C), (29) L221IDH (12.88 ^{0}C), (30) L046EVT (13 ^{0}C), (31) L050SVT (13 ^{0}C), (32) L051MED (13 ^{0}C), (33) L078ØNN (13.1 ^{0}C), (34) L081MED (13.2 ^{0}C), (35) L063SVT (14 ^{0}C), (36) L082MED (14.3 ^{0}C), (37) L048MED 14.5 ^{0}C), (38) L223ICH (14.75 ^{0}C), (39) L041KTJ (15 ^{0}C), (40) L198ØRN (15 ^{0}C), (41) L055SVT (15.5 ^{0}C), (42) L057SVT (15.5 ^{0}C), (43) L054147 (16 ^{0}C), (44) L056GVT (16 ^{0}C), (45) L096ØNN (16 ^{0}C), (46) L097ØNN (16 ^{0}C), (47) L069ØNN (16.4 ^{0}C), (48) L058EVT (16.5 ^{0}C), (49) L060DTJ (16.5 ^{0}C), (50) L088ØNN (16.5 ^{0}C), (51) L091ATN (16.7 ^{0}C), (52) L098ØNN (17 ^{0}C), (53) L107MED (17 ^{0}C), (54) L092ØNN (17.3 ^{0}C), (55) L093RNI (17.7 ^{0}C), (56) L103ØNN (18 ^{0}C), (57) L109MED (18 ^{0}C), (58) L095ØNN (18.3 ^{0}C), (59) L065AVT (18.6 ^{0}C), (60) L113ØNN (19 ^{0}C), (61) L123TØL (19 ^{0}C), (62) L204ØEN (19 ^{0}C), (63) L114ØNN (20 ^{0}C), (64) L134NET (20 ^{0}C), (65) L135MED (20 ^{0}C), (66) L125ØNN (20.5 ^{0}C), (67) L131TØL (20.5 ^{0}C), (68) L138TØL (20.5 ^{0}C). Key to lake abbreviations is given in Appendix 2.1.

chydorid taxa, *Alonella nana, Alonella excisa* and *Chydorus sphaericus* was also relatively high (Figure 6.10). However, two planktonic taxa, *Bosmina longispina* and *Bosmina coregoni* are widely distributed along the climatic gradients indicating their wider optima and tolerances to summer LSWT (Figure 6.10). The abundance of Cladocera in LCFR was dominated by two planktonic taxa, *B. longispina* and *B. coregoni* though the occurrence of Chydorids in this loch was also common (Figure 6.10). The increased abundance of littoral taxa such as *Acroperus harpae* and *Acroperus elongatus* are associated with low summer LSWT values (Figure 6.10). However, surprisingly, *A. harpae* did not show a significant response to summer LSWT in the HOF model, which will be discussed further in section 6.3.2.2.

Detrended canonical correspondence analysis (DCCA)

DCCA axes represent the response (gradient length) in standard deviation unit of the biological variables, in this case cladoceran assemblages, to environmental variables (ter Braak & Juggins, 1993; Lotter et al., 1997; Korhola, 1999). The DCCA was performed on summer LSWT with detrending-by-segments, non-linear rescaling, square-root transformed percentage data, rare taxa down-weighted, in which the eigenvalues and the length of gradient for the first constrained axis were 0.046 (λ_1) and 0.762 SD, and the eigenvalues and the gradient length of the second unconstrained axis were 0.059 (λ_2) and 1.372 SD respectively. The percentage variances explained by constrained (λ_1) and unconstrained ordination (λ_2) axes were 8.3% and 10.6% and their ratio (λ_1/λ_2) was 0.88 respectively. The eigenvalues, gradient lengths and variance explained by constrained ordination were somewhat smaller than the eigenvalues, gradient lengths and variance explained by unconstrained ordination, suggesting that there were large secondary gradients in the cladoceran species data, unrelated to mean lake surface water temperature (e.g. Korhola, 1999).

6.3.2. Niche species response (maximum likelihood) analysis

Niche species response analysis consists of determining the functional form of population response to parameters of interest through application of appropriate statistical techniques to field measurements (Stoermer and Ladewski, 1976). The major advantage of this approach is that it relates directly to the natural range of values, of both environmental and species parameters, occurring in the system studied. The major

environmental requirements are roughly the same for most species of Cladocera (Korhola and Rautio, 2001). Some species, however, show distinct variations with respect to ecological optima and tolerances (Harmsworth, 1968; Yurista, 1999; Hofmann, 2000). In order to define such optimal response of a cladoceran zooplankton taxon to a particular environmental variable, a taxon response analysis in a Huisman-Olff-Fresco (HOF) model was employed (e.g. Huisman et al., 1993). The HOF models are fitted using maximum likelihood with a Poisson error structure and a logarithmic link function and are restricted to all taxa with occurrences in 20% or more of the samples in the available species in the training sets.

6.3.2.1. Huisman-Olff-Fresco (HOF) models

The symmetric Gaussian response function is a widely used species response model in ecology, where the parameters can be estimated effectively. However, ecologists still have inadequate knowledge to test the significance of skewness of the species response. Huisman et al. (1993) proposed a set of hierarchical taxon response models (HOF models) which can describe the patterns of the occurrence and abundance of a species more accurately and unlike other regression models. In HOF the skewed response can also be statistically tested against a symmetric response (e.g. Oksanen and Minchin, 2002).

In HOF, a series of hierarchical taxon response models were proposed, in which the simplest statistically significant model was fitted by the most complex model first and progressively removing the parameters from the regression models and fitted by the other less complex and less significant models (Huisman et al., 1993). Initially, HOF fits the most complex skewed unimodal response model (model V) followed by dropping out the parameter to fit a symmetric unimodal response model (model IV). Further HOF dropped out the parameter to fit the monotonic sigmoidal increasing or decreasing model (model II) and finally, it fits the non-significant flat model (null model).

It was considered that the HOF models would be the best mathematical models to test the niche species response of Cladocera to the environmental parameters in the training set. The program HOF was then implemented to run the analysis (Oksanen and Minchin, 2002). However, before running the HOF, the species and environmental data

were stored in Excel and converted into normal CEP formats using the program Wintran (Juggins unpublished program). While running, the program asked the names of vegetation (in this case the cladoceran species) data and environmental data files, the number of the one and only environmental variable used, the minimum frequency of species analysed (in this case 10 cladoceran species), and the value of greatest theoretical value M (i.e. 100) (e.g. Huisman et al., 1993; Oksanen and Minchin, 2002). The summary screen after running HOF showed the parameter estimates, fit statistics, and significance of the removed term by the name of the file (e.g. HOFLOG.TXT). Observations against the scaled gradient, and the latest fitted significant curve were plotted in the graph. The model is simplified as long as the removed parameters are insignificant at $P < 0.05$. Estimation is stopped when first significant term is found. Thus the graph will show the curve from the largest significant model.

The number of taxa with statistical fits to the four types of response models is given in Table 6.18. From a total of 22 dominant taxa, only 8 taxa showed a significant response to mean summer LSWT, in which 5 taxa showed statistically significant increasing or decreasing sigmoidal monotonic response model (Model II), 2 taxa showed a symmetric unimodal response model (Model IV) and 1 taxon showed a skewed unimodal response model respectively (Table 6.19). Similarly, in a total of 8 significant taxa, 6 taxa showed significant increasing or decreasing sigmoidal monotonic response model (Model II) and only 2 taxa showed a significant symmetric unimodal response model to mean July air temperature (Table 6.18). With mean January air temperature, in a total of 9 significant curves, 6 taxa showed significant sigmoidal monotonic increasing or decreasing response (Model II) and 3 taxa showed significant unimodal response model (Table 6.18). However, only 3 taxa had a significant sigmoidal increasing or decreasing response and 2 taxa had a significant symmetric unimodal response to precipitation (Table 6.19). With SO_4, only 7 taxa showed a significant decreasing and increasing sigmoidal response model and 1 taxon showed a significant symmetric unimodal response model (Table 6.19). Only 1 taxon showed a significant sigmoidal decreasing response model and 2 taxa had significant symmetric unimodal response models to sampling depth (Table 6.19). With TOC, 1 taxon showed a symmetric unimodal and two taxa showed a significant sigmoidal decreasing and 1 taxon showed a significant sigmoidal increasing response models (Table 6.19). Among 8 significant response curves, 6 taxa showed a significant decreasing and increasing sigmoidal response

Table 6.19: Taxon-specific response to individual environmental parameters for the 22 cladoceran zooplankton taxa in Huisman-Olff-Fresco-HOF models. Abbreviations are presented in Table 6.4.

Variables	Skewed Unimodal (V)	Symmetric Unimodal (IV)	Sigmoidal Decreasing (II)	Sigmoidal Increasing (II)	Null Model (I)
pH	-	3	1	2	18
Alkalinity (μeql^{-1})	-	1	-	-	19
Conductivity (μScm^{-1})	1	1	-	1	17
Na (μeql^{-1})	-	1	-	1	19
NH4 (μeql^{-1})	-	-	-	-	22
K (μeql^{-1})	-	1	1	1	19
Mg (μeql^{-1})	-	2	-	1	17
Ca (μeql^{-1})	-	1	2	2	17
Cl (μeql^{-1})	-	1	-	1	18
NO3 (μeql^{-1})	-	-	-	-	-
SO4 (μeql^{-1})	-	1	3	4	10
A l-NL (μgl^{-1})	1	1	2	-	14
Al-L (μgl^{-1})	-	-	-	1	19
Abs –250	1	1	2	-	16
TOC (mgl^{-1})	-	2	2	1	16
SAMDEPTH (m)	-	2	1	-	14
JulT (^0C)	-	2	3	3	10
JanT (^0C)	1	2	3	3	11
LSWT (^0C)	1	2	2	3	14
PPT (mm)	-	2	2	1	9
LOI (%)	1	1	2	4	14

model, 1 taxon showed a significant symmetric response model, and 1 taxon showed a significant skewed unimodal response model to LOI (Table 6.19).

6.3.2.2. Weighted averaging optima and tolerances for Cladocera and their response curves in HOF models

The WA estimated optima and tolerances of the cladoceran taxa for the major environmental variables, mean summer LSWT, mean July air temperature, SO_4, sampling depth, LOI, TOC and pH in the calibration set with at least 4 significant hierarchical response curves (model V, IV, and II decreasing or II increasing) in HOF models are presented in Tables (6.20-6.26) and discussed in following sections. Sampling depth was considered important due to its relationship to water level, which often determines the area of littoral vs planktonic habitats of Cladocera as well as fossil deposition (Frey, 1988). The WA optima and tolerances of Cladocera to mean January air temperature, precipitation, Ca, conductivity, Mg, Na, Cl, K, Abs-250, Al-NL, Al-L, alkalinity are presented in the Appendices 6.3-6.14. Out of 22 cladoceran taxa, 19 taxa showed a significant response to at least one or more of four (V, IV, II increasing, II decreasing) statistically significant HOF models and they are presented as graphs. The remaining 3 taxa, *Alona rectangula, Alonella excisa, Rhynchotalona falcata*, showed a null model and are not presented and discussed below.

Daphnia spp.

The estimated WA optima suggests that *Daphnia* has ecological preferences for relatively high summer LSWT and high SO_4 and abundant in sites with high LOI with optima of about 17 ^{0}C for summer LSWT, 45 μeql^{-1} for SO_4, 43 % for LOI respectively (Table 6.20, Table 6.22, Table 6.24). The taxon has a statistically significant response to summer LSWT, mean January air temperature, precipitation, LOI, SO_4, Ca and K respectively in the HOF models (Figure 6.11). The result suggests that the occurrence and abundance of *Daphnia* sp. were well modelled by mean winter air temperature and precipitation. It has been argued that *Daphnia longispina,* in particular, is found across a wide climatic gradient (Tartari et al., 1998, Korhola, 1999) with increased alkalinity in lakes with forested catchments (Megard, 1964; Fryer, 1993). *D. longsipina* is abundant particularly in marsh loving plants such as *Typha* (Megard, 1964). Nilssen and Sandøy (1990) reported that this taxon might not survive in acidified lakes though it has been reported in lakes with pH less than 5.8 (also see Cammarano and Manca, 1997).

Table 6.20: Estimated Weighted Averaging (WA) of summer mean lake surface water temperature (LSWT) optima (Opt. ^{0}C) and tolerance (Tol ^{0}C) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway. The number of occurrence, maximum abundance (%), effective number of occurrence (N_2) and taxon response to mean lake surface water temperature in HOF models are presented.

Species	N. Occur	Maximum	N2	Optima (^{0}C)	Tolerance ($\pm^0$C)	Model
Daphnia spp	43	6.73	26.15	16.73	3.54	II increasing
Bosmina longispina	63	9.34	52.38	14.62	3.17	IV
Bosmina coregoni	68	9.21	57.45	14.00	3.61	II decreasing
Graptoleberis testudinaria	43	3.04	33.56	15.36	3.54	I
Eurycercus lamellatus	61	3.50	46.70	13.29	3.46	I
Camptocercus rectirostris	29	3.50	19.46	13.51	3.59	I
Acroperus harpae	67	5.43	53.08	13.30	3.61	I
Acroperus elongatus	59	3.15	44.75	12.96	3.10	IV
Alona rectangula	55	3.01	47.54	14.22	3.57	I
Alona guttata	59	2.88	51.84	15.06	3.54	II increasing
Alona costata	26	1.66	22.48	13.87	3.58	I
Alona rustica	60	4.32	50.62	14.75	3.28	II increasing
Alona intermedia	49	2.06	43.44	14.16	3.57	I
Alona affinis	62	7.13	47.70	13.99	3.31	I
Alona quadrangularis	37	4.81	22.99	12.89	3.32	II decreasing
Alonella nana	67	7.45	54.22	14.61	3.69	I
Alona excisa	62	3.32	53.20	14.67	3.62	I
Monospilus dispar	14	1.78	12.18	13.47	1.86	V
Chydorus sphaericus	68	5.53	54.574	13.81	3.68	I
Chydorus piger	59	3.55	44.54	13.69	3.18	I
Pleuroxus aduncus	13	1.16	11.97	14.49	3.22	I
Sida crystallina	39	1.82	34.86	15.49	3.43	I
Rhynchotalona falcata	7	1.17	6.35	15.72	2.94	I

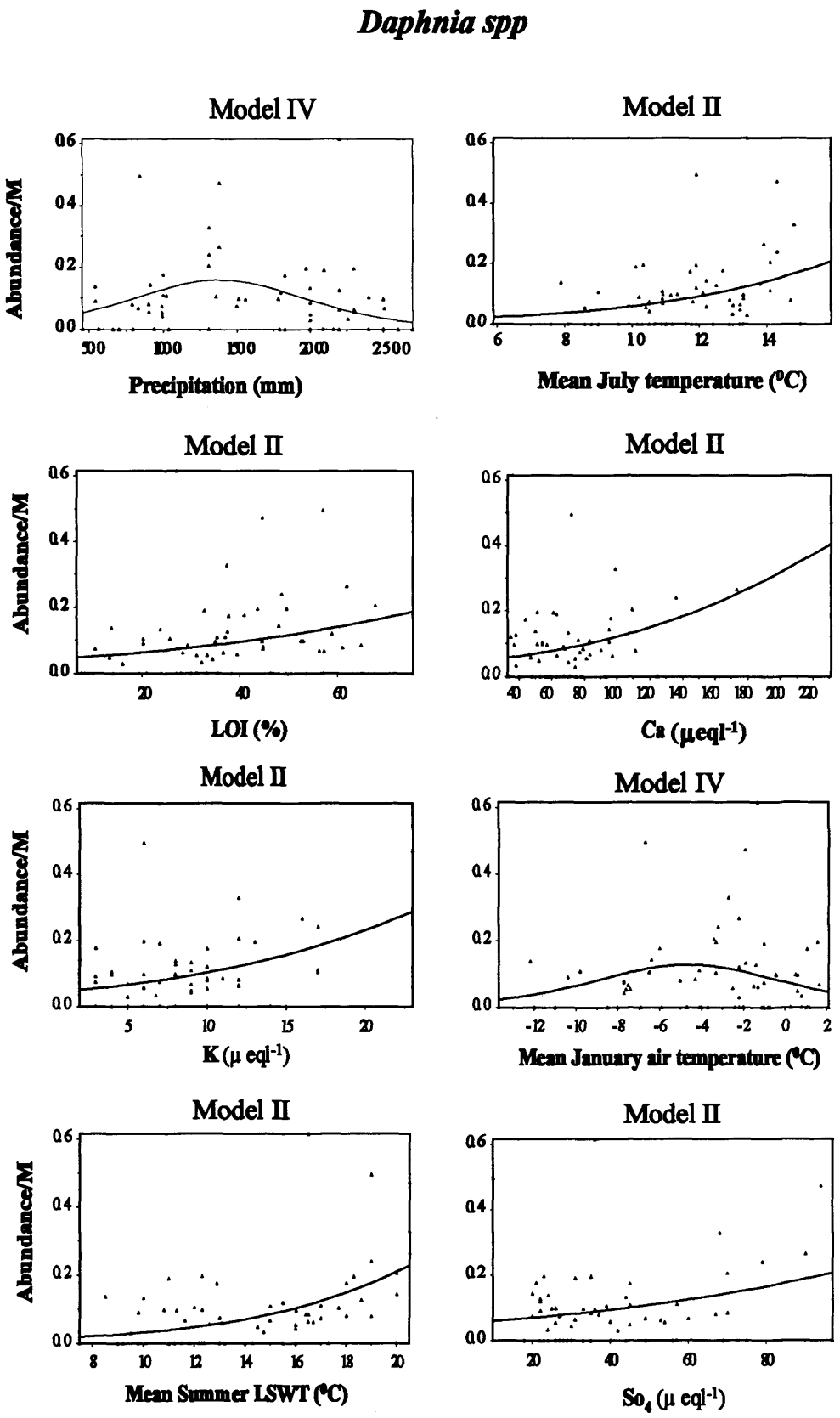


Figure 6.11: Relative abundances of *Daphnia* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

Because of its extensive use of deep water gradients, *D. longispina* is extensively reported in deeper lakes of Europe (Korhola, 2000).

Bosmina longispina

The WA optima for *Bosmina longispina* indicates that it has a preference for relatively high summer LSWT, low SO_4 and high TOC with optima of 15 ^{0}C for LSWT, 37 μeql^{-1} for SO_4 and 5 mgl^{-1} for TOC respectively (Table 6.20, Table 6.22, Table 6.23). The species showed a statistically significant response to summer LSWT, SO_4, TOC and conductivity in the HOF models (Figure 6.12). However, the occurrence and abundance of this taxon were best modelled by mean summer LSWT and conductivity (Figure 6.12). *B. longispina* is one of the most common taxa in the study sites. Flössner (1972) reported that the distribution of this taxon is restricted to boreal mountain regions of Europe. A recent study by Korhola (1992) suggested that *B. longispina* is also predominant in vegetation-filled wetlands of Europe. Hofmann (1978) reported that this taxon was common in late-glacial cladoceran communities suggesting its ability to withstand harsh climatic conditions. Its occurrence in sites with relatively high TOC in this study is in contrast to the study by Korhola (1999). He argued that this taxon is common in deep, large, cold and clear water sites with a low TOC. However, its response to low SO_4 and conductivity is in agreement with the studies of Boucherle and Züllig (1983). Hofmann (1986) and Fryer (1993) described *B. longispina* as an upland or high-altitude species favouring mostly acidic and ion-poor oligotrophic habitats. *B. longispina* is also one of the most common planktonic taxa in Loch Coire Fionnariach, Scotland, where the water temperature does not go below zero during winter and the temperature is rather high during summer compared to other high mountain lakes in the region (Chapter 4).

Bosmina coregoni

The WA optima and tolerances for *B. coregoni* indicate that this taxon has preferences for medium summer LSWT and July air temperature with moderate LOI and TOC respectively (Table 6.20, Table 6.21, Table 6.24, Table 6.25) in which the optima was 14 ^{0}C for summer LSWT, 12 ^{0}C for July air temperature, 36.5% for LOI and 4 mgl^{-1} for TOC. This taxon showed statistically significant responses to seven environmental variables: mean summer LSWT; mean July air temperature; LOI; TOC; Ca; Abs-250; and Al-NL in HOF models (Figure 6.13). *B. coregoni* was also one of the widely distributed taxa in Scottish and Norwegian training set sites. This taxon often co-

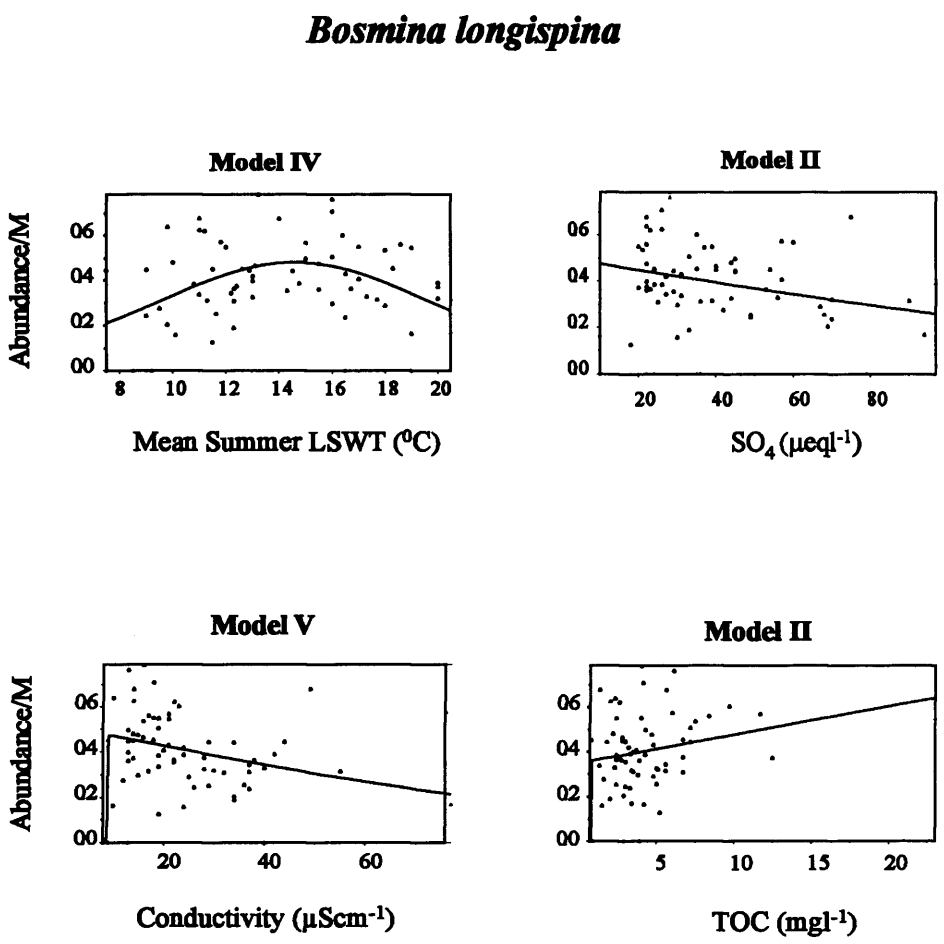


Figure 6.12: Relative abundances of *Bosmina longispina* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

Table 6.21: Estimated Weighted Averaging (WA) of mean July air temperature optima (Opt. ^{0}C) and tolerance (Tol ^{0}C) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway. The numbers of occurrences, maximum abundance (%), effective numbers of occurrences (N_2) are presented in Table 6.18. The taxon response curve to mean July air temperature in HOF models is also presented.

Species	Optima (^{0}C)	Tolerance ($\pm^0$C)	Model
Daphnia spp	12.52	1.69	I
Bosmina longispina	11.89	1.67	I
Bosmina coregoni	11.57	2.00	II decreasing
Graptoleberis testudinaria	12.56	1.67	II increasing
Eurycercus lamellatus	11.38	1.81	I
Camptocercus rectirostris	12.22	2.23	II increasing
Acroperus harpae	11.40	1.98	I
Acroperus elongatus	11.06	1.84	II decreasing
Alona rectangula	11.98	1.81	I
Alona guttata	12.18	1.73	I
Alona costata	11.66	1.94	I
Alona rustica	12.07	1.57	IV
Alona intermedia	11.73	1.79	I
Alona affinis	11.65	1.87	I
Alona quadrangularis	11.60	1.75	I
Alonella nana	11.73	2.10	I
Alona excisa	11.78	2.15	I
Monospilus dispar	11.38	1.68	I
Chydorus sphaericus	11.39	2.13	I
Chydorus piger	11.59	1.75	IV
Pleuroxus aduncus	11.25	2.01	II decreasing
Sida crystallina	12.32	1.70	I
Rhynchotalona falcata	12.77	1.71	I

Table 6.22: Estimated Weighted Averaging (WA) of SO_4 optima (Opt. μeql^{-1}) and tolerance (Tol μeql^{-1}) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway are presented in HOF models. The number of occurrence, maximum abundance (%) and effective number of occurrence (N_2) are presented in Table 6.18. Taxon response curve to SO_4 in HOF models is also presented.

Species	Optima (μeql^{-1})	Tolerance ($\pm\mu eql^{-1}$)	Model
Daphnia spp	45.11	26.33	II increasing
Bosmina longispina	36.70	16.71	II decreasing
Bosmina coregoni	38.27	17.95	I
Graptoleberis testudinaria	46.81	23.17	II increasing
Eurycercus lamellatus	38.93	18.34	I
Camptocercus rectirostris	43.17	19.34	I
Acroperus harpae	41.83	20.03	II increasing
Acroperus elongatus	37.52	16.62	II decreasing
Alona rectangula	40.27	20.52	I
Alona guttata	41.37	22.26	I
Alona costata	39.30	17.64	I
Alona rustica	39.01	20.12	I
Alona intermedia	40.28	21.38	I
Alona affinis	38.34	18.89	I
Alona quadrangularis	39.50	16.44	IV
Alonella nana	43.41	23.11	I
Alona excisa	41.43	21.58	I
Monospilus dispar	32.71	14.20	I
Chydorus sphaericus	42.07	20.82	II increasing
Chydorus piger	36.96	18.95	II decreasing
Pleuroxus aduncus	38.05	16.06	I
Sida crystallina	42.83	24.42	I
Rhynchotalona falcata	48.24	30.96	I

Table 6.23: Estimated Weighted Averaging (WA) sampling depth optima (Opt. m) and tolerance (Tol m) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway. The number of occurrence, maximum abundance (%), effective number of occurrence (N_2) are presented in Table 6.18. The taxon response curve to sampling depth in HOF models is also presented.

Species	Optima (m)	Tolerance (±m)	Model
Daphnia spp	9.84	5.40	I
Bosmina longispina	10.50	5.69	I
Bosmina coregoni	9.66	5.87	I
Graptoleberis testudinaria	9.50	4.60	I
Eurycercus lamellatus	8.33	6.07	I
Camptocercus rectirostris	8.57	4.30	IV
Acroperus harpae	8.70	6.25	I
Acroperus elongatus	9.08	6.49	I
Alona rectangula	9.02	5.54	I
Alona guttata	9.76	5.58	I
Alona costata	8.61	5.57	I
Alona rustica	9.87	5.82	I
Alona intermedia	8.08	5.50	II decreasing
Alona affinis	9.49	6.15	I
Alona quadrangularis	7.86	5.49	I
Alonella nana	8.38	5.47	I
Alona excisa	8.67	4.72	IV
Monospilus dispar	9.93	6.81	I
Chydorus sphaericus	8.70	5.65	II decreasing
Chydorus piger	9.95	6.21	I
Pleuroxus aduncus	8.19	4.31	I
Sida crystallina	9.86	5.24	I
Rhynchotalona falcata	7.46	4.57	I

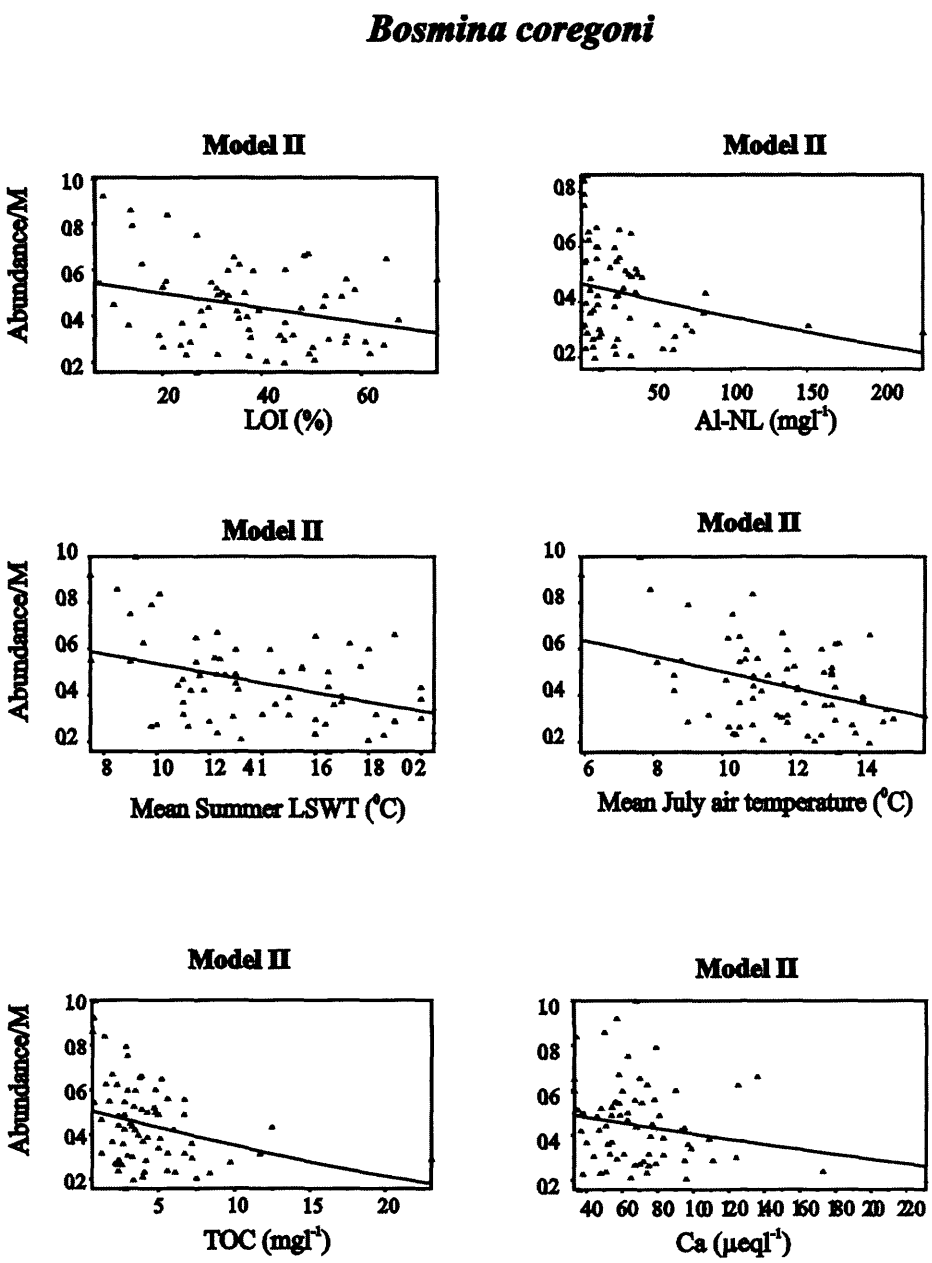


Figure 6.13: Relative abundances of *Bosmina coregoni* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

occurred with *B. longispina* suggesting that they have similar ecological preferences in the region. Fryer (1993) argued that this taxon should be *B. longisipina* though considerable debate is underway over the taxonomic and ecological differences between the two taxa. *B. coregoni* is abundant in upland lakes and prefers oligotrophic habitats. Megard (1964) reported that *B. coregoni* is common in most northern temperate lakes. However, its occurrence is not frequent in Greenland and Alaska. Hofmann (1996) argued that the abundance of *B. coregoni* might have been influenced by climatic amelioration during the Holocene. Røen (1981) found that *B. coregoni* was an important indicator for the trophic condition of lakes. The abundance of this taxon is found to be high in mesotrophic lakes (Røen, 1981). *B. coregoni* is also the most common cladoceran taxon in Loch Coire Fionnaraich, Scotland as revealed by the contemporary survey of the loch in Chapter 4.

Graptoleberis testudinaria

The WA optima for *G. testudinaria* indicate that it has ecological preferences for relatively high July air temperature and high SO_4 with optima of 13 ^{0}C for mean July air temperatures and 47 μeql^{-1} for SO_4 respectively (Table 6.21, Table 6.22). The taxon showed a significant response to eight environmental variables in HOF models: mean July air temperatures; mean January air temperatures; SO_4; precipitation; Cl; Mg; Na; and conductivity respectively (Figure 6.14). The occurrence and abundance of this taxon were best modelled (model IV) by five environmental variables, which were mean annual precipitation, Cl, Mg, Na and conductivity respectively (Figure 6.14). *G. testudinaria* was not a common species in the Scottish and Norwegian samples, and several studies suggest that *G. testudinaria* is rather a rare species of chydorid Cladocera (DeCosta, 1964; Megard, 1964; Whiteside et al., 1978). Its relative abundance in the training set sites with warmer-water is in agreement to the studies of Goulden (1964), Mezquita and Miracle (1997) and Korhola (1999). However, Harmsworth (1968) classified this taxon a 'north temperate' species. Megard (1967) also reports its abundance in moderately cold environments. Whiteside (1970) argued that this taxon prefers clear and soft water lakes in a vegetation-rich habitat in ponds and bogs. However, Brancelj et al. (1997) reported that this taxon could also colonise eutrophic lakes with shoreline vegetation. *G. testudinaria* does not prefer low pH, thus Krause-Dellin and Steinberg (1986) have described this taxon a 'circumneutral' species.

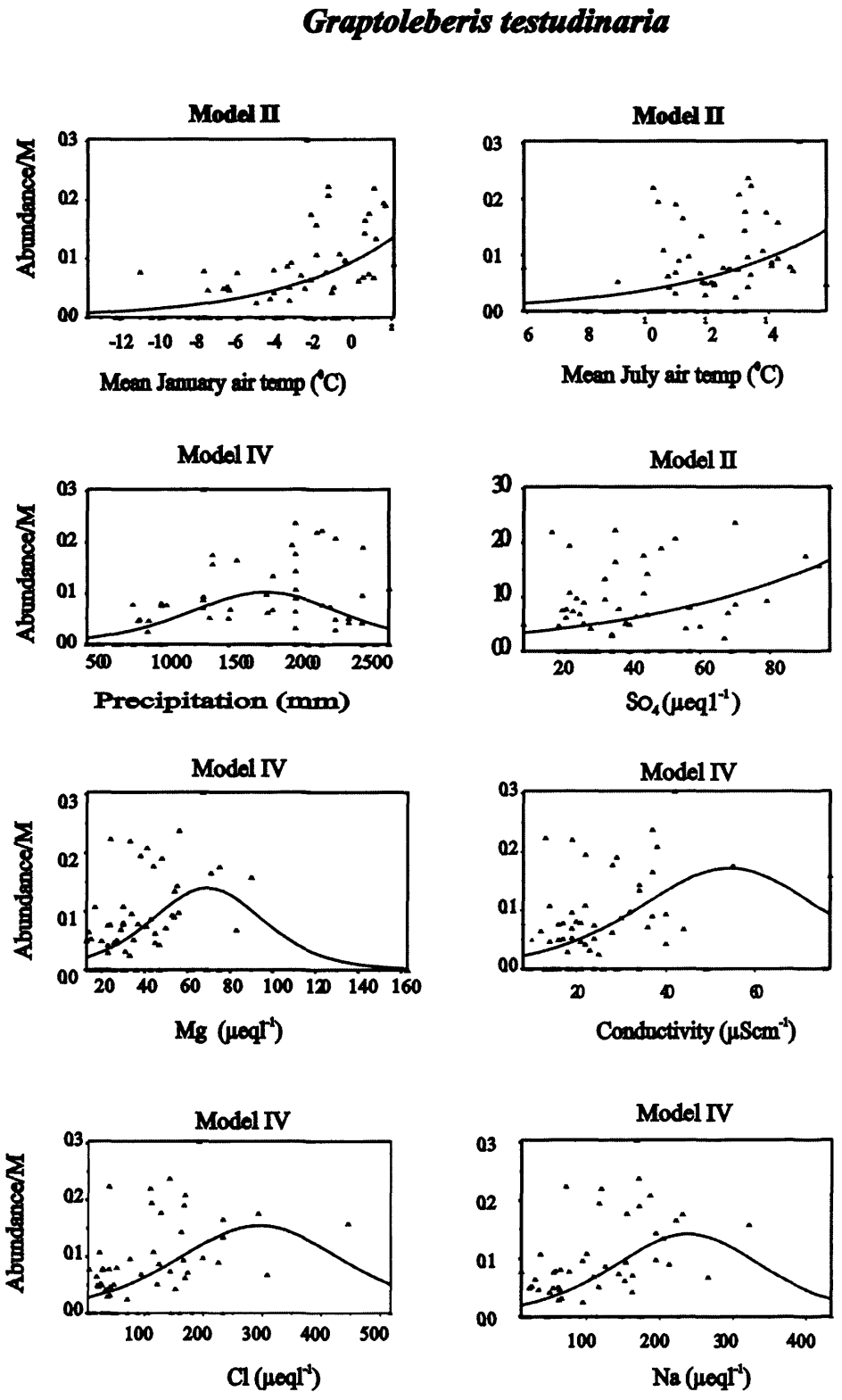


Figure 6.14: Relative abundances of *Graptoleberis testudinaria* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

Eurycercus lamellatus

The estimated WA optima for *E. lamellatus* suggest that this taxon has ecological preferences mainly for sites with moderate LOI and TOC with optima of 34.5 % for LOI and 4 mgl^{-1} for TOC respectively (Table 6.24, Table 6.25). This taxon showed significant responses to mean January air temperature, LOI, TOC and Al-NL (Figure 6.15). The unimodal response curves in HOF models suggest that the occurrence and abundance of this taxon were best modelled by LOI and TOC (Figure 6.15). *E. lamellatus* was relatively common in the training set especially in the sites with lower water temperature. The data indicate that this taxon in agreement with observation of Harmsworth (1968) and Korhola (1999). Harmsworth (1968) classified this taxon as a 'north temperate' species, while Korhola (1999) found it mostly in cold, deep and clear water lakes. Its intolerance to warm temperature is also reported by Megard (1964) and Frey (1975), and its preference for cold environments is further supported by its wide distribution in northern and central Europe, Arctic Alaska and the northern Mississippi River (Megard, 1967).

E. lamellatus is well distributed in ponds and bogs with a wide range of pH (Whiteside, 1970). Its response to acidity is, however, given as 'circumneutral' (Krause-Dellin and Steinberg, 1986). Sandøy and Nilssen (1986) recorded this taxon from lakes with relatively high conductivity. This taxon also prefers non-polluted, clear water lakes and is common in submerged macrophyte beds (Whiteside, 1970, Hofmann; 1978; Fryer, 1993). Duigan (1992) discovered that the abundance of this taxon is highest in *Chara* and muddy-vegetation substrates and is rarely found in water without any form of plant growth or detritus. Similarly, Carl (1940) and Korhola (1999) recorded this taxon as abundant in bottom-epiphytic substrates.

Camptocercus rectirostris

The estimated WA optima indicate that *C. rectirostris* has preferences for medium July air temperatures with respect to the range in the data-set and moderate sampling depth with the optima of 12 ^{0}C for July air temperature and 8.5 m for sampling depth respectively (Table 6.21, Table 6.23). This taxon showed a significant response to mean July air temperature, mean January air temperature, sampling depth, Abs-250, and Al-NL respectively in HOF models (Figure 6.16). The occurrence and abundance of this taxon were well modelled by sampling depth, Abs-250 and Al-NL respectively (Figure 6.16). *C. rectirostris* was one of the most infrequent chydorid taxa in the study region.

Table 6.24: Estimated Weighted Averaging (WA) of LOI optima (Opt. %) and tolerance (Tol %) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway. The number of occurrence, maximum abundance (%), effective number of occurrence (N_2) are presented in Table 6.18. The taxon response curve to LOI in HOF models is also presented.

Species	Optima (%)	Tolerance (±%)	Model
Daphnia spp	42.94	14.11	II increasing
Bosmina longispina	38.75	14.74	I
Bosmina coregoni	36.50	16.18	II decreasing
Graptoleberis testudinaria	41.50	15.79	I
Eurycercus lamellatus	34.54	14.24	V
Camptocercus rectirostris	32.34	14.63	I
Acroperus harpae	35.67	16.44	I
Acroperus elongatus	38.23	17.30	II increasing
Alona rectangula	38.98	15.85	I
Alona guttata	41.49	15.24	I
Alona costata	40.98	16.91	I
Alona rustica	40.32	14.43	II increasing
Alona intermedia	40.59	15.72	I
Alona affinis	36.58	16.36	II decreasing
Alona quadrangularis	36.17	13.67	I
Alonella nana	38.89	16.93	I
Alona excisa	39.91	16.74	I
Monospilus dispar	36.67	16.66	I
Chydorus sphaericus	35.37	16.40	I
Chydorus piger	38.57	15.41	I
Pleuroxus aduncus	32.30	11.57	IV
Sida crystallina	41.45	16.40	II increasing
Rhynchotalona falcata	45.73	17.99	I

Table 6.25: Estimated Weighted Averaging (WA) of TOC optima (Opt. mgl^{-1}) and tolerance (Tol mgl^{-1}) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway are presented in HOF models. The number of occurrence, maximum abundance (%) and effective number of occurrence (N_2) are presented in Table 6.18. Taxon response curve to TOC in HOF model is also presented.

Species	Optima (mgl^{-1})	Tolerance ($\pm mgl^{-1}$)	Model
Daphnia spp	4.84	3.31	I
Bosmina longispina	5.06	3.80	V
Bosmina coregoni	4.16	3.14	II decreasing
Graptoleberis testudinaria	4.79	3.58	I
Eurycercus lamellatus	3.70	1.92	IV
Camptocercus rectirostris	4.22	2.58	I
Acroperus harpae	3.96	3.29	I
Acroperus elongatus	3.88	2.87	I
Alona rectangula	4.28	3.03	I
Alona guttata	4.67	3.22	IV
Alona costata	4.96	4.96	I
Alona rustica	4.63	3.40	I
Alona intermedia	4.64	3.73	I
Alona affinis	4.01	2.91	I
Alona quadrangularis	3.51	1.89	II decreasing
Alonella nana	4.40	3.16	I
Alona excisa	4.65	3.81	I
Monospilus dispar	3.72	1.70	I
Chydorus sphaericus	4.20	3.59	I
Chydorus piger	3.98	2.74	I
Pleuroxus aduncus	4.56	2.91	I
Sida crystallina	4.66	2.33	I
Rhynchotalona falcata	4.53	1.57	I

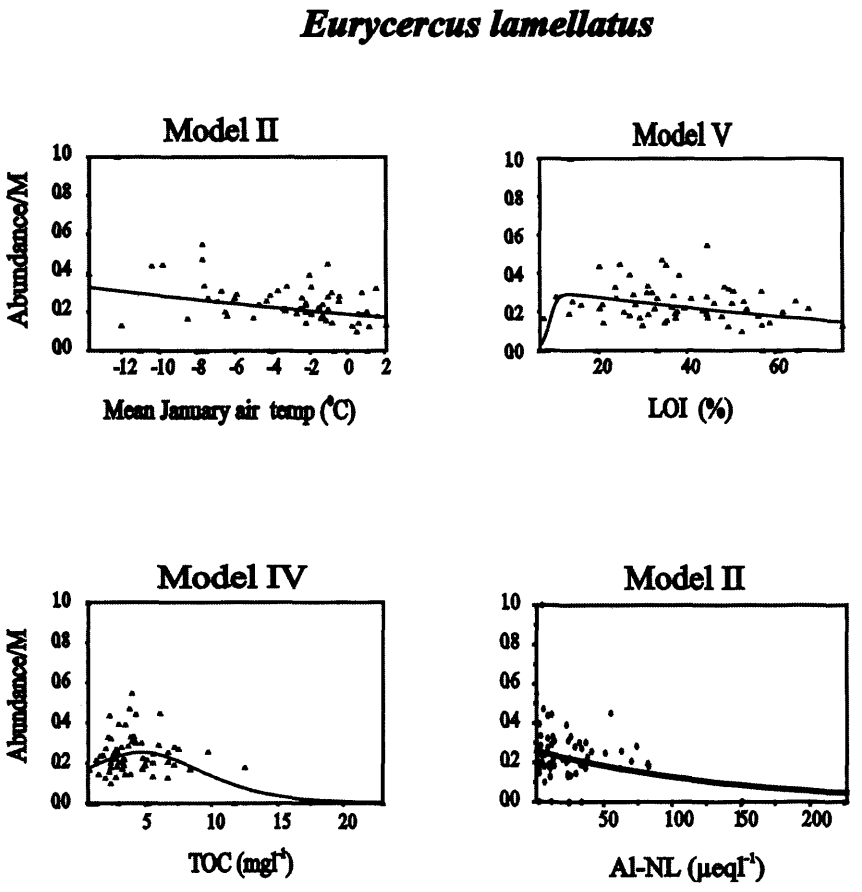


Figure 6.15: Relative abundances of *Eurycercus lamellatus* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

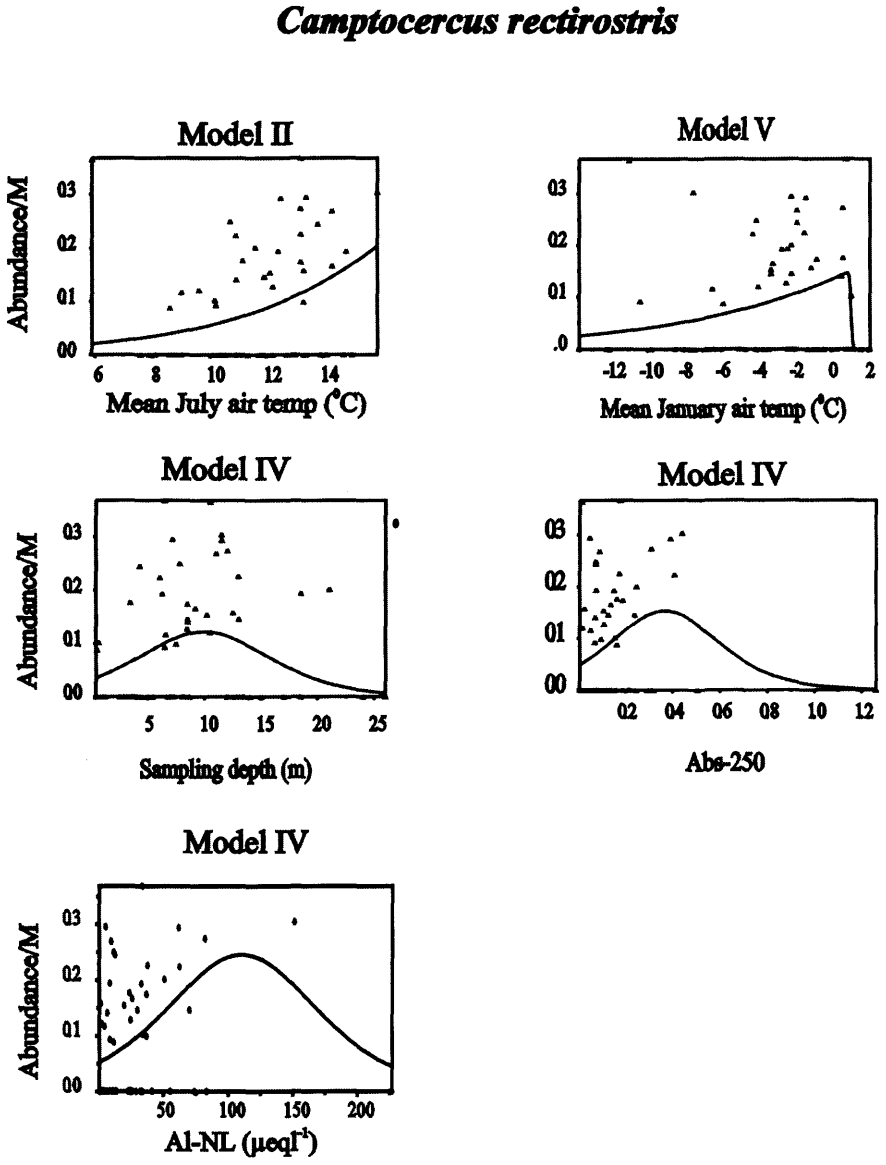


Figure 6.16: Relative abundances of *Camptocercus rectirostris* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

Simirnov (1998) reported that *C. rectirostris* is a rare taxon in Europe though it has a wider geographic distribution. Megard (1967) also reported that this taxon does not occur south of the Alps. Its preferences to medium July and January air temperatures with respect to the range in the data-set are supported by the observation of Harmsworth (1968), where this taxon was classified as a 'south temperate' species. It has a high frequency of occurrence in Europe but absent in Arctic (Harmsworth, 1968).

In terms of the response to the water-chemistry, Whiteside (1970) argued that *C. rectirostris* occurs in non-polluted lakes of low productivity with low pH. Krause-Dellin and Steinberg (1986) classified this taxon, as 'alkaliphilous' in which its abundance was highest when the pH was more than 7. Fryer (1993) reported that *C. rectirostris* is common in lowland Yorkshire in the United Kingdom preferably associated with habitats characterised by sand, gravel, grit, rocks, clay or soft mud. However, many authors have reported that this taxon also prefers wide range of vegetation habitats (Fryer, 1974; Hofmann, 1978; Whiteside et al., 1978; Synerholm, 1979; Korhola, 1999).

Acroperus harpae

The estimated WA optima suggest that *A. harpae* prefers relatively high SO_4 with optima of 42 μeql^{-1} (Table 6.22). This taxon showed a significant sigmoidal monotonic increasing response to SO_4 and Al-L in HOF models (Figure 6.17). This taxon was one of the most abundant chydorid taxa in the study sites. However, surprisingly, it did not have a significant relationship with any climatic parameters in the HOF models. Particularly, the distribution pattern of *A. harpae* along the altitudinal gradient in Figure 6.10 indicates that this taxon should show a significant relationship to summer lake surface water temperature (LSWT) in the HOF model. However, the result suggests that this taxon occurs across a significantly wider variation in temperature than expected. In this study, the temperature variation between the highest and the lowest values is 12 ^{0}C, where the lowest temperature (7.5 ^{0}C) is significantly higher than the average Arctic temperature during the Holocene (3 ^{0}C) (e.g. Moore et al., 1997). Harmswoth (1968) reported that *A. harpae* is most common in Arctic and sub-Arctic environments and classified this taxon as an 'Arctic' species. Hofmann (1978, 1987) also reported that *A. harpae* as a pioneer species of most clear water lakes of Arctic and sub-Arctic Europe. Hofmann (2000) discovered that the abundance of *A. harpae* was also predominant during the Younger Dryas, a cold climatic phase prior to the Holocene. Many other authors also found that an increased abundance of this taxon associated with cold

Acroperus harpae

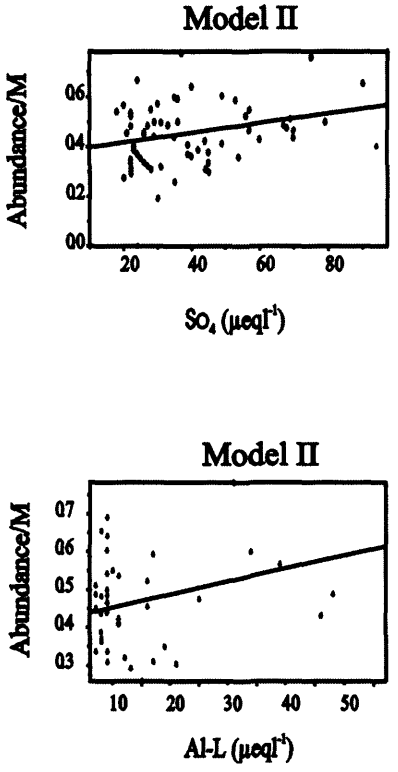


Figure 6.17: Relative abundances of *Acroperus harpae* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

climatic conditions. For example, Megard (1967) recorded it in Greenland more frequently than at low latitude sites. Rautio (1998) found it mostly in high altitude lakes of Finland. Similarly, Tartari et al. (1998) recorded this taxon from the very high altitude sites of the Himalayas. All earlier findings indicate that the training set sites available for this study were not suitable for *A. harpae*, as most of these sites have higher water temperature gradients.

The only significant relationship for *A. harpae* in the data-set were for SO_4 and labile aluminum (Figure 6.17). The reason for this are unclear although Whiteside (1970) and Fryer (1974) reported that *A. harpae* is commonly found in ponds, bogs and low productive lakes of the British Isles and Europe, in which atmospheric deposition of marine salts occur.

Acroperus elongatus

The estimated WA optima indicating that it has an ecological preference for medium summer LSWT with respect to the range in the data-set, medium LOI and pH with optima of 13 ^{0}C, 38 % and 6 respectively (Table 6.20, Table 6.24, Table 6.26). The taxon had a significant response to summer LSWT, January air temperature, LOI and pH in HOF models. However the occurrence and abundance of this taxon were well modelled by only one variable, mean summer LSWT (Figure 6.18). *A. elongatus* was also one of the most widely distributed species in the training set sites but its abundance was not as high as *A. harpae*. This taxon was found mainly in lower water temperature sites. This is also indicated by the significantly high abundance of this taxon in Loch Coire Fionnaraich, Scotland (Chapter 4). Fryer (1993) reported that *A. elongatus* is a pioneer species of northern and western Europe since it is a cold-water species in arctic and alpine regions. It has been argued that its distribution is determined largely by climate, mainly low summer temperature. As the ice retreated, at the end of the glacial period, its distribution would follow northwards. It probably became extinct in southern and eastern Britain as the climate became warmer in the early Holocene persisting only where summer temperature remained low (Fryer, 1993).

Surprisingly, the abundance of this taxon was not significantly related to any other measured environmental variables in the Scottish and Norwegian mountain lakes training set. It is commonly found in non-polluted, fairly oligotrophic and dystrophic lakes, ponds and bogs (Whiteside, 1970) characteristic of acidic, rocky and sandy shores

Table 6.26: Estimated Weighted Averaging (WA) of pH optima (Opt.) and tolerance (Tol) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway. The number of occurrence, maximum abundance (%), effective number of occurrence (N_2) are presented in Table 6.18. The taxon response curve to pH in HOF models is also presented.

Species	Optima	Tolerance	Model
Daphnia spp	6.16	0.25	I
Bosmina longispina	6.12	0.26	I
Bosmina coregoni	6.13	0.26	I
Graptoleberis testudinaria	6.18	0.24	I
Eurycercus lamellatus	6.12	0.32	I
Camptocercus rectirostris	6.14	0.24	I
Acroperus harpae	6.13	0.32	I
Acroperus elongatus	6.20	0.27	II increasing
Alona rectangula	6.14	0.28	I
Alona guttata	6.15	0.24	IV
Alona costata	6.18	0.34	I
Alona rustica	6.17	0.24	I
Alona intermedia	6.14	0.33	I
Alona affinis	6.20	0.23	IV
Alona quadrangularis	6.12	0.35	I
Alonella nana	6.14	0.28	I
Alona excisa	6.16	0.26	I
Monospilus dispar	6.22	0.18	IV
Chydorus sphaericus	6.13	0.32	II decreasing
Chydorus piger	6.22	0.25	II increasing
Pleuroxus aduncus	5.99	0.34	II decreasing
Sida crystallina	6.15	0.18	I
Rhynchotalona falcata	6.12	0.11	I

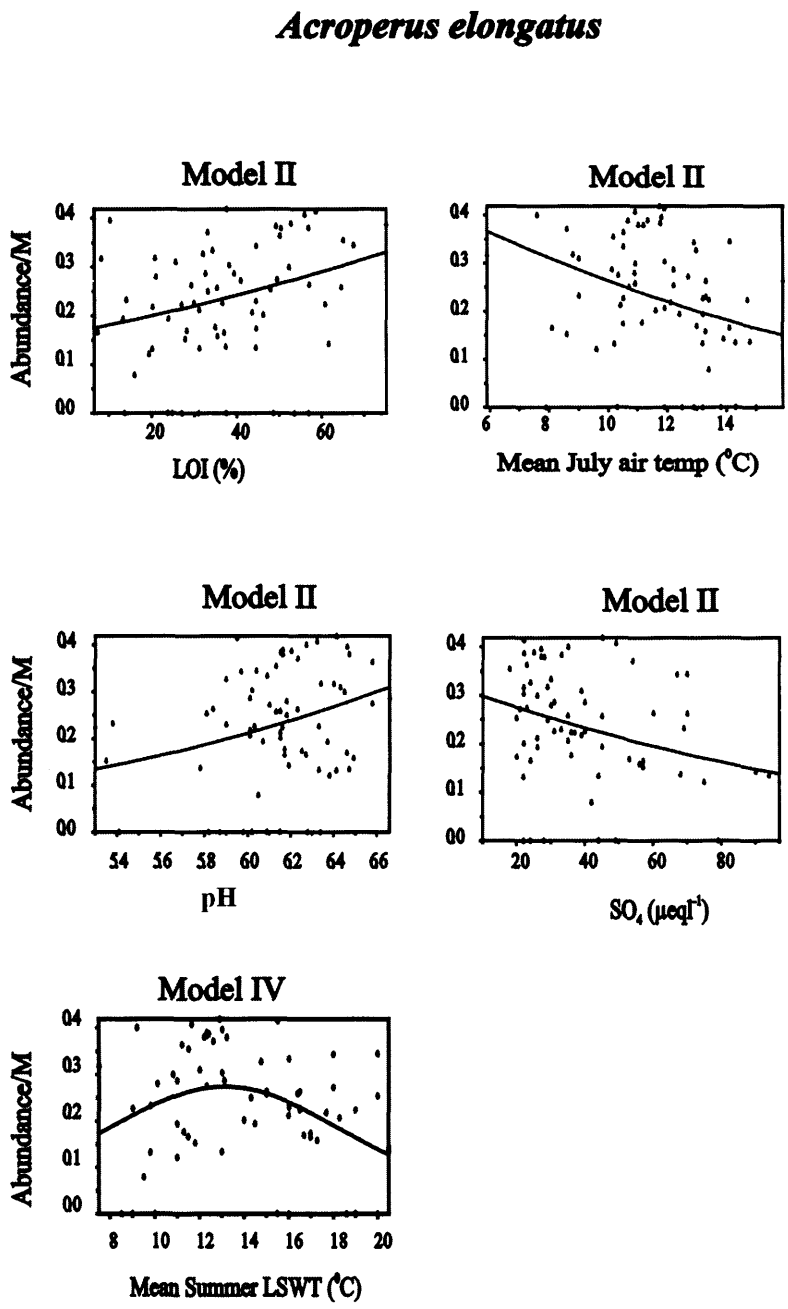


Figure 6.18: Relative abundances of *Acroperus elongatus* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

(Smyly, 1958; Fryer, 1993) as well as sparse vegetation or dense macrophyte (e.g. reed)-dominated swampy habitats (Flössner, 1972; Fryer, 1974). Sandøy and Nilssen (1986) and Rautio (1998), however, argued that this taxon is widely distributed in northern Europe regardless of lake type. Its distribution in sparse dense macrophyte beds (e.g. reed) in swamp habitats and also submerged vegetation indicates that it occurs in a wide range of vegetation substrates (e.g. Flössner, 1972; Fryer, 1974; Korhola, 1992 & 1999)

Alona rectangula

A. rectangula was widely distributed among the training set sites but its abundance was very low. It did not show a significant response to any of the measured environmental variables. However, this taxon can survive at temperature as low as –2 ^{0}C (Harmsworth, 1968) and often it is well distributed in warmer water with dense macrophyte growth (Hofmann, 1978; Fryer, 1993). Megard (1967) reported that *A. rectangula* is a temperate species but occurs abundantly in Greenland. Hofmann (1978) and Fryer (1993) argued that this taxon prefers littoral and marginal emergent macrophytes.

Alona guttata

The estimated WA optima suggest that *A. guttata* has ecological preferences for relatively high summer LSWT, TOC and pH values with optima of 15 ^{0}C for LSWT, 5 mgl^{-1} for TOC and 6 for pH respectively (Table 6.20, Table 6.25, Table 6.26). This taxon showed a significant response to four environmental variables, summer LSWT, January air temperature, TOC and pH respectively in HOF models (Figure 6.19). The occurrence and abundance of this taxon were well modelled by TOC and pH of the lake water (Figure 6.19). *A. guttata* was also widely distributed but in low abundance among the study sites. Previous studies suggest that this taxon prefers clean-water lakes in Arctic and temperate zones (Megard, 1967; Harmsworth, 1968; Whiteside, 1970), thus Harmsworth (1968) classified this taxon as a 'north temperate' species. An increased abundance of *A. guttata* has been reported in the late Holocene in Lake Varna, Croatia (Schmidt et al., 2000). However, its preference for warmer water is in agreement with Korhola (1999). The significant response of *A. guttata* to TOC found in this study is in agreement with Synerholm (1979), who found this taxon in greatest abundance in lakes with forested catchments with lowest conductivity.

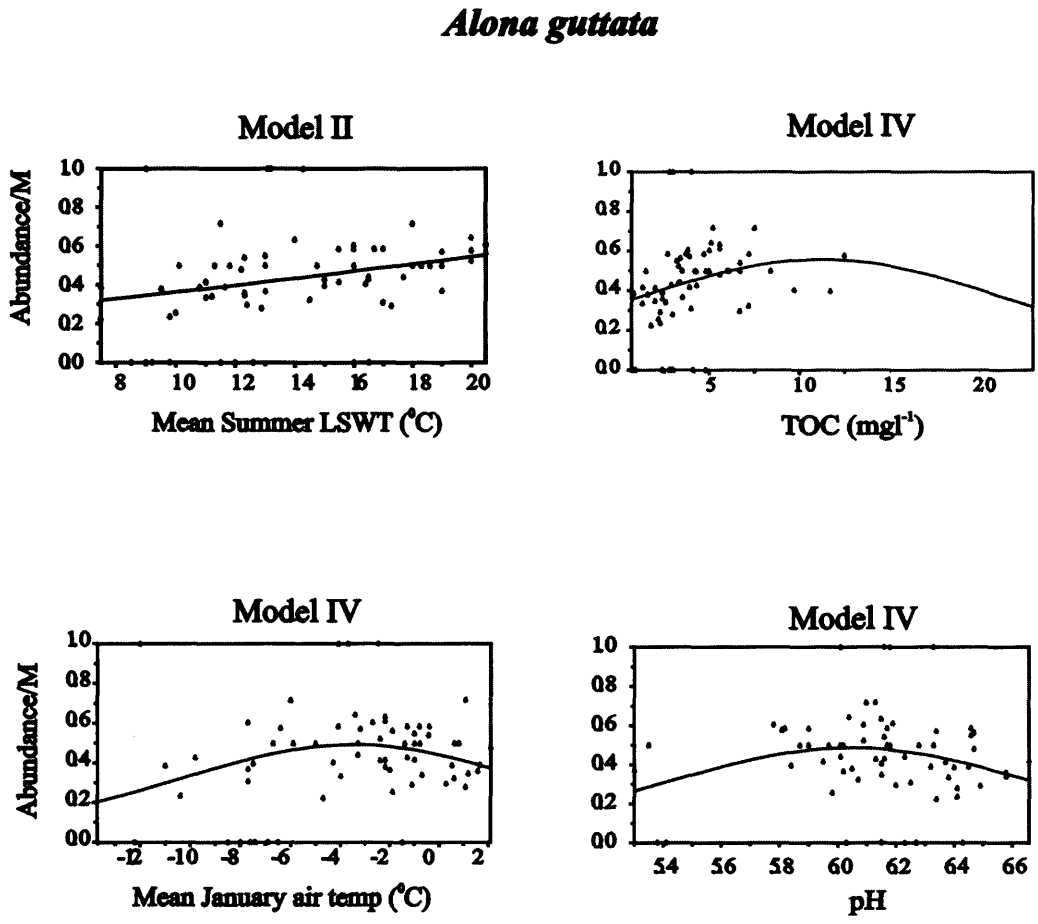


Figure 6.19: Relative abundances of *Alona guttata* plotted against environmental gradients for the training set sites. The fitted response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

Alona costata

A. costata showed a significant unimodal response to only one environmental variable, i.e. Ca in HOF models (Figure 6.20). It had an optimum of 69 μeql^{-1} to Ca (Appendix 6.5). *A. costata* was one of the rarest chydorid taxa in the training set sites. Harmsworth (1968) classified this taxon as a 'south temperate' species because of its high frequency over southern Europe. Fryer (1993), however reported that *A. costata* is common in Yorkshire lowlands, in habitats characterised by a wide range of substrata including stones, grit, sands, silts and soft organic material. Quade (1969) studied the habitat preference of *A. costata* in North American lakes, where the abundance of this taxon was restricted to vegetation types such as *Potamogeton natans* and *Chara*. Cluster and ordination analyses also showed that the abundance of this taxon was associated with lakes with low conductivity (Synerholm, 1979).

Alona rustica

The estimated WA optima indicate that *A. rustica* has ecological preferences for mean summer LSWT, July air temperature and LOI with optima of 15 ^{0}C, 12 ^{0}C and 40% respectively (Table 6.20, Table 6.21, Table 6.24). The taxon response model showed a significant relationship with mean summer LSWT, mean July air temperature and LOI respectively (Figure 6.21), however the occurrence and abundance of this taxon were well modelled by only the mean July air temperature (Figure 6.21). This taxon is more abundant in lower altitudinal and latitudinal sites with warmer water in the training set. Harmsworth (1968) classified this taxon as a 'temperate' species, and rare in the Arctic region. Usually it is predominant in low alkalinity ponds and bogs (Whiteside, 1970). It has also been reported from acidic seepage, and sometimes it is therefore regarded as an 'acid-loving' upland freshwater taxon (Fryer, 1993). Krause-Dellin and Steinberg (1986) have classified it as 'acidophylous' species. Quade (1969) found it abundantly in lakes with vegetation dominated by *Potamogeton amplifolius*, *P. zosteriformis*, *Ceratophyllum demersum* and *Elodea canadensis*. Synerholm (1979) recorded that this taxon was present mostly in lakes with coniferous forests with low values of conductivity.

Alona intermedia

The estimated WA optima indicate that the remains of *A. intermedia* were influenced by sampling depth with optimum of 8 m (Table 6.23). Five variables, precipitation, sampling depth, Na, Cl and Mg were significant in HOF models with monotonic

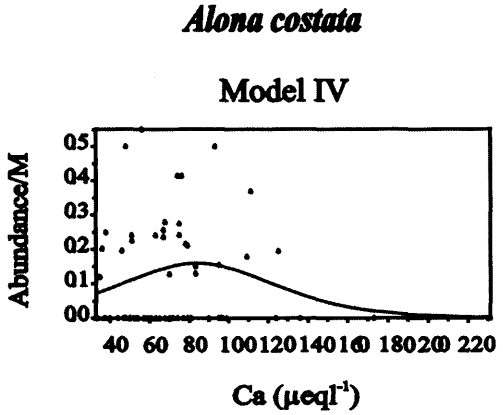


Figure 6.20: Relative abundances of *Alona costata* plotted against environmental gradients for the training set sites. The fitted response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

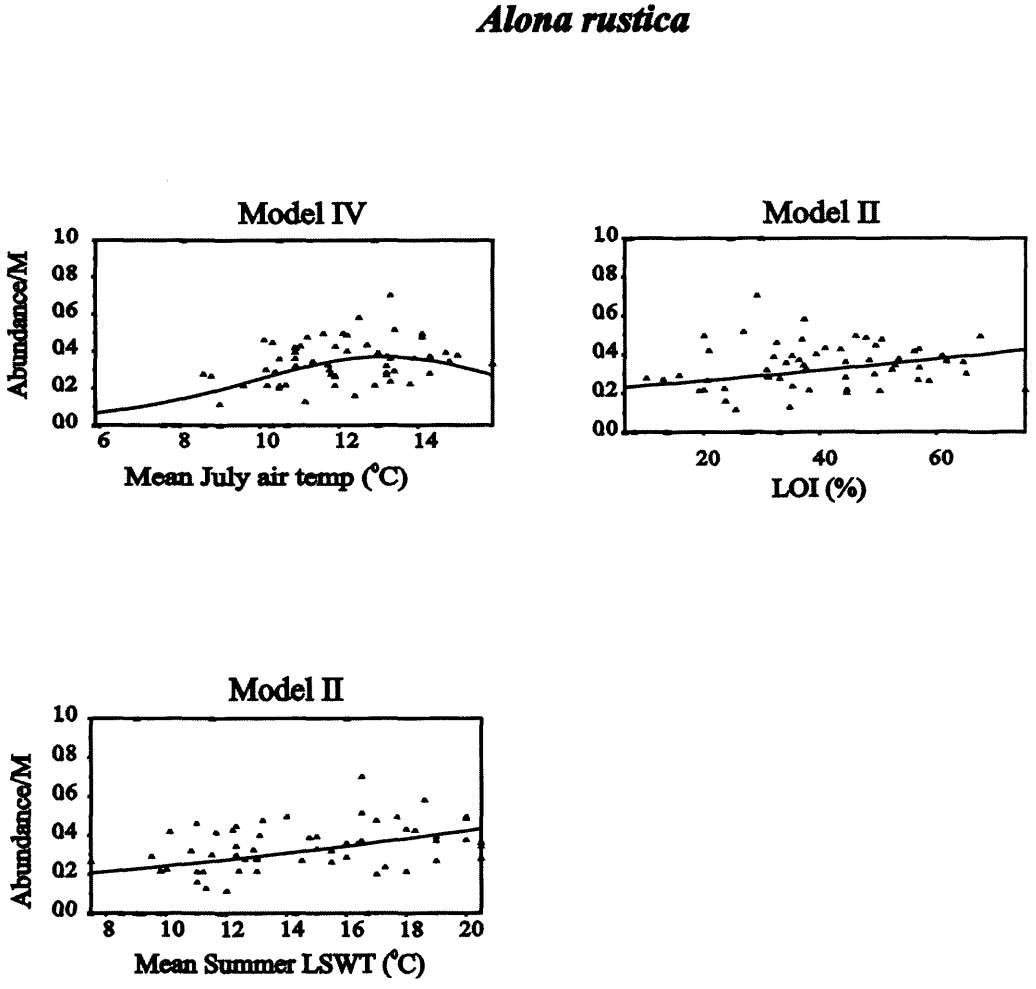


Figure 6.21: Relative abundances of *Alona rustica* and plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

increasing and/or decreasing responses (Figure 6.22). *A. intermedia* is not a common species in the Scottish and Norwegian training set sites but it is present in both upland and lowland environments. Harmsworth (1968) classified this taxon as a 'temperate species'. Fryer (1993) argued that *A. intermedia* is typically associated with nutrient poor, oligotrophic, often acidic, moorland situations, and has a predominantly northern and boreo-alpine distribution in Europe. Whiteside (1970) reported that this taxon is common in clear water sites, and is usually absent in polluted water. Krause-Dellin and Steinberg (1986) have classified this taxon as an 'acidophilous' species. *A. intermedia* is found mostly in upland lakes with low conductivity (Synerholm, 1979).

Alona affinis

The estimated WA optima suggest that *A. affinis* has preferences for LOI and pH with optima of 36% for LOI and 6 for pH (Table 6.24, Table 6.26). This taxon had a significant response to both environmental variables LOI and pH, however it was best modelled only by pH in HOF (Figure 6.23). *A. affinis* was one of the most common species in the training set but it was not present in the coldest sites. This taxon is considered one of the most cosmopolitan species in northern Europe (Whiteside, 1970; Korhola, 1999; Korhola et al., 2000). Harmswoth (1968) classified this taxon under the 'Sub-Arctic' group. Lotter et al. (1997) reported that this taxon has a cold tolerance behaviour, in which it occurred at more than 1500 m a.s.l. in the Swiss Alps. Its unimodal response to pH in Scotland and Norway suggests that it may withstand a wide range of acidic gradients. However, Fryer (1974) argued that it is absent in strongly acidic waters. The large shallow water bodies of Denmark and Finland have been reported to be good habitat types for this taxon (e.g. Korhola, 1999) since the submerged macrophytes of these water bodies are ideal for refuge (Nilssen and Sandøy, 1990). However, Fryer (1974) argued that, unlike other chydorids, this species does not appear to climb the parts of higher plants and its abundance is rather limited. Synerholm (1979) found that the abundance of this taxon was high in lakes with deciduous forests in their catchment.

Alona quadrangularis

The estimated WA optima indicate that *A. quadrangularis* has ecological preferences for summer LSWT, medium SO_4, low TOC with optima of 12 ^{0}C LSWT, 39.5 μeql^{-1} SO_4 and 3.5 mgl^{-1} TOC (Table 6.20, Table 6.23, Table 6.25). Altogether, the taxon showed a significant response to four variables mean summer LSWT, mean January air

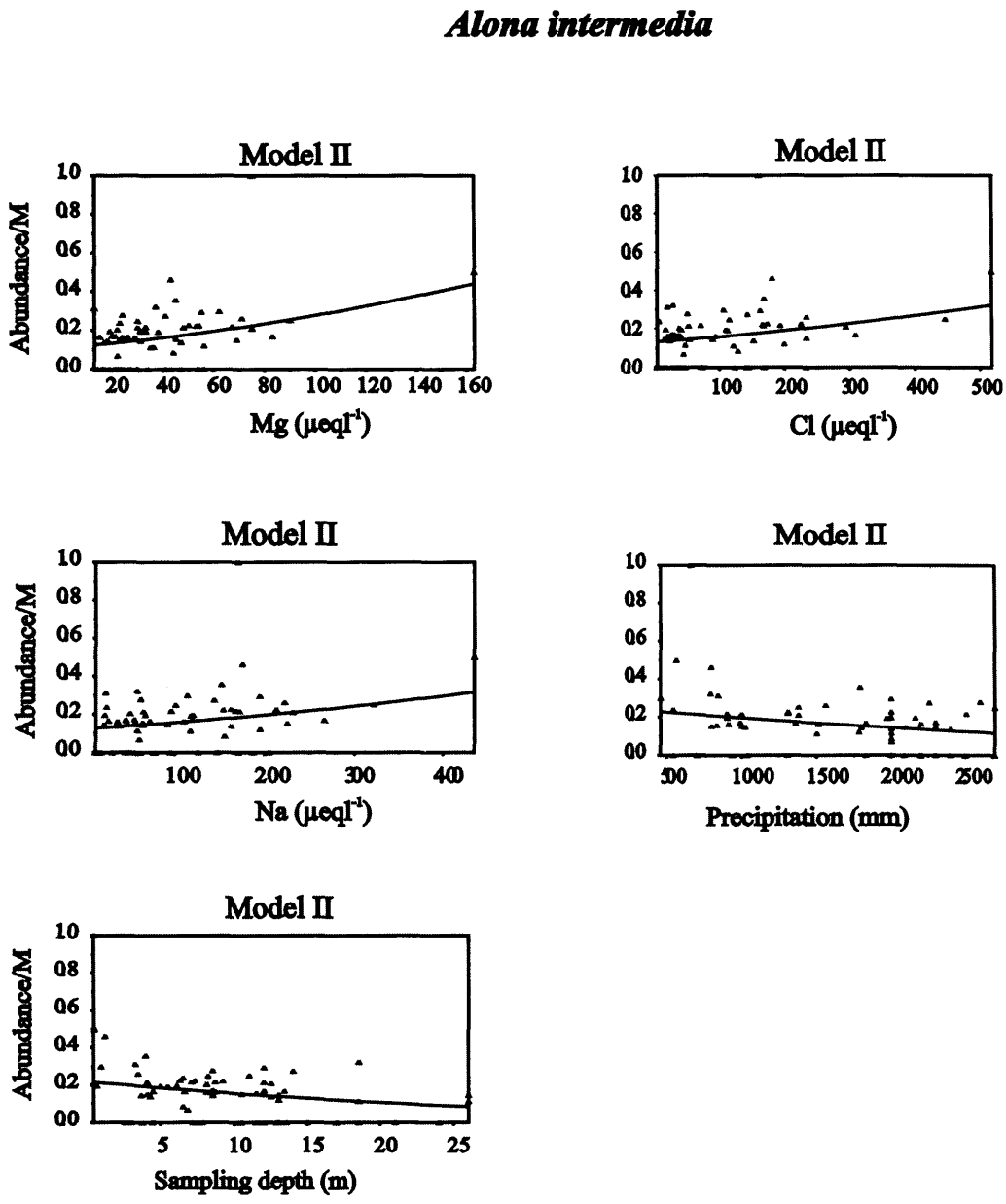


Figure 6.22: Relative abundances of *Alona intermedia* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

Alona affinis

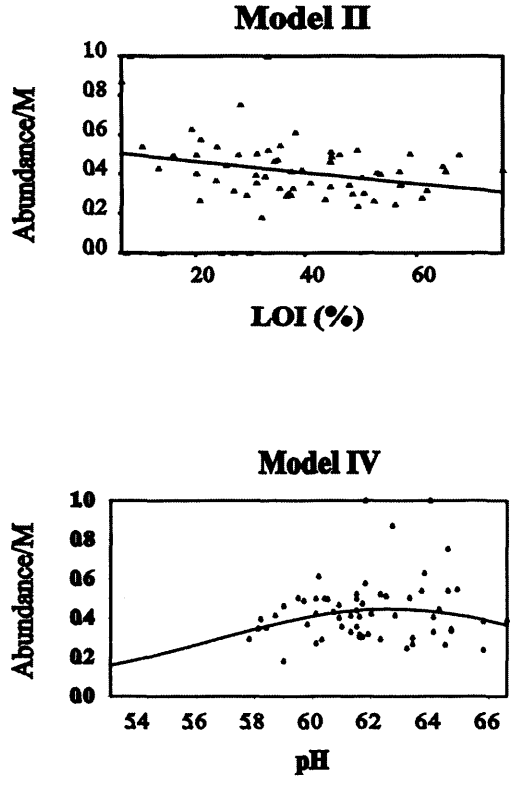


Figure 6.23: Relative abundances of *Alona affinis* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

temperature, SO_4 and TOC in HOF models, in which the significant symmetric unimodal response model was provided by SO_4 only (Figure 6.24). *A. quadrangularis* was common in sites with relatively low water temperature in Scotland and Norway. This is in agreement with Whiteside (1970) who reported that this taxon to be widely distributed in northern regions of Europe. Scourfield and Harding (1958) also reported that this taxon is very common in the British Isles. De Costa (1964) and Harmsworth (1968) classified it as a 'north temperate' species. It has low TOC and SO_4 optima suggesting its preference for clear water lakes with low salt concentration. However, Hofmann (1978) recorded it in polluted lakes of central Europe. It favours alkaline lowlands, but is also recorded from acidic upland sites (Fryer, 1974). However, in general, it is more abundant in alkaline environments and also regarded as an 'alkaliphilous' by Karuse-Dellin and Steinberg (1986). It occurs in a wide range of substrates including stones, sand and macrophytes (Fryer, 1974) and has been found associated with the macrophyte, *Ceratophyllum demersum* (e.g. Quade, 1969).

Alonella nana

A. nana was one of the most common chydorid taxa in the training set. Surprisingly this taxon did not show any clear relationship to any of the measured environmental variables. Harmsworth (1968) described *A. nana* as common in arctic and subarctic environments and classified it under the sub-arctic group. Whiteside (1970) regarded *A. nana* as a northern pioneer species, predominant in clear water and in ponds and bogs with a low productivity. Hofmann (2000) discovered that this taxon had a higher abundance during the Alleröd and the Preboreal, and a lower abundance during the Younger Dryas. Flössner (1972) argued that *A. nana* is an acidophilous species, in contrast, Krause-Dellin and Steinberg (1986) classified its response to pH as indifferent.

Alonella excisa

The WA optima show that abundance of *A. excisa* was only significantly related to sampling depth with an optimum of 8 m (Table 6.23). It is best modelled by a significant symmetric unimodal response in HOF models (Figure 6.25). *A. excisa* was one of the common taxa in the study site. Hofmann (1978) and Fryer (1993) have reported that it is abundant in arctic and subarctic regions of Europe. Lotter et al. (1997) reported that it can occur at sites more than 1500 m a.s.l. in alpine lakes of Europe. Harmsworth (1968) classified this taxon, as a 'north temperate' species. Ammann et al. (2000), Hofmann (2000) and Schmidt et al. (2000) all have showed that *A. excisa* was

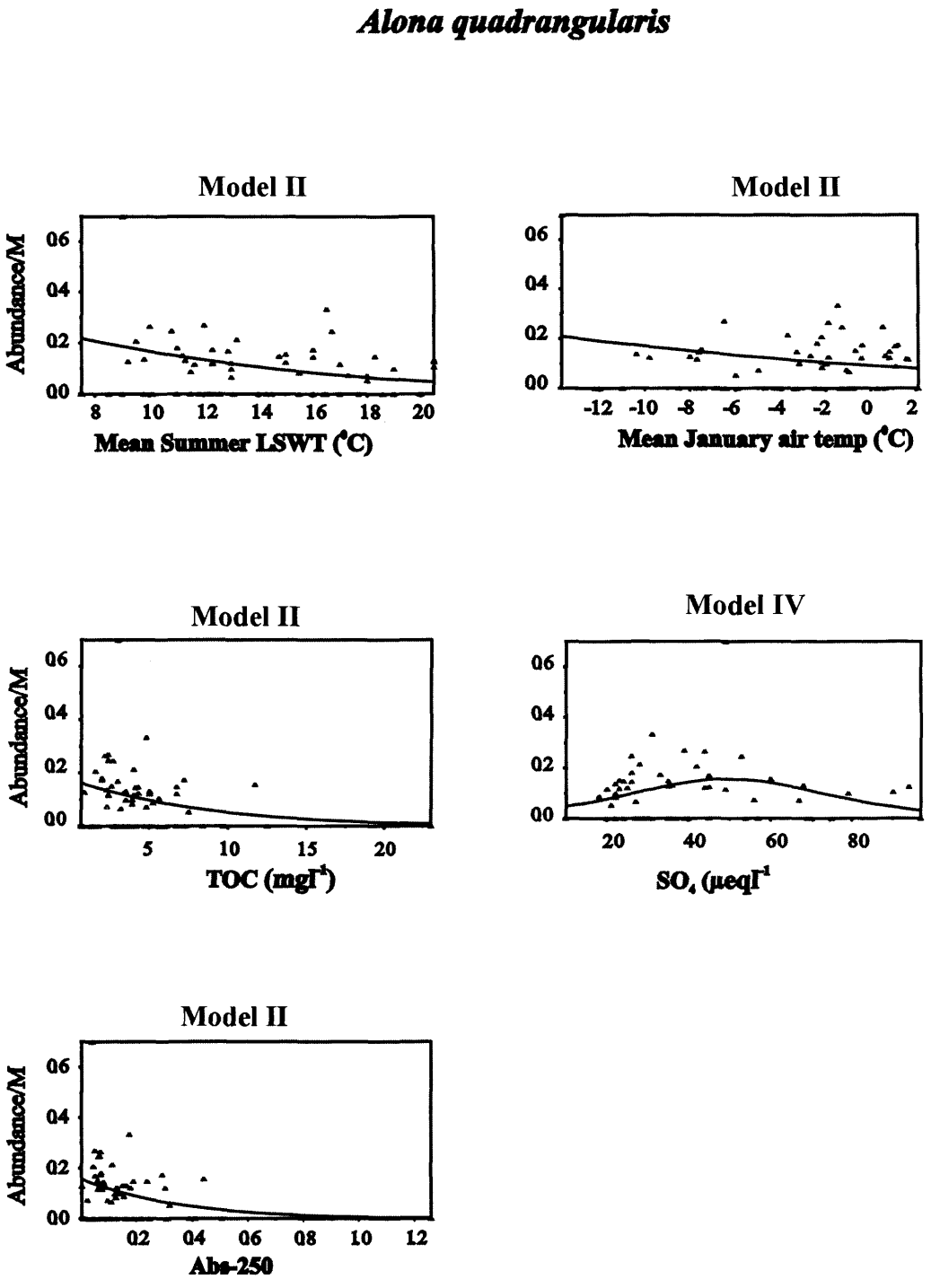


Figure 6.24: Relative abundances of *Alona quadrangularis* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

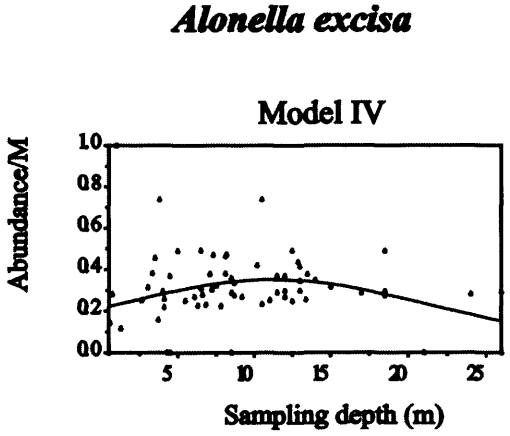


Figure 6.25: Relative abundances of *Alonella excisa* plotted against environmental gradients for the training set sites. The fitted response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

predominant in the Alleröd and the Pre-borial conditions, when the climate was rapidly ameliorating. A recent study by Ramdani et al. (2001) reported that this taxon is a rare species in North African lakes but a good indicator of low salinity and temperature. It prefers acid waters, in which the pH is sometimes is below 4 (Fryer, 1993). Sandøy and Nilssen (1986), Krause-Dellin and Steinberg (1986) and Rautio (1998) have all described this taxon as an acidophilous species. With respect to its habitat preference, it has been recorded frequently in vegetation beds (Whiteside, 1970). Nilssen and Sandøy (1990) described this taxon as a bottom dweller, living on detritus and *Sphagnum*, and Korhola (1992) reported that it becomes abundant during hydroseral succession in lake basins.

Monospilus dispar

The WA optima indicate that *M. dispar* prefers relatively mild summer LSWT and medium pH. The optima of this taxon are 13 ^{0}C for LSWT and 6 for pH (Table 6.20, Table 6.26). This species has significant response to 7 environmental variables, mean summer LSWT, mean January air temperature, pH, Ca, K, Abs-250 and Al-NL in HOF models. However, the occurrence and abundance of this taxon were well modelled by mean summer LSWT and Al-NL (model V) and pH, K, Abs-250 (model IV) (Figure 6. 26). *M. dispar* was one of the rarest species found in the majority of training set sites. However, its abundance was relatively high in Loch Coire Fionnaraich (LCFR). Habitat types in LCFR are ideal for the growth and development of this taxon. The contemporary survey of Cladocera in different habitat types of LCFR in Chapter 4 showed that this taxon is highly associated with sandy substrates, which is in agreement with Frey (1986) and Dole-Oliver et al. (2000). Whiteside (1970) and Hofmann (1986) described it as a taxon that prefers clean-water lakes, and Fryer (1993) described it from shallow ponds with sandy substrates and sometimes the lakes with muddy bottoms.

Chydorus sphaericus

The WA optima suggest that *C. sphaericus* has ecological preferences for medium SO_4 and sampling depth with optima of 42 μeql^{-1} and 9 m respectively (Table 6.22, Table 6.23). This taxon has significant response to five environmental variables, mean January air temperature, SO_4, Ca, precipitation and sampling depth in HOF models, where its occurrence and abundance were modelled by a sigmoidal increasing or decreasing response (Figure 6.27). *C. sphaericus* was one of the most common taxa in the training set. Its occurrence was relatively high in sites with low temperature. This is an

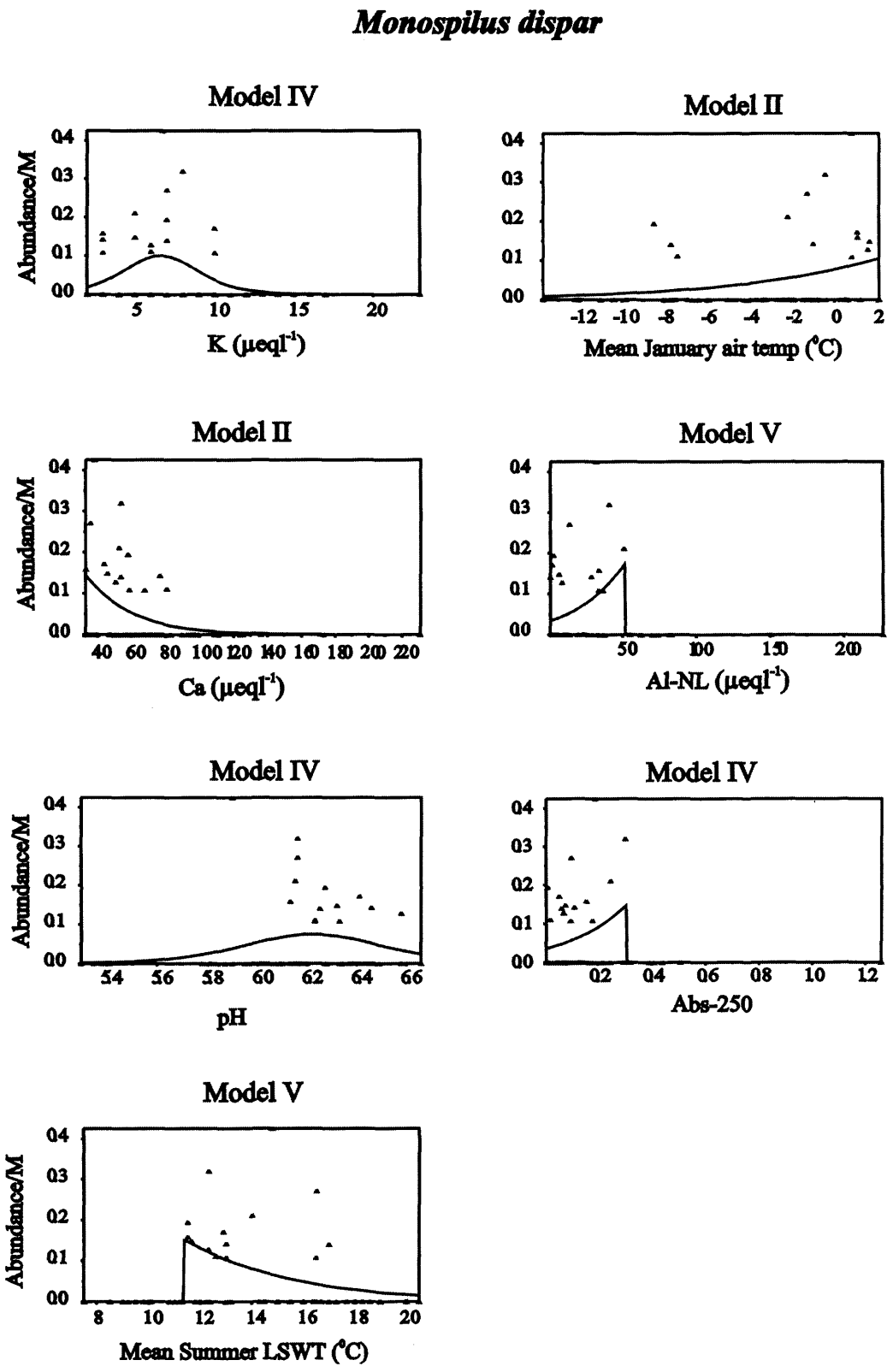


Figure 6.26: Relative abundances of *Monospilus dispar* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

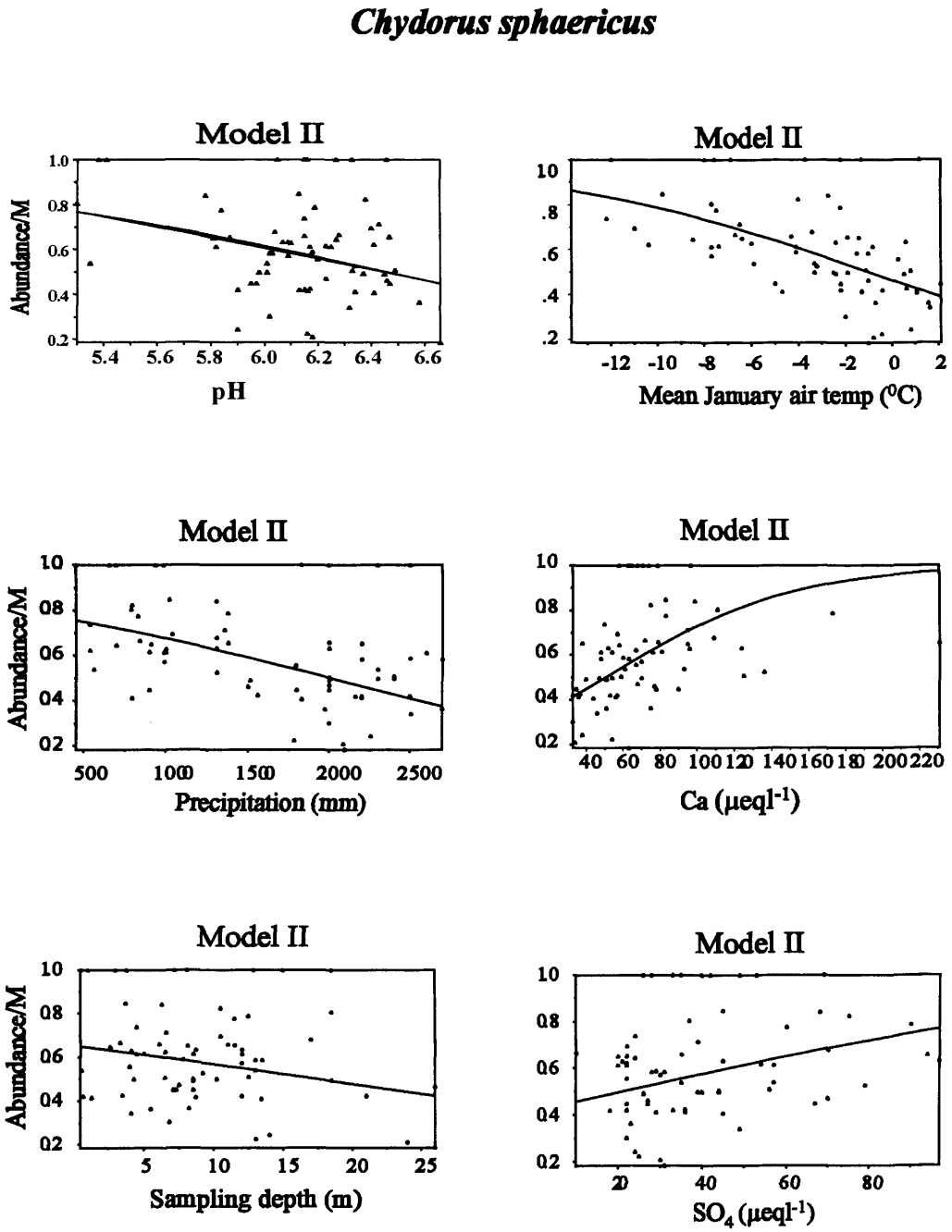


Figure 6.27: Relative abundances of *Chydorus sphaericus* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

agreement with a number of other studies. Megard (1967) reported it as a species with predominantly occurs in Greenland. Harmsworth (1968) classified this taxon, as an 'Arctic' species, and Lotter et al. (1997) have recorded it at sites over 1500 m a.s.l. in the Swiss Alps. Tartari et al. (1998) collected *C. sphaericus* from lakes in the Himalayas situated around 5000 m a.s.l. In contrast, Frey (1980) argued that *C. sphaericus* could survive in the tropics.

Krause-Dellin and Steinberg (1986) classified this taxon as an indifferent species to pH. Korhola (1999) also found that *C. sphaericus* did not have a specific preference to pH, conductivity or other water chemical parameters. However, a study of Sarvala and Halsinaho (1990) on southern Finish lakes reported that *C. sphaericus* was found to be typical of high pH, conductivity, Ca, and organic carbon rich sites. Ramadani et al. (2001) on the other hand reported that *C. sphaericus* can tolerate low concentrations of dissolved oxygen and can be found in lakes pH 3.4-9.2. The wide tolerance of this taxon indicates that it is frequently recorded in a wide range of water bodies from upland and lowlands and from benthic, littoral and deep open-water habitats (Whiteside, 1970; Fryer, 1974; Fryer, 1993; Korhola, 1999; Korhola et al., 2000; Ramadani et al., 2001). This taxon is also present in extremely polluted and eutrophic conditions (Frey, 1976; Hofmann, 1978; Fryer, 1993; Cattaneo et al., 1998). Birks et al. (1976), Frey (1986) and Hofmann (1987) also argued that the abundance of this taxon could be very high in lakes with thick blue-green algal blooms. Fryer (1993) has recorded this taxon frequently in flooded marshlands, and from tarns with acidic and muddy bottoms. It has been suggested that the wide tolerance of this species is because of its body structure, which is well adapted both morphologically and physiologically for a wide range of situations. The shape of the carapace of *C. sphaericus* offers protection against small predators such as cyclopoid copepods (Fryer, 1993). However, the actual physiological mechanism for the tolerance is unknown.

Chydorus piger

The estimated WA optima show that *C. piger* has preferences for relatively low July air temperatures and medium pH with optima of 12 ^{0}C and 6 respectively (Table 6.21, Table 6.26). The occurrence and abundance of this taxon were well explained by only mean July air temperature in HOF models (Figure 6.28). The unimodal response of this taxon to July air temperature suggests that it have a wide temperature tolerance in training set sites. Harmsworth (1968) classified this taxon as a 'Temperate' species.

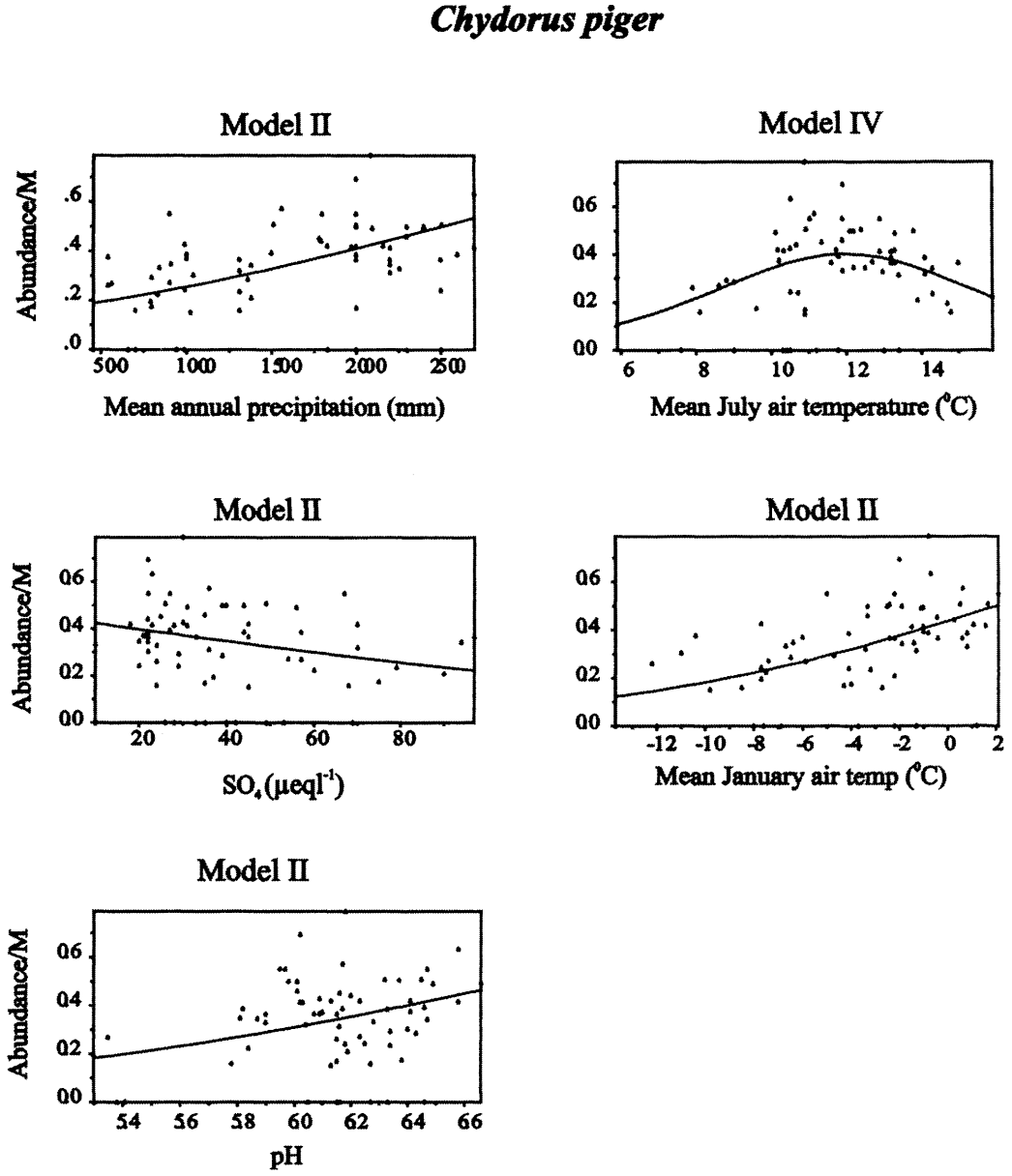


Figure 6.28: Relative abundances of *Chydorus piger* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

Fryer (1974) reported that this taxon was a cold-tolerant stenotherm in European and North American lakes. However, Korhola (1999) described this taxon from shallow, relatively warm water environments of many European lakes. *C. piger* prefers clear water lakes (Whiteside, 1970). With 'circumneutral' pH (Krause-Dellin and Steinberg, 1986). It is found predominantly associated with sediments rather than macrophytes. Whiteside et al. (1978) found that this species lives almost exclusively in muddy habitats, and Hofmann (1986) and Fryer (1993) reported that *C. piger* is typically associated with nutrient poor, often acidic moorland situations in northern latitudes.

Pleuroxus aduncus

The occurrence of *P. aduncus* was very low, so the results here are uncertain. The estimated WA optima for this taxon suggest that this taxon prefers rather low July air temperature and low LOI and pH with optima of 11 ^{0}C for July air temperature, 32.3% for LOI and 6 for pH respectively (Table 6.21, Table 6.24, Table 6.26). The taxon showed a significant response to all three environmental variables, mean July air temperature, LOI and pH in HOF models. However, the occurrence and abundance of this taxon were well explained by LOI and alkalinity (Figure 6.29). Carl (1940) reported it from a wide altitudinal and latitudinal range.

Sida crystallina

The WA optima indicate that *S. crystallina* abundant at sites with a relatively high LOI with optima of 41% (Table 6.24). The taxon had a significant sigmoidal response to LOI (model II increasing) and significant symmetric unimodal response (model IV) to Mg in HOF models (Figure 6.30). The abundance of *S. crystallina* was relatively low in the training set but it was more common in sites with warmer water. Its climate preferences are not well documented, though Flössner (1972) and Korhola (1999) noted that it seems to occur in warmer water. Lotter and Boucherle (1984) reported that it is a plant-dwelling species, usually abundant in macrophyte-dominant habitats. In the British Isles, Europe and North America, it is found attached to large-leaved plants of *Potamogeton* (Scourfield and Harding, 1958; Quade, 1969) and *Nymphaea* (Flössner, 1972). However, it can also be found in the open-water (Fairchild, 1981).

The WA summer LSWT optima of cladoceran zooplankton is presented in Figure 6.31 and the summary statistics for the Cladocera summer lake surface water temperature (LSWT) calibration data-set are presented in Table 6.27. In Table 6.27, the mean,

Pleuroxus aduncus

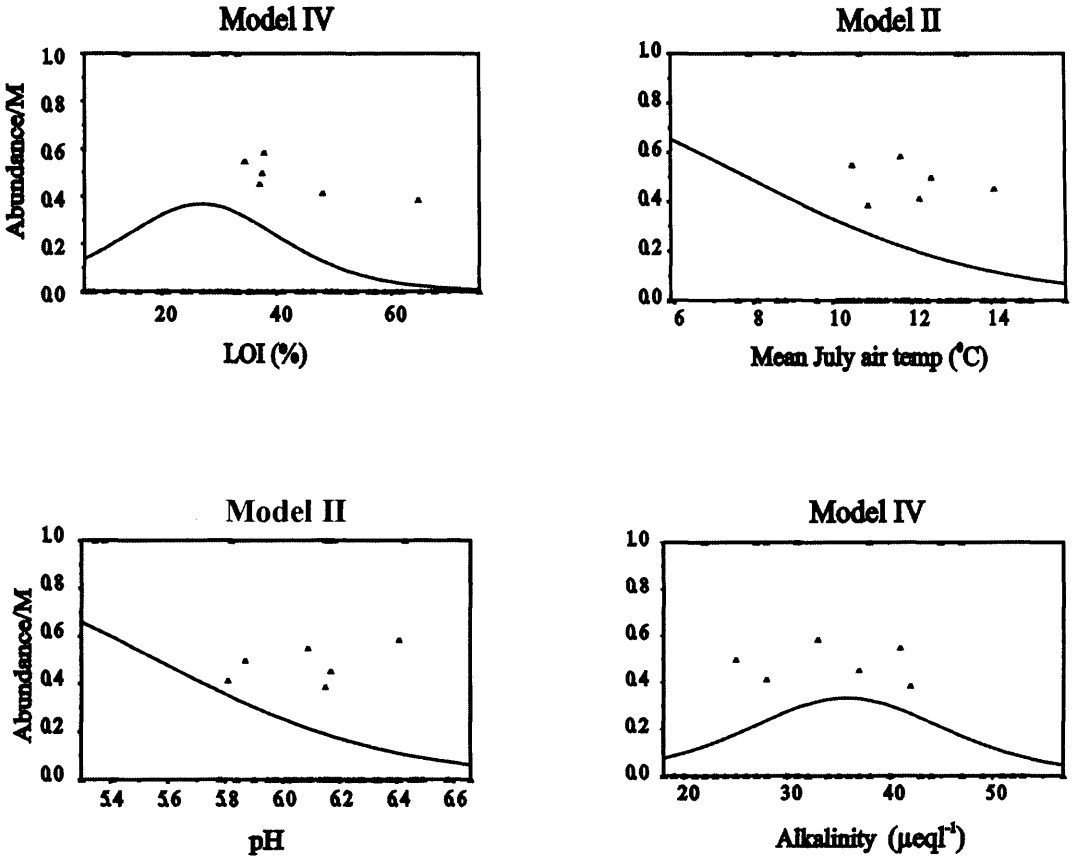


Figure 6.29: Relative abundances of *Pleuroxus aduncus* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

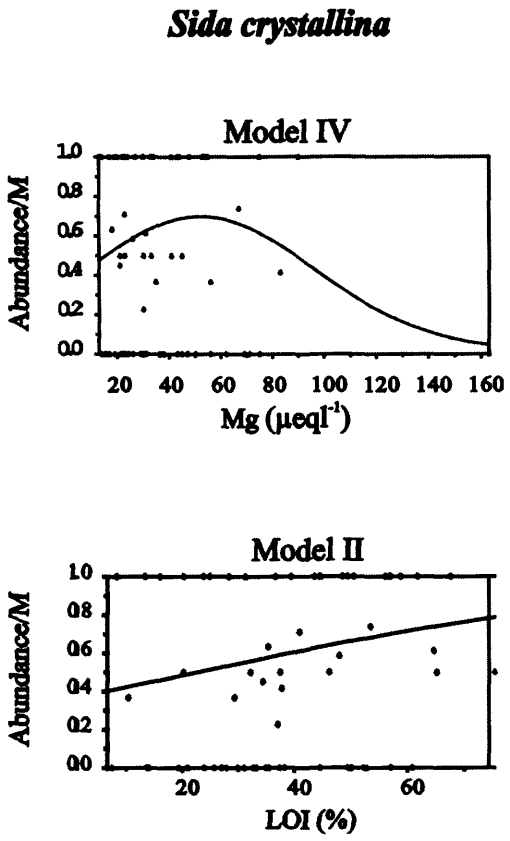


Figure 6.30: Relative abundances of *Sida crystallina* plotted against various environmental gradients for the training set sites. The fitted species response model is shown only for the significant environmental variables (model II-V) in HOF. The relative abundance is divided by M, which is the greatest theoretical value (i.e. 100%) in the model.

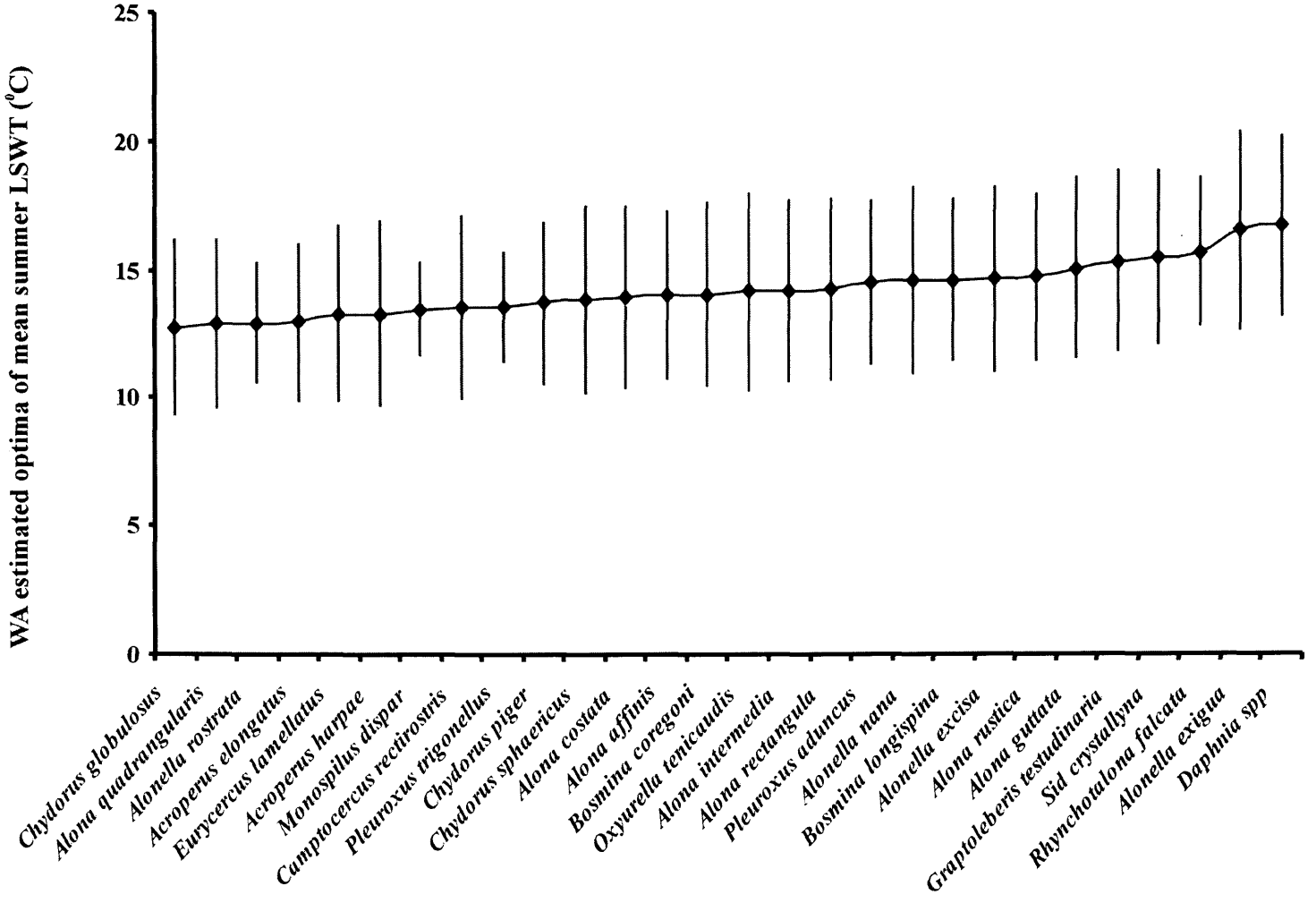


Figure 6.31: Estimated weighted averaging (WA) summer lake surface water temperature optima (°C) tolerances (°C) of the Cladoceran taxa in the data-set. The 'abundance' of each taxon was determined by multiplying the number of occurrences with the maximm abundace of the taxon in the data-set. The WA was implemented by the computer program CALIBRATE..

Table 6.27: Summary statistics for the Cladocera summer LSWT calibration data-set.

Number of samples	68
Number of taxa used in ordination	28
N2 for samples	
Mean	10.14
Maximum	15.65
Minimum	3.17
N2 for taxa	
Mean	32.82
Maximum	57.46
Minimum	4.48
DCCA axis 1 (constrained with LSWT)	
λ_1	0.046
Gradient length (SD)	0.762
% variance	8.3
DCA axis 2	
λ_2	0.06
Gradient length (SD = standard deviation of compositional turnover)	1.37
% Variance	10.6
λ_1/λ_2	0.76
Summer Lake surface water temperature (LSWT)	
Minimum	7.5
Mean	14.15
Median	13.60
Maximum	20.50
Standard deviation	3.57
Range	13
Taxon response model generated from a total of 22 taxa	
Skewed unimodal model	1
Symmetric unimodal model	2
Sigmoidal monotonic model - increasing	3
Sigmoidal monotonic - decreasing	2
Null or flat model	14

maximum and minimum as well as the effective number of taxa or Hill's N2-diversity (Hill 1973), the presence of large primary and secondary gradients as indicated by DCCA axis 1 (constrained) and unconstrained DCA axis 2, the niche response model as shown by cladoceran taxa and the mean, median and standard deviation of summer LSWT are included.

6.3.3. Development of summer LSWT transfer function models

In the data-set presented here from Scotland and Norway, the summer LSWT has been shown to be one of the important variables in explaining cladoceran distributions among lakes, and thereby provides the basis for the development of Cladocera-temperature transfer functions. Overall results based on Table 6.27 indicated that the best approach for developing a Cladocera-based inference model on the summer LSWT was PLS regression and calibration. However, other non-linear based WA and WA-PLS regression and calibrations were also performed. Ter Braak et al. (1993) argued that although the compositional length of a biological data-set is linear, in some situations unimodal-based methods can outperform the linear-based methods. Weighted Averages with tolerance (WA_{tol}), and without (WA) tolerance down-weighting were performed using classical and inverse deshrinking (Birks et al., 1990), and Weighted Averaging-Partial Least Squares (WA-PLS; ter Braak and Juggins, 1993) methods. WA with WA_{tol} down-weighting and without tolerance down-weighting was performed since Birks et al. (1990) argued that taxa with a narrow tolerance to the environmental gradient (in this case, the summer LSWT) might be given greater weight in WA than taxa with a wide tolerance to that environment. In the following sections, results of calibration models based on WA, PLS and WA-PLS are presented.

6.3.3.1. Weighted Averaging (WA) method

The summary statistics of WA regression and calibration are presented in Table 6.28. A significant variation was observed between cross-validated (jack-knifed) RMSE and apparent RMSE. Similarly, the apparent r^2 was higher than the jack-knifed r^2. Usually the apparent statistics are over-optimistic since all the individual samples being inferred are included in the calibration model. However, a more realistic error of prediction (RMSEP) is obtained by leave-one-out jack-knifing in which each sample is left in turn from the model, but its temperature value is predicted by the model and the difference between (predicted temperature – observed temperature) for that sample is recorded. On

the basis of jack-knifed RMSE the inverse-deshrinking regression and calibration model appears to perform the best WA regression and calibration results, where RMSE, r^2 and maximum bias were 2.29 ^{0}C, 0.58 and 5.28 ^{0}C respectively (Table 6.28).

Table 6.28: Summary statistics for mean lake surface water temperature WA and tolerance down-weighted (Tol d/w) WA regression with cross-validation by jack-knifing of the data-set with 68 samples used for the derivation of a transfer-function. Results for both classical and inverse deshrinking are presented. Bold numbers represent the best inference results.

Inference model	Classical deshrinking			Inverse deshrinking		
	RMSE (^{0}C)	r^2	Max-bias (^{0}C)	RMSE (^{0}C)	r^2	Max-bias (^{0}C)
Simple WA	2.3314	0.6978	2.975	1.9476	0.6978	3.986
Tol d/w WA	2.3695	0.6909	3.177	1.9696	0.6909	4.149
Cross-val. WA	2.5079	0.5912	4.783	**2.2923**	**0.5829**	**5.285**
Cross-val. Tol d/w WA	2.6506	0.5459	5.119	2.4096	0.5386	5.53

6.3.3.2. Partial-Least squares regression (PLS) method

The results of the PLS transfer functions are presented in Table 6.29. The prediction error (RMSEP) was the lowest (2.28^{0}C) for the one-component PLS model. Similarly the maximum bias was also lower (4.92 ^{0}C) in one-component model than the two-component (5.07 ^{0}C) (Table 6.29).

Table 6.29: Summary statistics for mean lake surface water temperature PLS models applied to the 68 surface sediment training set sites. The performance of the models in relation to the number of components is assessed in terms of apparent RMSE and leave-one out RMSEP. Bold numbers represent the best inference results.

Number of components	Apparent errors			Predicted errors		
	RMSE (^{0}C)	r^2	Max-bias (^{0}C)	RMSEP (^{0}C)	r^2	Max-bias (^{0}C)
1	1.9413	0.6998	3.317	**2.2841**	**0.5854**	**4.9223**
2	1.7564	0.7542	3.622	2.2985	0.5855	5.0708
3	1.6484	0.7835	2.7022	2.3946	0.5654	4.4526

6.3.3.3. Weighted Averaging Partial-Least Squares regression (WA-PLS) method

The results of WA-PLS transfer functions are presented in Table 6.30. The prediction error (RMSEP) was the lowest (2.29 ^{0}C) for the one-component WA-PLS model.

The prediction errors, apparent RMSE and jack-knifed RMSEPs in WA, PLS and WA-PLS suggest that the PLS model had the lowest RMSEP value. When samples with high residuals (outliers) or low Cook's D (<4/*n*, where *n* is the number of samples) (Lotter et al. 1997), L033ATN, L113ØNN, L148ATN, L163NET, were removed from

Table 6.30: Summary statistics for mean lake surface water temperature WA-PLS models applied to the 68 surface sediment training set sites. The performance of the models in relation to the number of components is assessed in terms of apparent RMSE and leave-one out RMSEP. Bold numbers represent the best inference results.

Number of components	Apparent errors			Predicted errors		
	RMSE (^{0}C)	r^2	Max-bias (^{0}C)	RMSEP (^{0}C)	r^2	Max-bias (^{0}C)
1	1.9480	0.6978	3.9748	**2.2911**	**0.5834**	**5.2798**
2	1.7211	0.7641	2.3044	2.4756	0.5457	4.3598
3	1.6629	0.7880	2.6339	2.6137	0.5041	4.9325

the data-set and re-run, the PLS regression and calibration, the RMSEP, r^2 and maximum bias were improved significantly with an RMSEP of 1.8090 ^{0}C, r^2 of 0.7158 and low maximum bias of 1.8949 ^{0}C in the component-two model (Table 6.31, Figure 6.32).

Table 6.31: Summary statistics for mean lake surface water temperature PLS models applied to the 64 surface sediment training set sites after deletion of sites (L033ATN, L113ØNN, L148ATN, L163NET) with high residuals and Cook's D. The performance of the models in relation to the number of components is assessed in terms of apparent RMSE and leave-one out RMSEP. Bold numbers represent the best inference results.

Number of components	Apparent errors			Predicted errors		
	RMSE (^{0}C)	r^2	Max-bias (^{0}C)	RMSEP (^{0}C)	r^2	Max-bias (^{0}C)
1	1.5649	0.7853	1.9596	1.8552	0.7017	3.1648
2	1.3234	0.8464	1.0000	**1.8090**	**0.7158**	**1.949**
3	1.2253	0.8684	0.7886	1.8493	0.7061	1.9390

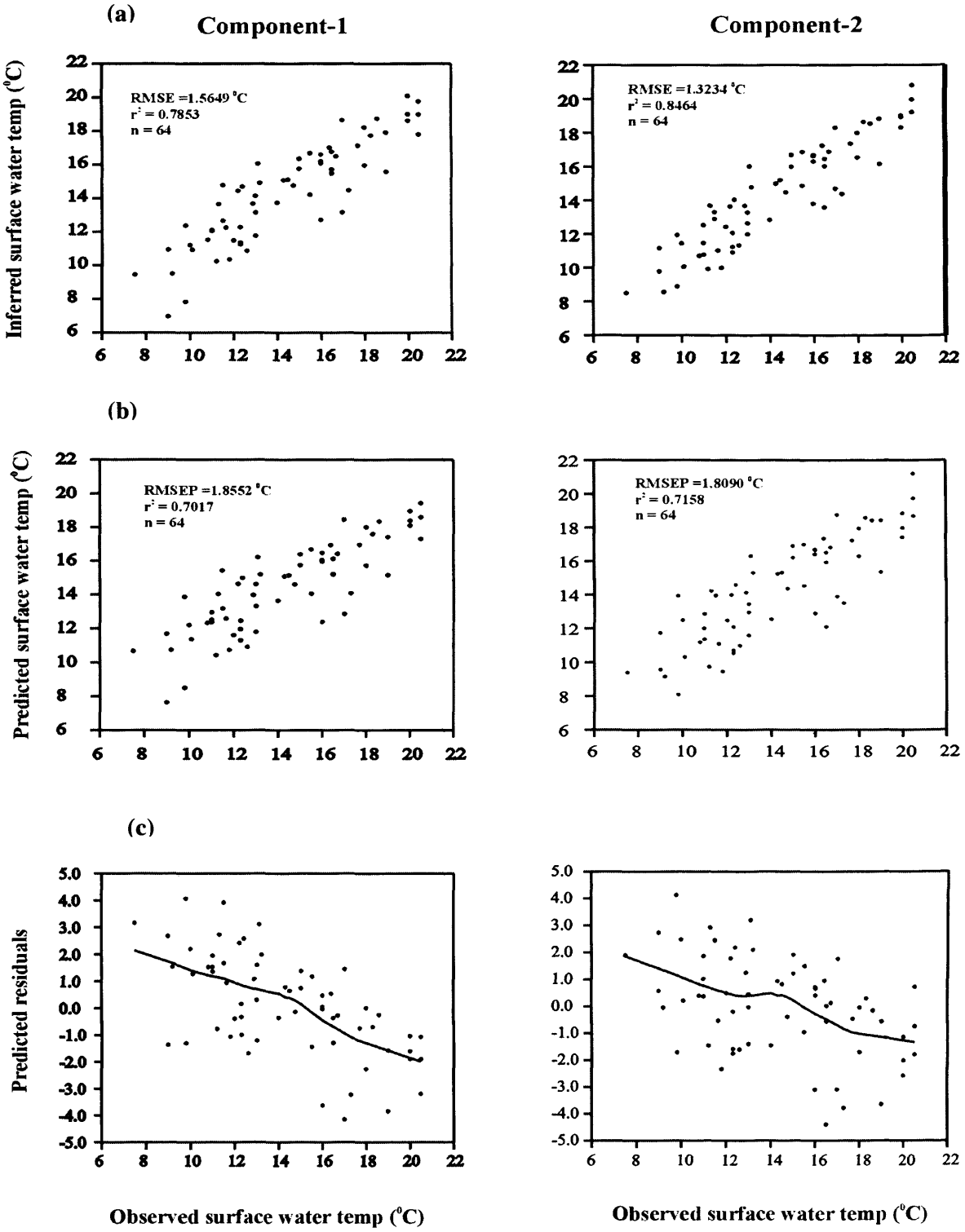


Figure 6:32: PLS models of Cladocera-inferred mean summer lake surface water temperatures of 64 sites in Scotland and Norway. (a) apparent v observed, (b) predicted vs observed and (c) Residuals (predicted – observed) mean summer LSWT as a function of observed summer water temperature. LOESS scatter-plot smoother (span = 0.45).

Those outliers removed were from Norway and they had very high or low temperatures possibly due to altitudinal and latitudinal factors. Site L033ATN is located at a low altitude but it has an exceptionally low mean lake surface water temperature perhaps due to a sampling error or to weather conditions at the time of sampling, compared to other sites in the same altitudinal ranges.

Site, L113ØNN however, has a very high mean lake surface water temperature compared to its counterparts in the similar altitudinal and latitudinal gradients. Since this site is located at 59.68^{0}N and 720 m altitudes, the high temperatures in the sampling day could be due to local weather conditions. Two sites L148ATN and L163NET are located at extremely high altitudinal ranges so have very low lake surface water temperatures.

6.4. Discussion

6.4.1. Training set sites

Although the training set sites were selected from two different regions of north-west Europe with significant latitudinal, longitudinal and altitudinal variations, the development of a transfer function combining the data was regarded as appropriate due to many similarities among the sites selected from two regions. All the sites are remote lacking human disturbance in their catchments, and all are formed by glacial erosion with slow-weathering, siliceous bedrock. In terms of their climatic setting, they all fall within high rainfall regions. Scotland and Norway have shown very similar figure for rainfall (Appendix 2.2). In particular, the pattern of precipitation in this region of Northwest Europe is influenced by the year-to-year and decadal variations in the North Atlantic Oscillation (NAO) (Busuioc et al., 2001; Fowler and Kilsby, 2002) and it can be expected that mountain lakes in the region respond to such climate influence in a similar way (e.g. Ventura et al., 2000). The sensitivity of upland lakes to the NAO has been recently reported by George et al. (2004). Combining the data-sets also provides a longer climate gradient for mean summer LSWT, the climatic variable of central interest, and consequntly allows the species optima to be better defined than would be the case with only the Scottish training set. On the other hand, by lengthening the temperature gradient in this way, there has been an increase in variation between sites related to chemical composition. This has been minimised by attempting to keep

alkalinity within a narrow range, but the remaining variation, principally in marine ions, sulphate and chloride has a significant influence as shown by the PCA ordinations.

6.4.2 Factors affecting the composition and abundance of Cladocera in the calibration data-set

This is the first attempt in quantifying the modern relationships between Cladocera and summer lake surface water temperature in Scottish and Norwegian mountain lakes. Most mountain lakes in northwest Europe have low base status (Jones et al., 1993), and the cladoceran zooplankton assemblage structure in these lakes is particularly sensitive to variations in alkalinity. Consequently, in this study, to maximize the temperature-Cladocera relationship, an attempt was made as pointed out above to minimize the alkalinity effect by holding alkalinity approximately constant in the selection of the calibration data-set. In principle, this approach then allows Cladocera to be used as indicators of climate change.

The significantly large amount of variation in the cladoceran species data is accounted by summer lake surface water temperature (LSWT) as revealed by direct gradient analysis (RDA), and this result supports the presumption that the Northwest Scottish and Norwegian mountain lakes are sensitive to climate change. Many studies suggest that climate is one of the most important factors in driving the abundance and richness of Cladocera in mountain lakes (e.g. Patalas, 1990) through either direct or indirect mechanisms (Battarbee, 2000). Temperature plays a direct role on productivity, life history and reproduction (Keller et al., 1999). Laboratory studies demonstrate the importance of temperature on physiology and bio-energetic processes of Cladocera (Yurista 1999, de Eyto and Irvine 2001). Indirect mechanisms are also important. When lakes are influenced by factors other than climate change such as changes in nutrients and bio-geochemical processes, temperature continues to play the paramount roles on the dynamics of these mechanisms and thereby the assemblages of Cladocera. In addition, it is expected that during ice-free seasons, lakes particularly located in the more northerly continental region of the training set become more sensitive to UV radiation due to longer light hours, which in turn can influence lake stratification (e.g. Sommaruga and Psenner 1997). During stratification, the thermocline acts as a barrier between epilimnetic and hypolimnetic water masses. During global warming, particularly, deep small lakes are likely to be influenced by thermocline migration

resulting in the enlargement of metalimnetic and shrinkage of hypolimnetic habitats for the most aquatic communities including Cladocera (Pompilio et al., 1996; Schindler, 1998). The epilimnetic layer is ecologically important (Fee et al.1996) for vertically migrating Cladocera such as *Daphnia* and *Bosmina* (Gliwicz, 1986). These animals frequently use the photosynthetically available irradiance and dissolved oxygen conditions in the mixed layer (Pompilio et al. 1996). However, for the majority of lakes in Scotland and Norway located close to the ocean, stratification may be less strong due to NAO-associated weather conditions. As a result, the winter ice-cover decreases significantly and the growing season increases affecting the population dynamics of most species of planktonic Cladocera (e.g. George and Harris, 1985; George, 2000). The Greenland ice-core data (Crowley, 1993) and the variation in the NAO indices (Delworth and Dixon, 2000) indicate that the northward heat transport in the North Atlantic has been increasing in recent years, and such heat transport mechanism causes changes in the North Atlantic thermohaline circulation (THC) (Wood et al., 1999; Delworth and Dixon, 2000) that controls seasonal climate in the study region (Hurrel, 1995).

Changes in summer water temperature should exert equal amount of influence on both littoral and planktonic Cladocera in most warm, small, temperate lakes (Walker et al., 1991), In addition, significant altitudinal and latitudinal distribution patterns of both planktonic and littoral Cladocera have been described by various authors for northern Hemispheric lakes (DeCosta, 1964; Harmsworth, 1968; Lotter et al., 1997; Rautio, 1998; Korhola, 1999) suggesting that both groups of Cladocera are sensitive to climate change. For example, common littoral and planktonic Cladocera such as *Alona rustica* and *Daphnia* spp. prefer warmer conditions in the training set (Figure 6.11, Figure 6.21). These results are in accordance with Korhola (1999) for Fennoscandian lakes. Lotter et al. (1997) found a significant relationship between the assemblage structures of Cladocera and mean July air temperature along altitudinal gradients in the Swiss Alps. Since the LSWT is positively correlated with atmospheric air temperature (Livingstone et al. 1999) and given that there are *a priori* reasons to expect a relationship between the cladoceran community and surface water temperature, it is not surprising that summer LSWT is a significant explanatory variable for the composition of the fossil assemblage of Cladocera in the calibration data-set.

However, it is unexpected that a significant amount of variation in the Cladoceran assemblages should also be explained by SO_4. Since SO_4 is one of the major contributors to the salinity gradient (Cumming et al. 1995), a gradual increase in acidity across Scotland, Ireland and Norway due to sea salt deposition has been reported earlier (Harriman et al., 1995). Apart from sea salts, the main sources of sulphate in this region may also be from the forested catchments and atmospheric aerosols. Eimers and Dillon (2002) argued that climatic variability such as temperature and precipitation often has influences on temporal patterns of annual sulphate concentrations and sulphate export in forested catchments of upland streams and the dynamics of sulphate in upland lakes could possibly be regulated by those streams that drain into these lakes. Climate induced stream flooding is also found to be associated with anthropogenic greenhouse gases and sulphate aerosols (Milly et al., 2002). However, the mechanism on how the assemblage structure of Cladocera is driven by SO_4 independently is not known.

A significant amount of variation is also explained by the maximum depth, and this appears to be consistent with the most previous studies on cladoceran and other biotic assemblages in lakes (Korhola et al., 2000, Porinchu et al., 2002). Lake depth influences cladoceran assemblages through various mechanisms. Increased lake level results in an increased volume of the pelagic zone allowing extended planktonic habitats (Sarmaja-Korjonen and Alhonen 1999), and a relative reduction of littoral habitats (Schindler, 1998) causing distinct variations in the ratio of planktonic and littoral Cladocera (Alhonen 1970, Frey 1988, Hofmann 1998a, Korhola et al. 2000). The maximum depth is also reported to have a significant influence on the littoral community through lake stratification and changes in lake surface water temperature as discussed above (Walker et al. 1991; Shuter and Ing, 1996). As the fossil assemblages of Cladocera are well integrated before being preserved in the sediments (Frey 1988) they may also be used as indicators of lake level change (Korhola et al. 2000). However, Hofmann (1998a) cautioned that faunal assemblages preserved in deep water cores may not be sensitive to changes in lake level, while Birks (1998) highlights the use of the sub-fossil assemblages of biota retrieved from the lake centre to reconstruct the past hydrologic conditions of the lake including the depth and lake morphometry.

6.4.3 Transfer function model for Cladocera-inferred summer lake surface water temperature

The two-component PLS regression and calibration model was found to be the best inference model to predict summer LSWT in the calibration data-set. The performance of the model as indicated by a large λ_1/λ_2 (>0.50) value suggests that a reliable inference model for summer LSWT could be developed (e.g. Dixit et al., 1991). However, the rather low DCCA λ_1 compared to DCA λ_1 suggests that secondary environmental gradients are also important (Lotter et al., 1997; Pla et al., 2003). As a large number of low altitude lakes (100-500 m) with forested catchments were included in the calibration data-set, other environmental variables such as total phosphorous (TP) and fish predation (Jeppesen et al., 2003) may be additionally important. Unfortunately the calibration data-set lacks data for both total phosphorous and fish populations.

Until recently, only a few Cladocera-inferred air temperature models have been developed in Europe and none has been developed for summer LSWT. Lotter et al. (1997) developed the first model on Cladocera-inferred July air temperature model in the Swiss Alps. Their study yielded a two-component WA-PLS model for benthic cladocera ($r^2_{(jack)}$ = 0.821, RMSEP $_{(jack)}$ = 1.597 ^{0}C and maximum bias = 3.375 ^{0}C) and a PLS model for planktonic Cladocera ($r^2_{(jack)}$ = 0.715, RMSEP $_{(jack)}$ = 1.773 ^{0}C and maximum bias = 2.984 ^{0}C) as the best models. The results presented here are in accordance with those by Lotter et al. (1997) even though their inference model was based on mean July air temperature. Prediction models based on surface water temperature should not vary much from models associated with atmospheric temperature since air temperature and lake surface water temperature are usually highly correlated (Livingstone and Lotter 1998). Even though the air temperatures data were incorporated into RDA, the July air temperature data were not expected to be as important as summer LSWT in the training set. This is because on site air temperature data were generated using data from the nearest stations (e.g. Agusti-Panerada & Thompson, 2002), and those data might not always be reliable due to differences in temperature with respect to altitude and aspect (Odland et al. 1995). As described earlier, the prediction of summer LSWT appears to perform as well for July air temperature since a number of studies suggest that the growth and development of Cladocera are dependent on the changes in lake surface water temperature (Hofmann, 1996, Lotter et al., 1997; Korhola, 1999). The significance of LSWT on Cladocera

assemblages is further supported by the study of Hofmann (1993), where he found that Cladocera responded to deglaciation at the onset of the Holocene.

Korhola (1999) developed a Cladocera-inferred July lake surface water temperature model in sub-Arctic Fennoscandian lakes. The result of the PLS regression model on lake water temperature with $r^2_{(jack)} = 0.30$, RMSEP $_{(jack)} = 1.19\ ^0C$ and maximum bias = $0.94\ ^0C$) was as robust as this study. However, the low correlation coefficient in his model was due to a short temperature gradient in the training set. It has been widely accepted that expanding the training set sites would improve the quality of the inference model due to an increase in the heterogeneity of the biological and environmental variables (Korhola 1999, Porinchu et al. 2002). In the 'screened' calibration dataset with a range of $13\ ^0C$, the coldest lake (L186MED) during summer had a temperature about $7.5\ ^0C$. The temperature range in this study is still lower than the air temperature range ($>15\ ^0C$) in Lotter et al. (1997) suggesting that the inference model could be improved by expanding the calibration data-set.

6.5. Conclusions

Mountain lakes of northwest Europe are potentially good sensors of climate change. The assemblage structure of the surface sediment fossil remains of Cladocera across the 68 training set sites from the Scottish and Norwegian mountain lakes described here are significantly driven by mean lake surface water temperature in a direct gradient analysis. A variety of inference models for mean summer LSWT suggests that a two-component linear PLS model was the best inference model with $r^2_{(jack)} = 0.715$, RMSEP $_{(jack)} = 1.809\ ^0C$ and maximum bias = $1.895\ ^0C$ respectively. This is the first Cladocera-inferred transfer function model on lake surface water temperature developed for the region. The statistical data indicate that the model is suitable for reconstructing the past summer LSWT using the subfossil assemblage structure of cladocera preserved in late Holocene lake sediments. This is explained in the next chapter, which attempts to use the model to reconstruct temperature from the cladoceran record of Loch Coire Fionnaraich.

Most low altitude sites of Scotland and Norway are likely to be less sensitive to climate change than those sites located in high altitude regions, because low altitude lakes have warmer water and longer growing seasons. In addition, unlike high-altitude sites, these

sites can also be influenced by anthropogenic acitivity. Palaeoclimatologists always have difficulty in separating the impacts of human activity from natural climatic variability. As a result, palaeoclimate reconstruction from low altitude sites is not considered to be ideal (e.g. Battarbee, 2000). However, in spite of its relatively low altitude, Loch Coire Fionnaraich (LCFR) is a remote site with little catchment disturbance and is the key site for this study for reasons given above (Chapter 2, section 2.2.2).

Although not positioned in the centre of the temperature gradient represented on the training set, LCFR was considered a good site for palaeocliamte reconstruction due to the excellence of the sediment record, the diversity of its cladoceran fauna and the abundance of pre-existing chemical and biological data from other projects. Sediment core analysis and its climatic significance forms the subject of the next chapter.

Chapter 7

Recent Climate Change in Northwest Scotland: Inferred from subfossil assemblages of Cladocera

7.1 Introduction

This chapter highlights recent climate change in Northwest Scotland inferred from changes in the subfossil assemblage of Cladocera in a Scottish mountain loch, Loch Coire Fionnaraich. Many Northwest European mountain lakes are sensitive to climate change, caused by a combination of natural (e.g. solar radiation, volcanic aerosols, changes in earth's orbit) and internal forcing. More recently, greenhouse gas emissions from human activity are also considered to be an additional cause of rapid climate change (Wood et al., 1999). However, the pattern of climate variability over recent centuries and its expression on a regional basis is not yet fully established. In this chapter, an attempt is made to contribute to the understanding of recent climate variability based on a high-resolution study of changes in cladoceran assemblages in a core taken from Loch Coire Fionnaraich (LCFR), situated in a remote and climatically sensitive mountain region of Scotland. It explores the use of Cladocera as indicators of lake water temperature over this period using a Cladocera-inferred summer lake surface water temperature (LSWT) transfer function model described in Chapter 6.

7.2 Materials and methods

7.2.1 Field and laboratory methods

Descriptions of the study site, and field and laboratory methods are presented in detail in Chapter 2 (section 2.2) and Chapter 3 (sections 3.2.4 and 3.3.4). The analytical methods used for fossil Cladocera from LCFR2 are described in Chapter 3 in detail. At least 200 Cladocera remains from each sample were counted from the LCFR2 core. A list of cladoceran species recovered from LCFR2 is presented in Appendix 7.1.

Since the core LCFR1 was used for diatom and chrysophyte analyses in a separate NERC-funded project (Award No.: NER/B/S/2000/00752), this is not described in

detail here. However, results from LCFR1 were needed in this project for age modelling and comparison between diatom and chrysophytes data in LCFR1 and cladoceran data in LCFR2.

7.2.2 Numerical analyses

7.2.2.1 Zonation

The fossil assemblages of Claocera in LCFR2 were zoned by various cluster analysis techniques. All possible zonation methods such as, Optimal Binary Division, SPLITSQ, CONSLINK and CONISS (Birks and Gordon, 1985) were used in the program ZONE version 1.2 in order to obtain the best divisions (Juggins, University of Newcastle-upon-Tyne 1991, unpublished). ZONE combines CONSLINK, CONISS, binary splitting by least-square methods and information content and optimal splitting by least squares, and the variable barriers approach. The subsequent comparison of the partitions was made using the program BSTICK version 1.0 (Bennett, 1996; Birks, 1998).

The stratigraphic sequences are zoned with the concept of the 'assemblage zone'. It means that the part of sediment sequence is characterised by distinctive natural assemblages of microfossils (e.g. Hedberg, 1976). One way of zonation of sedimentary assemblages of microfossils including the Cladocera sequence can be carried out using splitting methods. In these methods, the sequence is divided stratigraphically in such a way that the sum of the variances of each zone is reduced as much as possible relative to the total variance in the whole data-set. The approach is either 'binary' or 'optimal'. In the binary approach, the data-set is divided into two best divisions, and the best division of one of those zones is again divided into two best divisions, and so on. In the optimal approach, the data-set is split directly into the desired number of zones. The 'best' division is the one that minimises the sum of variances at each stage. The variance is then measured using the least squares and information content (Bennett, 1996).

(a) Least squares:

$$\sum_{i} \sum_{k} (p_{ik} - q_{ik})^2 \qquad \textit{Equation 7.1}$$

(b) Information content:

$$\sum_{i} \sum_{k} (p_{ik} \log (p_{ik}/ q_{ik}))^2 \qquad \textit{Equation 7.2}$$

where,

p_{ik} l = proportion of microfossil type k in sample i

q_{ik} = mean proportion of microfossil type k in group of samples including i

The other way of zonation of sedimentary assemblages of microfossils including the Cladocera core sequence is carried out using agglomerative methods. In these methods, the data-set is searched for the most similar, stratigraphically-adjacent samples and those samples are then combined (van Tongeren, 1995). Gordon and Birks (1972) developed the method called constrained single link cluster analysis or CONSLINK and later Grimm (1987) developed a slightly modified agglomerative method from the previous one, called constrained incremental sum of squares clustering or CONISS.

7.2.2.2 Ordination

Detrended correspondence analysis (DCA) was used for cladoceran species present in the sediment core with detrending by segments, down-weighting of the rare taxa and non-linear rescaling of axes. Since the gradient length in DCA was less than 2 standard deviation unit, PCA was the most appropriate approach for indirect gradient analysis of the species data (Birks, 1995). A time trajectory analysis of the core sequence was also performed in PCA for Cladocera. Apart from cladoceran subfossil samples, PCA was also performed on the diatom and chyrsophyte subfossil samples in LCFR1, where data were obtained from Monteith and Pla (personal communication) for a multiproxy comparison.

7.2.2.3 Shannon-Wiener Diversity Index

The Shannon-Wiener Diversity index of Cladocera for samples in core LCFR2 was calculated on the basis of categories in a dataset and their proportions (http://math.hws.edu/javamath/ryan/DiversityTest.html). For example, there are n possible categories (species) in a data-set (sample) and their proportions are ρ_i,.....ρ_n. Then the measure of diversity for this system is defined as described by Levesque et al. (1996),

$$H^1 = - \sum_{i=1}^{n} \rho_i \log_n \rho_i \qquad \textit{Equation 7.3}$$

The Cladocera-inferred summer lake surface water temperature (LSWT) reconstructions were made using two independent approaches. First, a contemporary analogue approach was used, in which the response of sub-fossil assemblages of Cladocera to climate was assessed using a PCA time trend ordination by incorporating the subfossil samples into the modern temperature data-set as passive variables. Second a transfer function approach was used, in which the summer LSWT of Loch Coire Fionnaraich was reconstructed on the basis of the Cladocera-inferred linear PLS regression and calibration model developed in Chapter 6. The reconstruction of the past summer LSWT was performed in the programme CALIBRATE (version 0.81, Juggins and ter Braak, unpublished).

Correlations and regression techniques were also used to compare the relationship between the Cladocera-inferred reconstructed temperatures and the instrumental air temperature records as well as the North Atlantic Oscillation Indices during winter.

7.3 Results

7.3.1 Dry weight (DW) and loss-on-ignition (LOI)

No highly visible differences were observed between two core sequences, LCFR1 and LCFR2. Except for a short lighter section, 2-4 cm from the top of the cores, the sediment was homogeneously dark-brown organic mud. The percentage DW and LOI of the two cores were very similar (Figure 7.1a & b). The DW was almost constant until 10 cm where it gradually increased to a maximum at 8.5 cm. It remained high until near the core-top where it decreased markedly due to the high water content close to the mud-water interface (Figure 7.1a & b). The trend in LOI between the two cores was also similar. The LOI of LCFR1 was relatively high in the lower part of the core and then declined sharply from 9 cm depth (Figure 7.1a). The LOI profile of LCFR2 also declined from 9 cm and became constant for a short period and again increased sharply close to the top of the core. The highest and lowest records of LOIs in the two cores, however, did not match perfectly with depths suggesting that it was due to the variations in sediment resolution between two cores. The highest LOIs recorded in LCFR1 and LCFR2 were at 22.5 cm (37.67%) and 11.75 cm (35.73%) respectively while the lowest LOIs recorded were at 1.9 cm (17.27%) and at 8.75 cm (14.02%) respectively. A

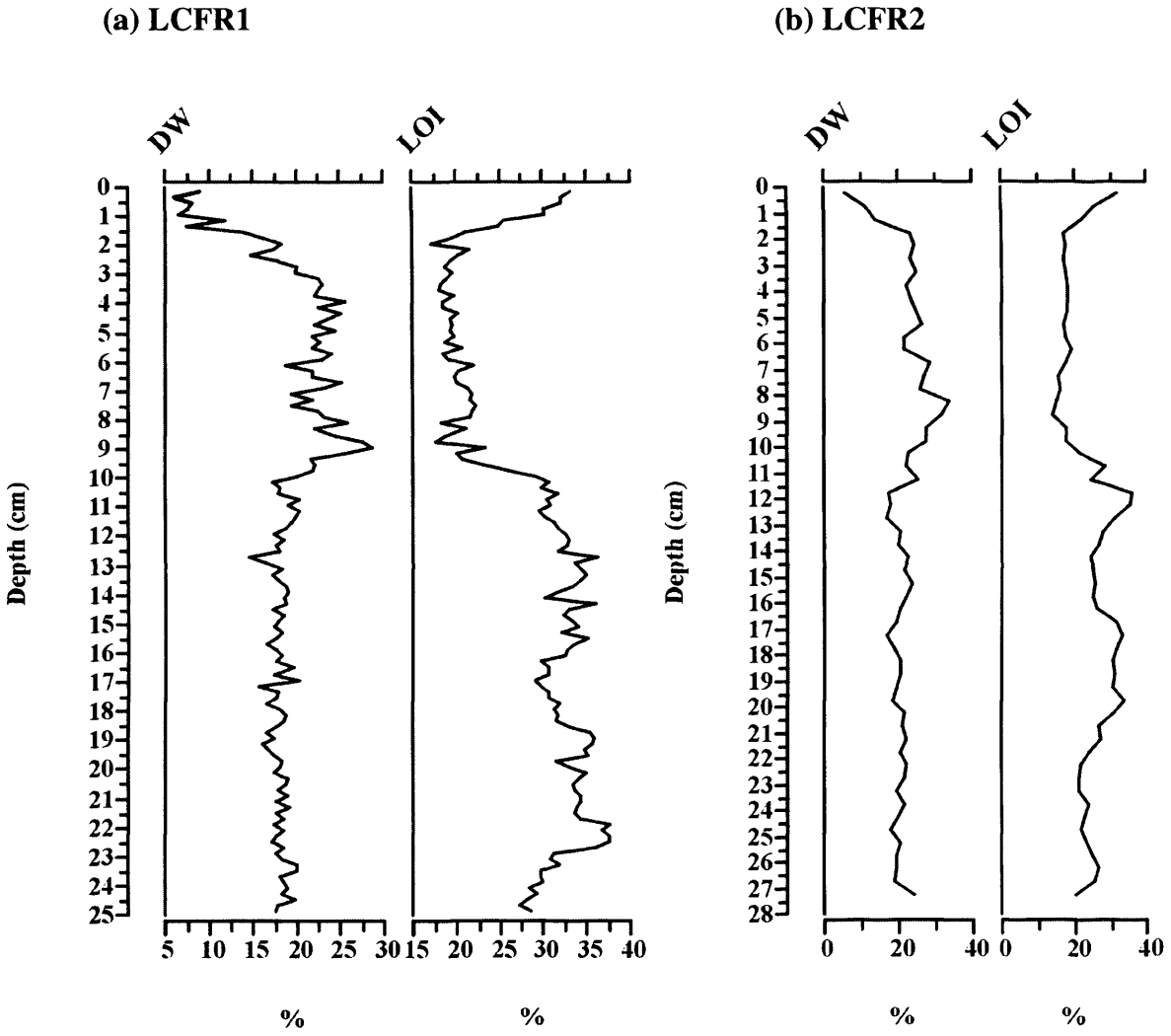


Figure 7.1: Percentage dry weight (DW) and loss on ignition (LOI) profiles of two core sequences (a. LCFR1 and b. LCFR2) retrieved from Loch Coire Fionnaraich, Scotland in May 2001. The resolution of LCFR1 and LCFR2 was 0.2 cm and 0.5 cm respectively.

comparison of the LOI records of the sediment cores is further highlighted in the cross correlation of LCFR1 and LCFR2 in section 7.3.3.

7.3.2 Chronology of LCFR1

The dried sediment samples from core LCFR1 were analysed for ^{210}Pb, ^{226}Ra and ^{137}Cs by direct gamma assay in the Liverpool University Environmental Radioactivity Laboratory, using Ortec HPGe GWL series well-type coaxial low background intrinsic germanium detectors (Appleby et al. 1986). The ^{210}Pb was determined via its gamma emissions at 46.5keV, and ^{226}Ra by the 295keV and 352keV γ-rays emitted by its daughter isotope ^{214}Pb following 3 weeks storage in sealed containers to allow radioactive equilibration. The ^{137}Cs was measured by its emissions at 662keV. The absolute efficiencies of the detectors were determined using calibrated sources and sediment samples of known activity. Corrections were made for the effect of self-absorption of low energy γ-rays within the sample (Appleby *et al.* 1992).

The results of the radiometric analyses are given in Table 7.1 and shown graphically in Figure 7.2. Unsupported ^{210}Pb activity in each sample was determined by subtracting ^{226}Ra activity from total ^{210}Pb activity.

Table 7.1. Fallout radionuclide concentrations in Loch Coire Fionnaraich core LCFR1 (Source: P. G. Appleby).

Depth		^{210}Pb						^{137}Cs	
		Total		Unsupported		Supported			
cm	g cm^{-2}	Bq kg^{-1}	±	Bq kg^{-1}	±	Bq kg^{-1}	±	Bq kg^{-1}	±
0.7	0.06	565.0	40.9	521.5	41.6	43.5	7.6	319.5	13.1
1.5	0.14	385.0	21.3	350.6	21.7	34.4	4.4	298.2	8.6
2.9	0.41	276.0	17.6	235.5	18.0	40.5	3.7	422.2	7.9
4.1	0.73	165.4	14.7	140.8	14.9	24.5	2.3	432.1	5.4
5.5	1.10	128.9	7.9	97.6	8.1	31.3	1.9	243.5	3.8
6.7	1.40	94.6	10.6	54.4	10.9	40.2	2.5	83.8	3.4
8.1	1.76	51.1	8.4	22.9	8.7	28.2	2.2	24.6	2.0
8.8	1.96	36.8	5.2	5.2	5.3	31.7	1.4	15.6	1.0
9.5	2.16	27.8	14.6	-9.2	14.8	37.1	2.7	7.3	2.1
10.7	2.41	31.3	9.3	-9.9	9.5	41.2	2.3	6.4	1.8
13.5	2.97	28.3	12.0	-4.0	12.2	32.2	2.0	0.0	0.0
14.7	3.22	40.4	11.0	0.0	11.5	40.3	3.1	2.2	1.9
16.1	3.49	29.2	10.2	-4.4	10.4	33.6	2.4	0.0	0.0

7.3.2.1 ^{210}Lead activity

Total ^{210}Pb activity reaches equilibrium with the supporting ^{226}Ra at a depth of around 9 cm (Figure 7.2a). The unsupported ^{210}Pb activity versus depth profile (Figure 7.2b) closely follows a simple exponential relation, suggesting relatively uniform sediment accumulation rates through time. There are however small but significant changes in the gradient of the ^{210}Pb profile at around 4 cm that coincide with a reduction in dry bulk density of the sediments. These changes may indicate some relatively minor changes in accumulation rates in recent decades.

7.3.2.2 Artificial Fallout Radionuclides

The ^{137}Cs activity versus depth profile (Figure 7.2c) has a relatively well-resolved peak at a depth of between 2.8-4.2 cm that almost certainly records the 1963 fallout maximum from the atmospheric testing of nuclear weapons.

7.3.2.3 Core Chronology of LCFR1

Figure 7.3 shows ^{210}Pb dates calculated using the constant rate of supply (CRS) and constant initial concentration (CIC) dating models (Appleby and Oldfield, 1978), together with the 1963 depth determined from the ^{137}Cs record. The two ^{210}Pb models are in relatively good agreement above 4.1 cm, and consistent with the ^{137}Cs date, both placing 1963 at between 3.8-4.0 cm. In the deeper sections of the core there is however a widening discrepancy between the CIC and CRS models. The CIC model places gives a date of c.1900 for the sample at 8.1 cm. In contrast, the CRS model dates sediments at this depth to the mid-19th century.

Due to a combination of relatively small samples sizes and low activities it was difficult to obtain accurate ^{210}Pb measurements in samples close to ^{210}Pb/^{226}Ra activity and it is likely that the ^{210}Pb results given in Table 7.1 for samples below 8.1 cm under-estimate the true activity. Nonetheless, using the methods described in Appleby (2001) a date of 1846 ± 22 years was obtained for sediments at the deepest level at which unsupported ^{210}Pb was detected (8.8 cm). This date was used as a reference point to calculate revised CRS model dates for the more recent samples. The results are shown in Figure 7.3, and given in detail in Table 7.2.

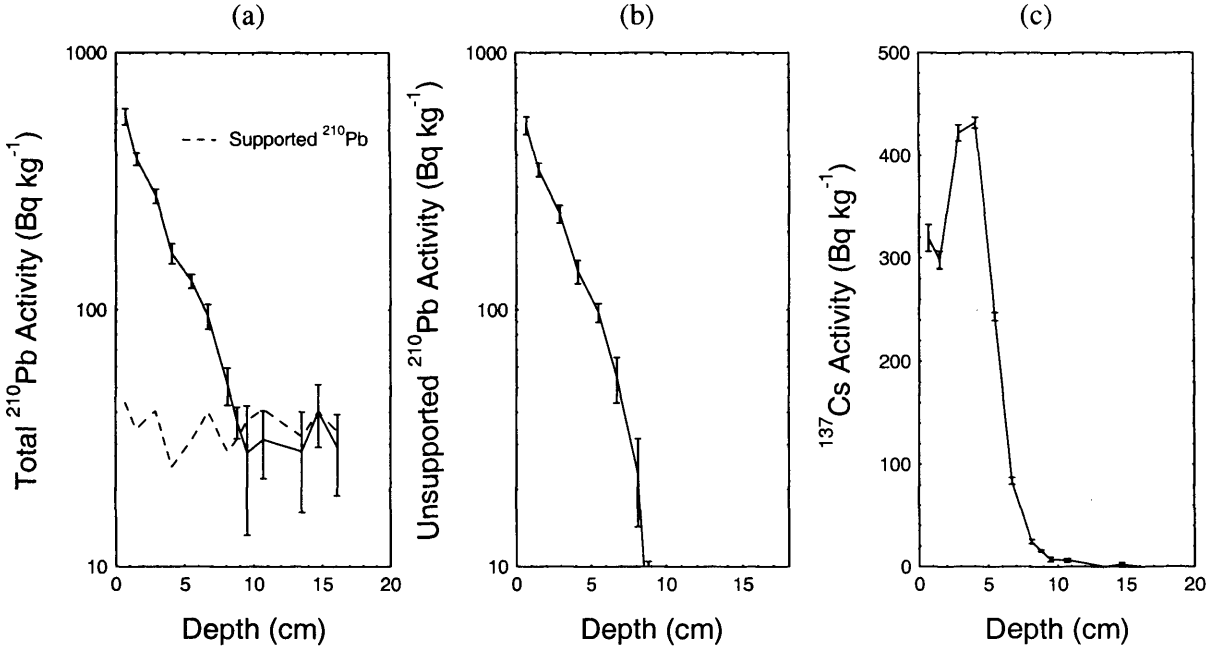


Figure 7.2: Fallout radionuclides in the Loch Coire Fionnaraich sediment core LCFR1 showing (a) total and supported ^{210}Pb, (b) unsupported ^{210}Pb, (c) ^{137}Cs concentrations versus depth (Source: P. G. Appleby).

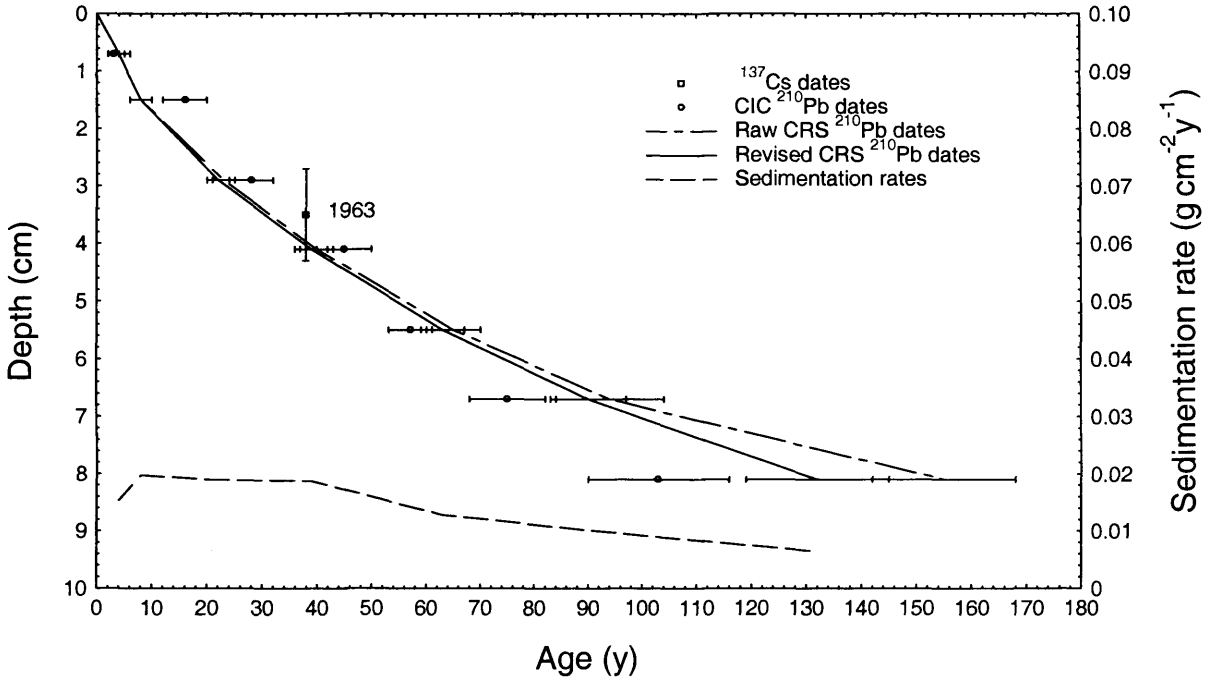


Figure 7.3: Radiometric chronology of Loch Coire Fionnaraich sediment core LCFR1 showing the raw CRS and CIC model ^{210}Pb dates, and the 1963 depth determined from the ^{137}Cs stratigraphy. Also shown are the corrected CRS model ^{210}Pb dates calculated using the estimated sediment accumulation rate near the base of the ^{210}Pb record, and the accumulation rates versus time (Source: P.G. Appleby).

Table 7.2. ^{210}Pb chronology of Loch Coire Fionnaraich core LCFR1 (Source: P. G. Appleby).

Depth		Chronology			Sedimentation Rate		
cm	g cm^{-2}	Date AD	Age y	±	g cm^{-2} y^{-1}	cm y^{-1}	± (%)
0.0	0.00	2001	0	0			
0.2	0.02	1999	2	1	0.015	0.20	8.9
0.4	0.03	1999	2	1	0.015	0.20	9.0
0.6	0.05	1998	3	1	0.015	0.27	9.1
0.8	0.07	1997	4	2	0.016	0.16	9.0
1.0	0.09	1996	5	2	0.017	0.16	8.7
1.2	0.11	1994	7	2	0.018	0.16	8.3
1.4	0.13	1993	8	2	0.019	0.13	8.0
1.6	0.16	1992	9	2	0.020	0.13	8.0
1.8	0.20	1990	11	2	0.020	0.11	8.3
2.0	0.23	1988	13	2	0.019	0.10	8.5
2.2	0.27	1986	15	2	0.019	0.10	8.8
2.4	0.31	1984	17	2	0.019	0.10	9.1
2.6	0.35	1982	19	2	0.019	0.09	9.3
2.8	0.39	1980	21	2	0.019	0.080	9.6
3.0	0.44	1977	24	2	0.019	0.080	10.0
3.2	0.49	1974	27	2	0.019	0.073	10.5
3.4	0.54	1972	29	2	0.019	0.073	11.0
3.6	0.59	1969	32	2	0.019	0.073	11.6
3.8	0.65	1966	35	2	0.019	0.067	12.1
4.0	0.70	1963	38	3	0.019	0.067	12.6
4.2	0.75	1960	41	3	0.018	0.062	13.0
4.4	0.81	1957	44	3	0.017	0.062	13.3
4.6	0.86	1953	48	4	0.017	0.057	13.6
4.8	0.91	1950	51	4	0.016	0.057	13.8
5.0	0.97	1946	55	4	0.015	0.062	14.1
5.2	1.02	1943	58	5	0.014	0.057	14.4
5.4	1.07	1940	61	5	0.013	0.053	14.6
5.6	1.13	1936	65	5	0.013	0.050	15.9
5.8	1.18	1931	70	6	0.012	0.044	18.0
6.0	1.23	1927	74	7	0.012	0.044	20.2
6.2	1.28	1922	79	8	0.011	0.047	22.3
6.4	1.33	1918	83	9	0.011	0.042	24.5
6.6	1.38	1914	87	10	0.010	0.040	26.7
6.8	1.43	1908	93	10	0.010	0.036	28.1
7.0	1.48	1902	99	11	0.009	0.033	29.0
7.2	1.53	1896	105	11	0.009	0.033	29.8
7.4	1.58	1890	111	10	0.008	0.033	30.6
7.6	1.63	1884	117	11	0.008	0.033	31.5
7.8	1.68	1878	123	12	0.007	0.033	32.3
8.0	1.73	1872	129	13	0.007	0.033	33.1

7.3.3 Core correlation bewtween LCFR1 and LCFR2

If two or more cores are taken from the same lake, it is often possible to date all cores using a stratigraphic correlation with a single dated master core. This can be achieved usually on the basis of bulk sediment analysis such as LOI profiles of two cores. However, depending on sampling methods, a variety of techniques have been used for core correlation. A visual inspection technique can be used based on LOI plots of two cores. Core smoothing can also be carried out and if necessary numerical sequence slotting methods can be used. Since the cores, LCFR1 and LCFR2 had different sampling resolutions the sequence slotting method was not considered appropriate here due to the possibility of a 'blocking' error (Birks pers. com.). Therefore, the LOIs of the two cores were correlated by visual inspection after smoothing (Figure 7.4).

The ages for the undated sections of the cores were estimated on the basis of a linear extrapolation presented in Figure 7.4. For example, the sediment accumulation rates and ^{210}Pb dating of LCFR1 suggest that for the last six measurements, there was a constant accumulation rate of 0.033 cm yr^{-1} and the age at 8 cm was 1872 A.D. Thus it was assumed that the accumulation rate of LCFR2 at 8 cm was also 0.033 cm yr^{-1} and the date was also 1872 A.D. Since the length of the LCFR2 was 27.5 cm, the undated section of the core would be 27.5 – 8 cm = 19.5 cm. The approximate amount of time required for sediment accumulation over 19.5 cm was, 19.5/0.033 = 590.90 years. When converted into A.D., the date for 27.5 cm depth would be about 1872 -591 = 1281 A.D.

There are other methods available for dating recent sediments and the core cross-correlation. Rose et al. (1995) developed the spheroidal carbonaceous particle (SCP) dating technique. This technique is particularly useful for mid-to late-nineteenth century sediments where, because of radiactive decay ^{210}Pb dating is progressively less useful (e.g Rose et al., 1995). The comparison between ^{210}Pb (Appleby unpublished data) and SCP (Rose unpublished data) dating of LCFR1 was found to be in good agreement (Figure 7.5).

7.3.4 Chronology of LCFR2

The age-depth data for LCFR2 is shown in Table 7.3 and plotted in Figure 7.6. The chronology is based on a visual correlation between the LOI profiles of two cores LCFR1, the ^{210}Pb-dated core, and LCFR2 (Figure 7.4).

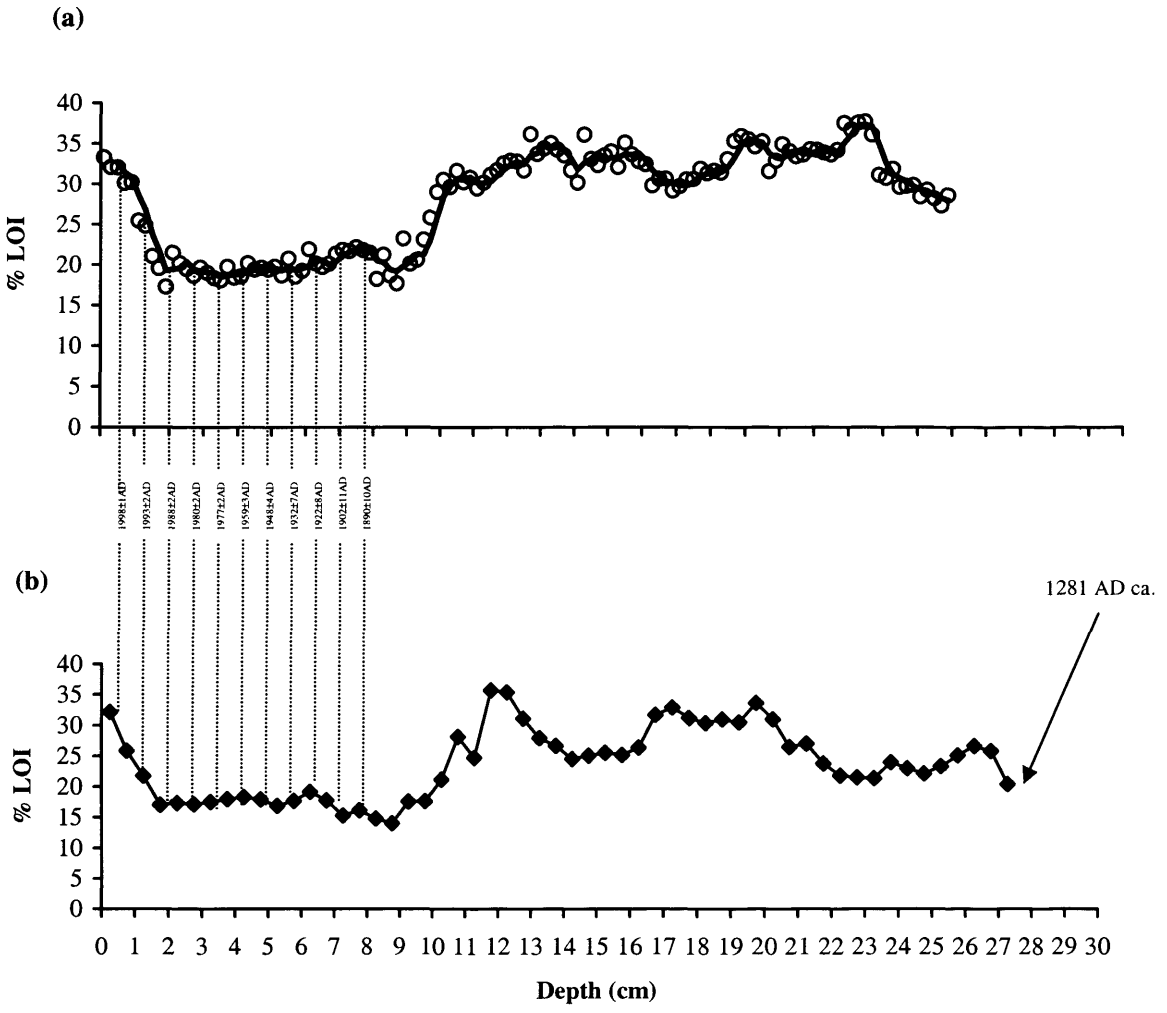


Figure 7.4: Core cross-correlations between (a) LCFR1 and (b) LCFR2 on the basis of their LOI profiles. The core, LCFR1 was dated (^{210}Pb) down to 8 cm. The dating for the end of LCFR2 was based on a linear extrapolation; the rate of accumulation of the LCFR1 sequence at 7-8 cm. The accumulatioin rate of LCFR1 is presented in Table 7.2. Smoothing of curve = 2 units moving average.

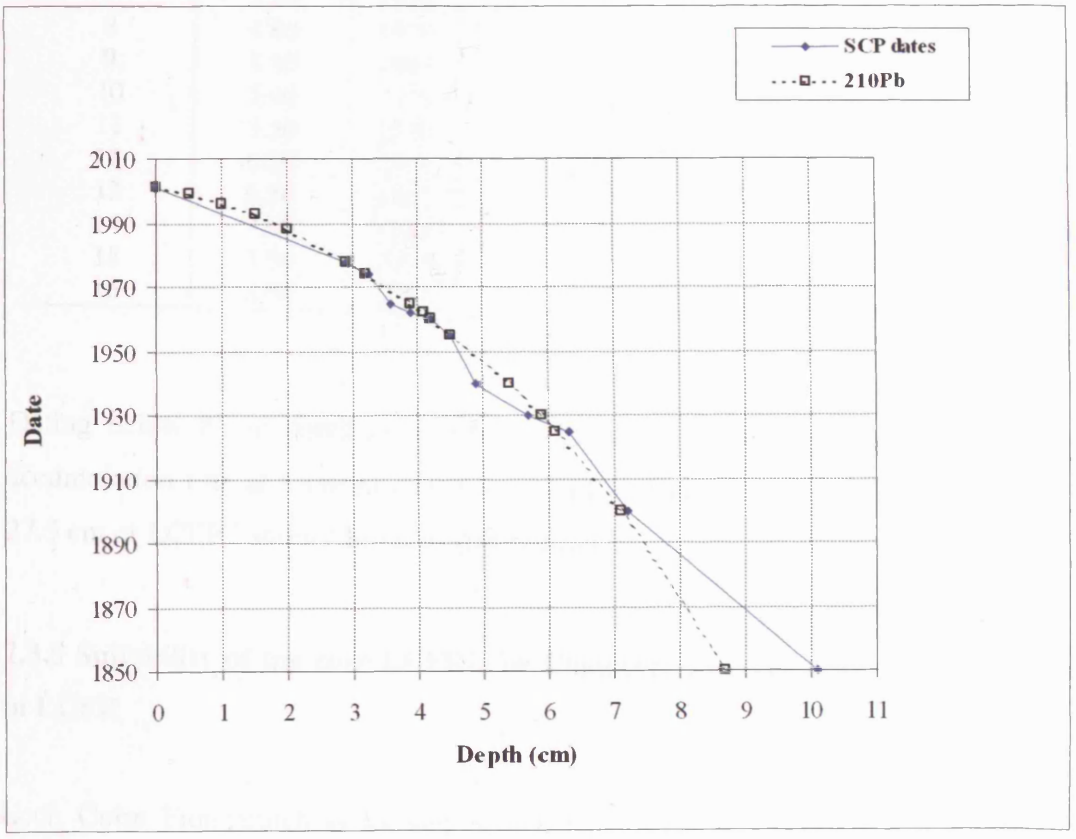


Figure 7.5: Cross correlation between ^{210}Pb and SCP dating of sediment of Loch Coire Fionnaraich, Scotland. (Source: Neil Rose)

Table 7.3: Chronology of LCFR2 correlation with LCFR1. Details of the sediment accumulation rates for LCFR1 is presented in Table 7.2 (Source: P. G. Appleby).

Sample no.	Depth (cm)	Date	Age (year before present	±	Sedimentation rate ($g\ cm^{-2}\ y^{-1}$)
0	0	2001	0	0	
1	0.50	1998	3	1	0.015
2	1.00	1996	5	2	0.017
3	1.50	1993	8	2	0.019
4	2.00	1988	13	2	0.019
5	2.50	1984	17	2	0.019
6	3.00	1980	21	2	0.019
7	3.50	1978	23	2	0.019
8	4.00	1970	31	2	0.019
9	4.50	1962	39	3	0.019
10	5.00	1959	42	3	0.018
11	5.50	1948	52	4	0.016
12	6.00	1932	69	7	0.012
13	6.50	1922	79	10	0.011
14	7.00	1918	83	10	0.011
15	7.50	1902	91	12	0.009
16	8.00	1890	111	14	0.008

Dating below 8 cm depth in LCFR2 is based on extrapolation using the sediment accumulation rate at 8 cm as shown by LCFR1. Thus the dating between 8.5 cm and 27.5 cm of LCFR2 should be used with caution.

7.3.5 Suitability of the core LCFR2 for Cladocera-inferred climate reconstruction in LCFR

Loch Coire Fionnaraich is located in a remote Scottish mountain range, and has a relatively undisturbed catchment. The contemporary survey and the taphonomic study of Cladocera described in Chapter 4 and 5 show that the loch contains a diverse group of Cladocera and that these animals are well-represented in the calibration data-set (Chapter 6). However, changes in the loss on ignition over the last 100 years or so indicate that some disturbances in the catchment has occurred (Figure 7.1). The reason for this is not known, although diatom analysis (Flower pers. comm.) suggests that there was little impact on the lake. LCFR was therefore considered a good site.

For the analysis of subfossil assemblages of Cladocera and the reconstruction of climate change using the Cladocera-inferred temperature transfer function developed in Chapter 6. In addition, unlike many remote oligotrophic lakes, the LCFR cores have a rapid

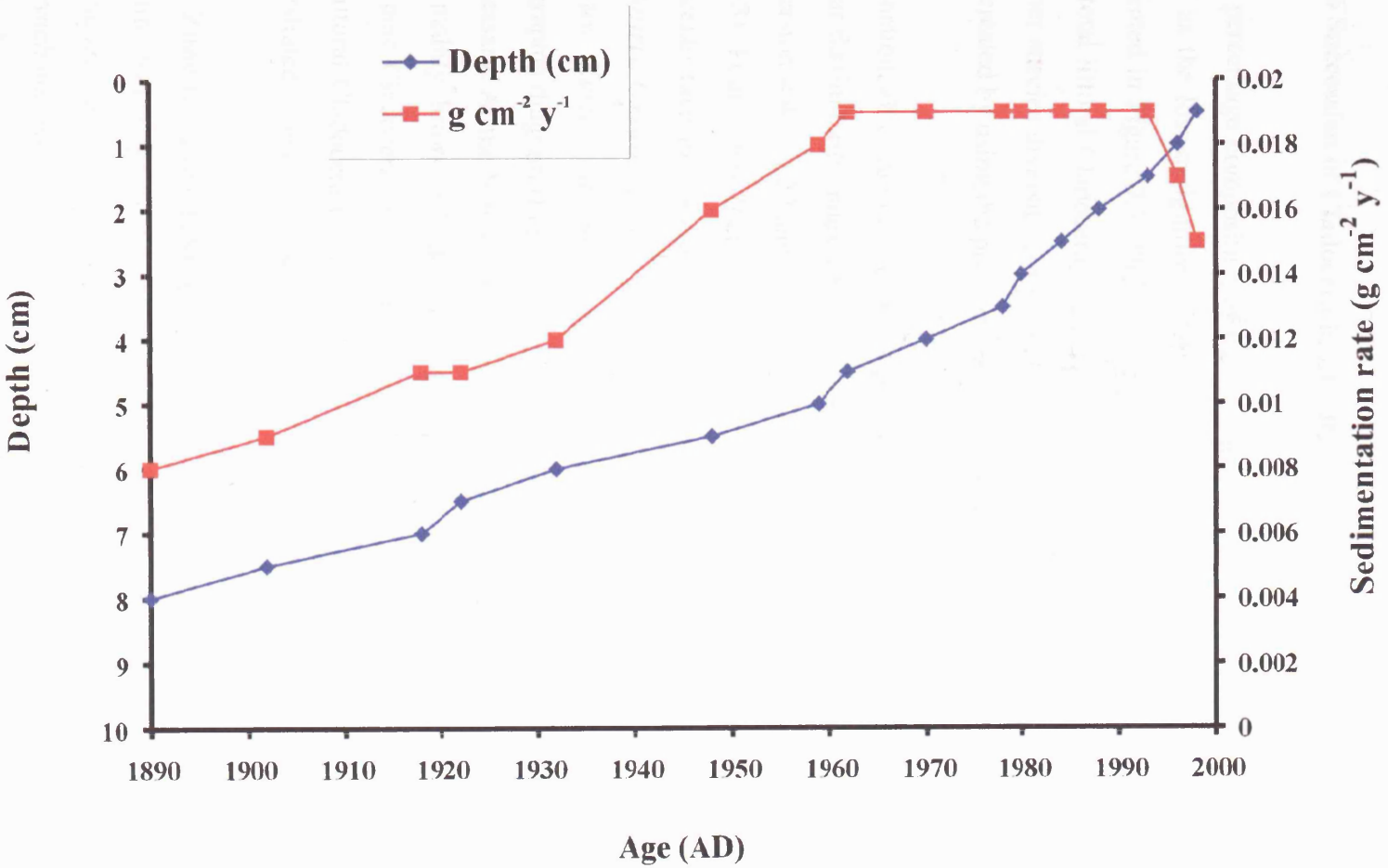


Figure 7.6: Age-depth model of LCFR2 based on ^{210}Pb chronology to 8cm depth profile of Loch Coire Fionnaraich after comparision with LCFR1. For detail, also see Table 7.3 and the sediment accumulation rates presented for LCFR1 in Table 7.2 (Source: P.G. Appleby).

sediment accumulation rate. As a result, the cores provide a decadal and sub-decadal time resolution, enabling the sediment record to be matched with the instrumental meteorological records.

7.3.6 Succession of Cladocera in LCFR2

The percentage composition of the total planktonic and the littoral cladoceran taxa as well as the loss-on-ignition (LOI) of the core sequence is plotted against depth and presented in Figure 7.7. The percentage composition of principal taxa, total planktonic and total littoral Cladocera, the LOI, PCA axes and the species richness and Shannon-Wiener species diversity are plotted in Figure 7.8. The Cladocera stratigraphic diagram was created by using the programme C2 (Juggins, 2003).

In zonation, all techniques (Optimal Binary Division, SPLITSQ and CONISS) showed a similar dissimilarity index where high dispersion was obtained in between 6 and 6.5 cm (dispersion = 4.74), 22 and 22.5 cm (dispersion = 2.18) and 25.5 and 26 cm (dispersion = 3.13). Four zones (Lcf-1, Lcf-2, Lcf-3 and Lcf-4) were therefore identified. Rare cladoceran taxa in the core sequence such as, *Eurycercus lamellatus*, *Camptocercus rectirostris*, *Oxyurella tenuicaudis*, *Alonella rostrata*, *Alona quadrangularis*, *Pleuroxus aduncus*, *Kurzia latissima*, *Anchistropus emarginatus* are clearly visible in the stratigraphic diagram (Figure 7.7) so are not emphasised in the discussion section unless if necessary. At the bottom of the core, the Cladocera fauna was dominated by littoral taxa, mainly littoral Chydorids, and gradually the relative abundance of the total planktonic Cladocera, mainly *B. coregoni*, increased with a reciprocal decrease in the total littoral Cladocera (Figure 7.8). The Shannon Wiener species diversity index also demonstrated a decline of species diversity over time (Figure 7.8).

7.3.6.1 Zone Lcf-1 (ca. 1281 AD – ca. 1327 AD; 27.25-25.75 cm)

According to the age model, this zone lasted for about 50 years. The main features of this zone are the absence of *Daphnia* and some littoral taxa such as *Monospilus dispar* and *Rhynchotalona falcata*, and the low abundance of other planktonic taxa, *B. coregoni* and *B. longispina,* and the relatively higher abundance of three littoral taxa *Graptoleberis testudinaria, Alona intermedia* and *Chydorus piger* (Figure 7.8). The species richness and the Shannon Wiener species diversity index are also high at the initial phase of this zone and declined gradually (Figure 7.8).

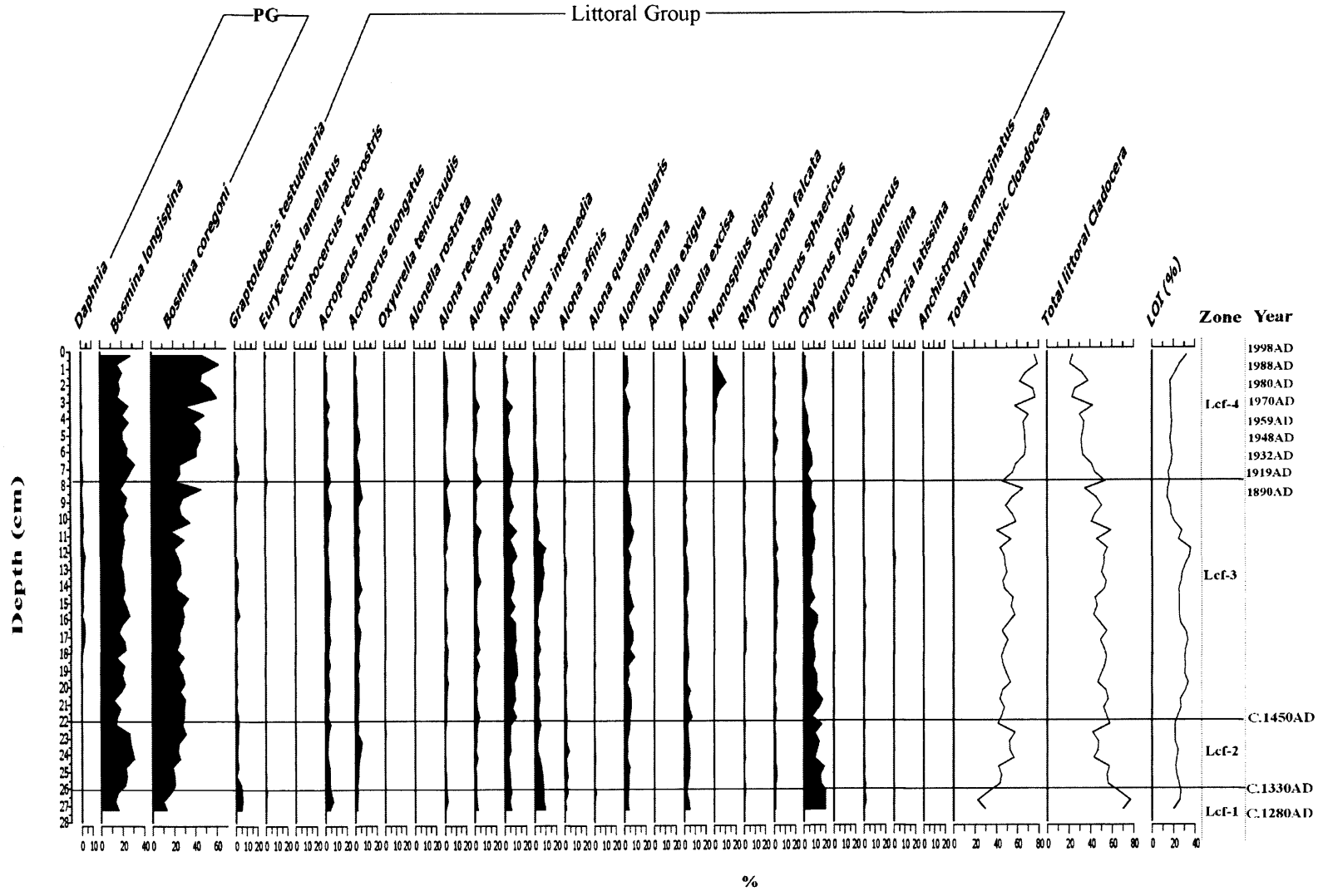


Figure 7.7: Stratigraphic representation of sub-fossil assemblage of Cladocera taxa recovered from the Loch Coire Fionnaraich, Scotland. The ^{210}Pb chronology is given on the right side of the diagram. The zones (Lcf-1 to Lcf-4) are determined by minimum-variance cluster analysis (CONISS). PG stands for Planktonic Group..

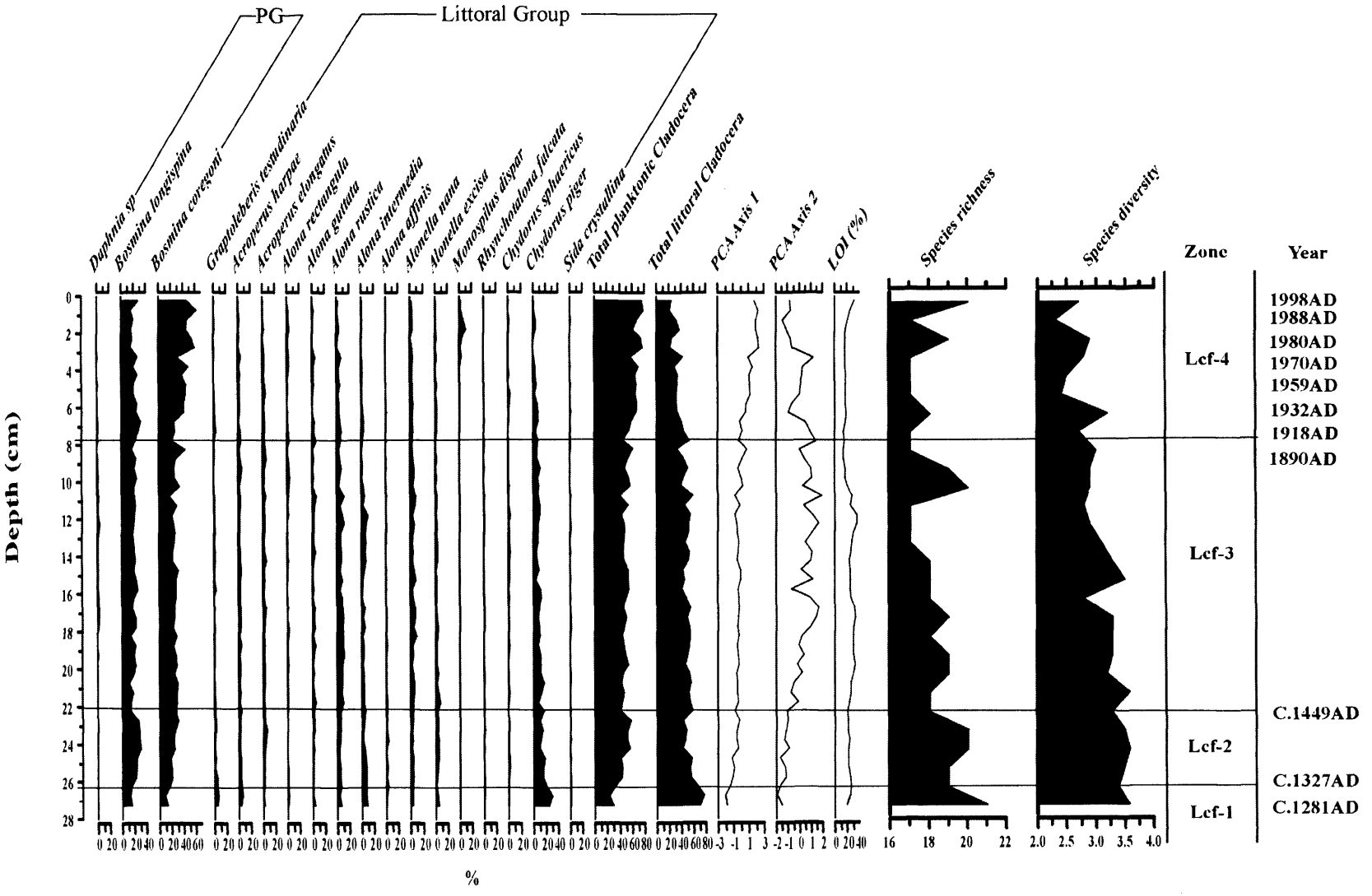


Figure 7.8: Stratigraphic representation of sub-fossil assemblage of principal Cladocera and the PCA axis 1 and PCA axis 2 of each taxon recovered from the Loch Coire Fionnaraich, Scotland. The ^{210}Pb chronology is given on the right side of the diagram. The zones (Lcf-1 to Lcf-4) are determined by minimum-variance cluster analysis (CONISS). PG stands for Planktonic Group.

7.3.6.2 Zone Lcf-2 (ca. 1327 AD – ca. 1439 AD; 25.75-22.25 cm)

This zone lasted for about 100 years according to the age model. This zone is more stable in terms of the abundance of total planktonic and littoral Cladocera, though the abundance of planktonic taxa, *B. coregoni* and *B. longispina* increases rapidly and there is a sharp decrease of some littoral taxa such as *Chydorus piger* and *Graptoleberis testudinaria*. The planktonic taxon, *Daphnia* and the two littoral taxa, *R. falcata* and *M. dispar*, were absent in this zone (Figure 7.8). The species richness and the Shannon Wiener species diversity index are variable in this zone. The species diversity increased from about 1327AD and became highest, and again declined to the lowest in about 1449AD (Figure 7.8).

7.3.6.3 Zone Lcf-3 (ca. 1439 AD – ca. 1919 AD; 22.25-6.25 cm)

This zone is the longest zone, lasting for more than 400 years. The assemblages of Cladocera were fairly constant throughout the period. However, there is a sharp decline at the end of the 18th century being lowest at the Lcf-3 and Lcf-4 boundary. Another important feature of this zone is the appearance of the planktonic taxon, *Daphnia,* and littoral taxa *Rhynchotalona falcata* and *Kurzia latissima* (Figure 7.8). The Shannon Wiener species diversity index continues to decline in this zone (Figure 7.8).

7.3.6.4 Lcf-4 (ca. 1919 AD – ca. 1998 AD; 6.25 –0.25 cm)

This zone is the most varied zone in the whole sequence and lasted about 80 years. The large planktonic Cladocera, *Daphnia,* disappeared, while the smaller taxon, *B. coregoni* increased significantly. Except for *Monospilus dispar*, the abundance of most littoral Cladocera, particularly *Chydorus piger*, declined significantly. *M. dispar,* however, was absent in the beginning but became dominant after 1950 AD. A littoral taxon, *Eurycercus lamellatus*, also appeared briefly around the Lcf-3 and Lcf-4 boundary (Figure 7.8). Some littoral Cladocera, such as *R. falcata*, *Alona affinis* and *Sida crystallina,* were uncommon in this zone. The loss-on-ignition increased sharply after 1990 AD (Figure 7.8). Similarly, in this zone, the Shannon Wiener species diversity index also declined significantly (Figure7.8).

7.3.7 Cladocera analysis through ordinations

7.3.7.1 Detrended correspondence analysis (DCA)

Of 26 cladoceran species present in 55 sub-fossil samples of Loch Coire Fionnaraich, DCA showed that the first two axes together accounted for 47% of the cumulative

variation of the species data (Table 7.4). The gradient length or standard deviation of species data after DCA was 0.79 (<2 SD) suggesting that the overall species data were linearly distributed with depth. Thus PCA was chosen as the most appropriate method to determine the response of the Cladocera fauna to the latent variables.

Table 7.4: Summary of DCA ordination of Cladocera assemblage in 55 core samples in Loch Coire Fionnaraich, Scotland.

DCA axes	1	2	3	4
Eigenvalues (λ)	0.061	0.024	0.009	0.006
Lengths of gradient (standard deviation units)	0.791	0.637	0.437	0.447
Cumulative percentage (%) variance of species data	33.8	46.8	51.0	54.8
Sum of all unconstrained eigenvalues				**0.182**

7.3.7.2 Principal components analysis (PCA)

The PCA of species data shows that the PCA axis 1 and 2 explained the maximum variation in the species data where those two axes accounted for 44.0% and 13% of the total variation (Table 7.5).

Table 7.5: Summary of PCA of 55 core samples Cladocera in Loch Coire Fionnaraich.

PCA Axes	1	2	3	4
Eigenvalues (λ)	0.440	0.131	0.071	0.054
Variance explained (cumulative %) in the environmental data	44.0	57.1	64.2	69.6

7.3.7.3 Succession of Cladocera as shown by PCA axes

When the percentage composition of principal Cladocera taxa, total planktonic and total littoral Cladocera, the LOI, and the species richness and the Shannon-Wiener species diversity index is plotted together with the first two PCA axes in the stratigraphic diagram, the PCA axis 1 curve shows a very similar trend with *B. coregoni* and total planktonic Cladocera (Figure 7.8). The PCA axis 1 curve increases gradually from the bottom to the top. According to the age model, the pace of increment of the PCA axis 1 is, however, slow until the boundary zone between Lcf-3 and Lcf-4. In about 1920 AD, it became rapid (Figure 7.8). Unlike the PCA axis 1, the PCA axis 2 shows a rather variable trend (Figure 7.8). The PCA axis 2 shows a positive relation with littoral taxa, mainly *Alona rustica, Alona intermedia* and *Alonella nana* in the first three zones (Figure 7.7). According to the age model, except for some species of littoral Cladocera

(e.g. *M. dispar*, *R. falcata*), the percentage composition of littoral taxa in zone Lcf-3 (ca. 1439 AD - ca. 1919 AD) is rather high and subsequently declines after that period (Figure 7.8). The PCA axis 1 curves show a reciprocal trend to the Shannon-Wiener species diversity index, but the PCA axis 2 does not seem to have important relationships with the species diversity index (Figure 7.8).

7.3.7.4 Succession of Cladocera as shown by the PCA time-track

The PCA solution file from CANOCO 4.5 was used to construct a time trajectory in the programme CALIBRATE (version 0.81, Juggins and ter Braak, unpublished). The main objective of the time-track analysis was to show the depths where the significant changes in sub-fossil assemblages of Cladocera in LCFR2 occurred. While doing this, the graph style was modified by joining the samples into a time series. The PCA sample scores for axis 1 and axis 2 showed a clear time trajectory, where the major changes were observed at 2.5/3.0 cm, 6.25/6.5 cm and 22.5/23 cm depths (Figure 7.9). The time track along PCA axis 1 and 2 indicates significant environmental gradient for a rapid change of the recent cladoceran community in the Loch Coire Fionnaraich (Figure 7.9).

7.3.8 Cladocera-inferred summer lake surface water temperature (LSWT) reconstruction using the transfer function approach

On the basis of the screened calibration data-set (n=64), a summer (June, July, August) lake surface water temperature (LSWT) transfer function model was developed in Chapter 6. Here the model is applied to reconstruct the past summer LSWT of Loch Coire Fionnaraich using the samples of the cladoceran assemblages from the core LCFR2.

The model is considered to be robust due to the relatively low RMSEP (1.8 ^{0}C), high r^2 (0.71) values and low maximum bias (1.94 ^{0}C). More than 85% of the cladoceran species in LCFR2 are also represented by Cladoceran taxa present in the modern calibration data-set indicating that the reconstruction of past summer LSWT of Loch Coire Fionnaraich should be reliable (e.g. Birks, 1998). There are also good analogues for the core samples in the modern training set as shown by a joint PCA ordination of modern and subfossil samples of the cladoceran assemblages (Figure 7.10).

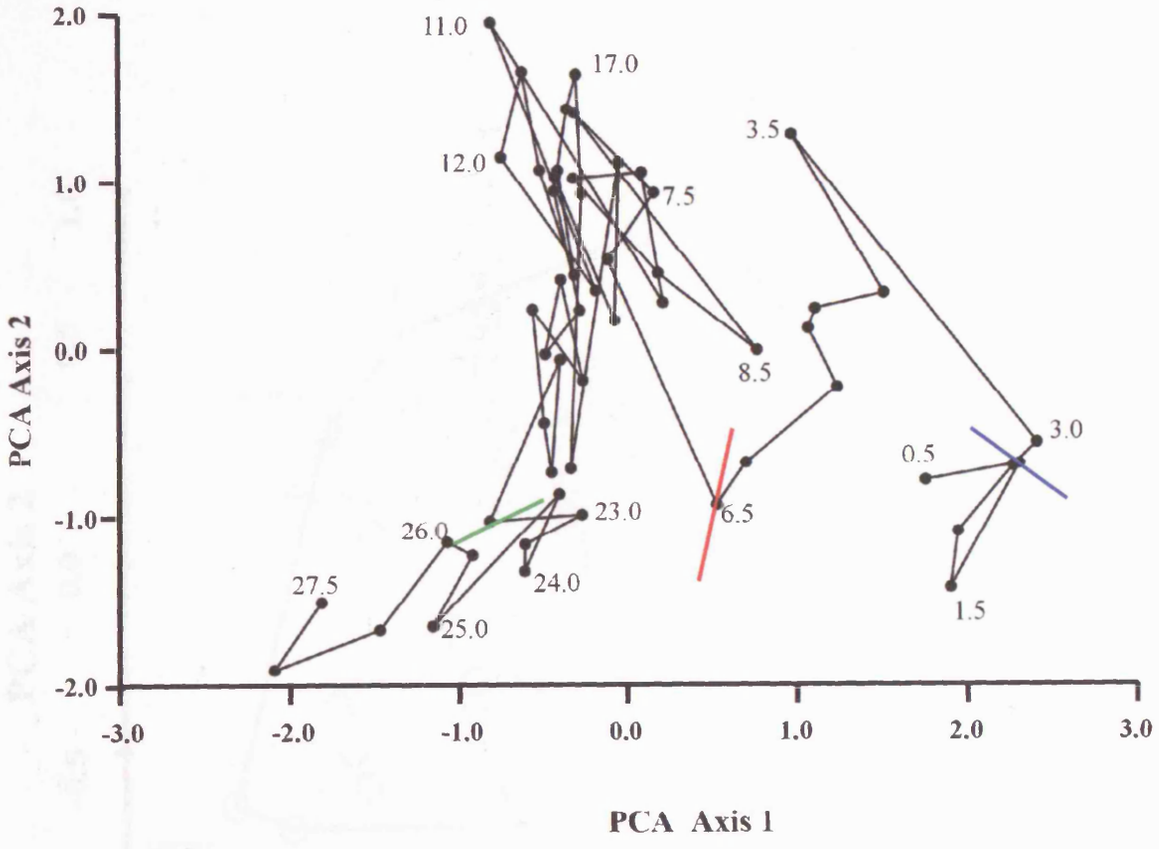


Figure 7.9: Time-track analysis of 55 Cladocera samples using a PCA biplot ordination along axis 1 and 2 in Loch Coire Fionnaraich, Scotland. The labelled numbers are depth (cm) of the sediment core, LCFR2. Major changes of subfossil assemblages of Cladocera in LCFR2 are shown by markers (_____).

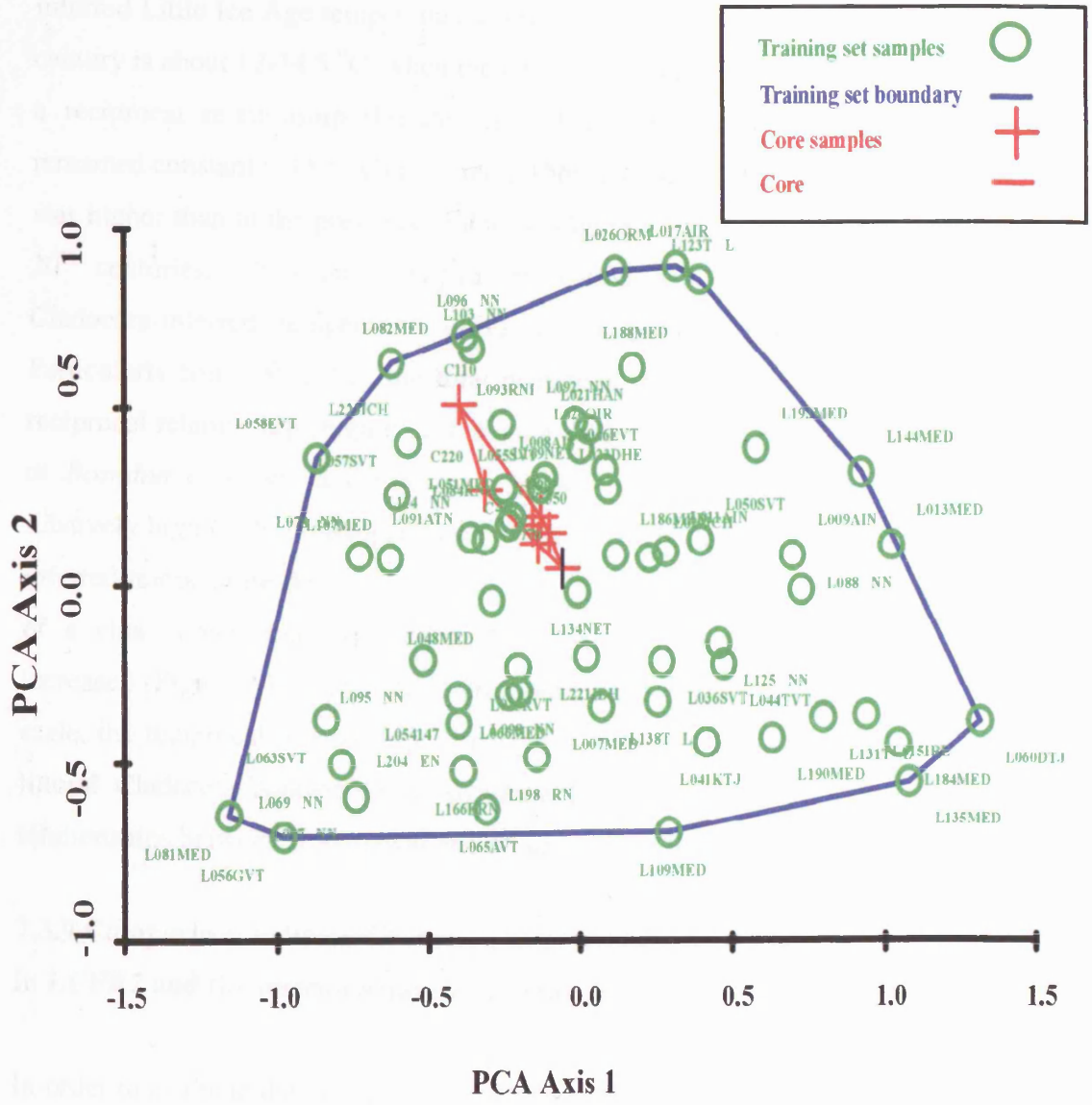


Figure 7.10: PCA of subfossil assemblages of Cladocera in core samples (red) and modern samples (green with blue boundary). The subfossil samples are passively incorporated in the ordination.

The ^{210}Pb dating for the lake sediment was carried out only for the top 8 cm of the core, thus there is increased uncertainty in the age model before about 1890 AD. However, assuming a constant accumulation rate, the base of the core is estimated to be 1281 AD, the start of the Little Ice Age (Figure 7.11, Figure 7.12). Application of the Cladocera-inferred summer LSWT model to the Cladocera stratigraphic data shows that the inferred Little Ice Age temperature at the end of 13th century and the beginning of 14th century is about 12-14.5 ^{0}C, when the total planktonic and total littoral Cladocera shows a reciprocal relationship (Figure 7.11). However, mostly the inferred temperature remained constant (~15.5 ^{0}C) between c.1569AD and c.1782 AD, when the temperature was higher than in the previous centuries (Figure 7.11). In the late 19th and most of the 20th centuries, when the industrial revolution was already well established, the Cladocera-inferred temperature curve shows a very marked climatic variability. Particularly from 1920 AD, the total planktonic and littoral Cladocera show a strong reciprocal relationship (Figure 7.11, Figure 7.12). At about 30 years BP, the abundance of *Bosmina coregoni*, a mesotrophic planktonic taxon (Hofmann, 1986) indicates a relatively high (>15 ^{0}C) temperature (Figure 7.11). Following 1970 AD, the Cladocera-inferred temperature declined to about 12.5 ^{0}C for a short period, when the abundance of a clear water and sand-preferring taxon, *Monospilus dispar* (Hofmann, 1986) increased (Figure 7.11). The temperature inference curve shows that, on a century time scale, the reciprocal relationships between the total planktonic Cladocera and the total littoral Cladocera appears to be significant, but for a decadal scale, the reciprocal relationships between *B. coregoni* and *M. dispar* are significant (Figure 7.11).

7.3.9 Comparison between Cladocera-inferred reconstructed summer LSWT using in LCFR2 and the instrumental temperature records

In order to evaluate the performance of the model, the Cladocera-inferred reconstructed summer LSWT in LCFR using the transfer function approach was compared with the CET data series and the local instrumental temperature records. The CET data series is taken as one of the most representative instrumental data-series in Northwest Europe (Jones et al., 1997). However, the Cladocera-inferred-summer LSWT does not match with the CET pattern and the correlation between two is not significant either (Figure 7.13). The Cladocera-inferred summer LSWT in early 1900 AD was somewhat comparable with the CET records (Figure 7.13), however, after this period the patterns diverge until 1980 AD, when the both temperature profiles were close to 15^{0}C. Around

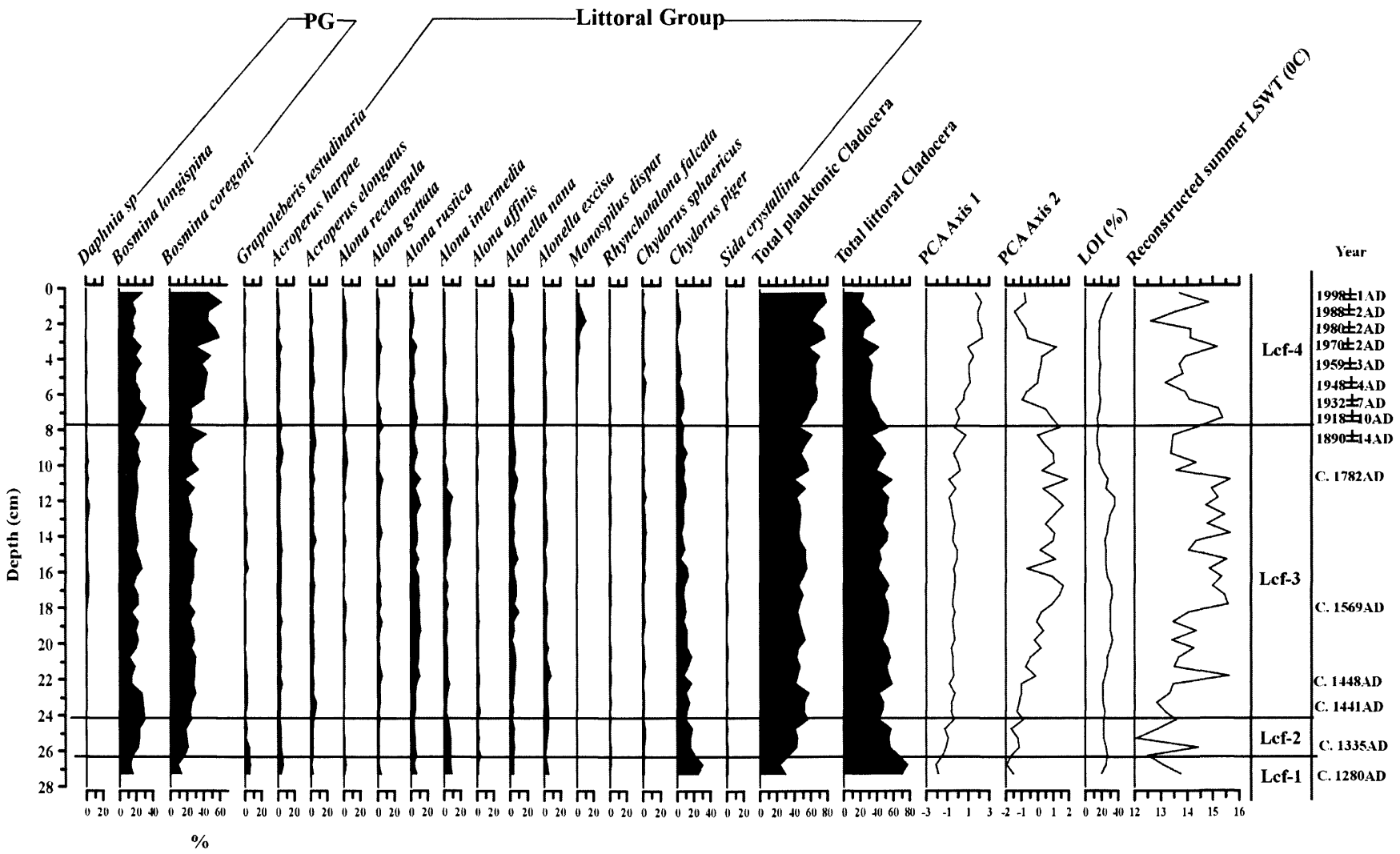


Figure 7.11: Stratigraphic representation of sub-fossil assemblage of principal Cladocera and their inferred temperature reconstruction in LCFR2 of Loch Coire Fionnaraich, Scotland. The ^{210}Pb chronology is given on the right side of the diagram. The zones (Lcf-1 to Lcf-4) are determined by minimum-variance cluster analysis (CONISS). PG stands for Planktonic Group.

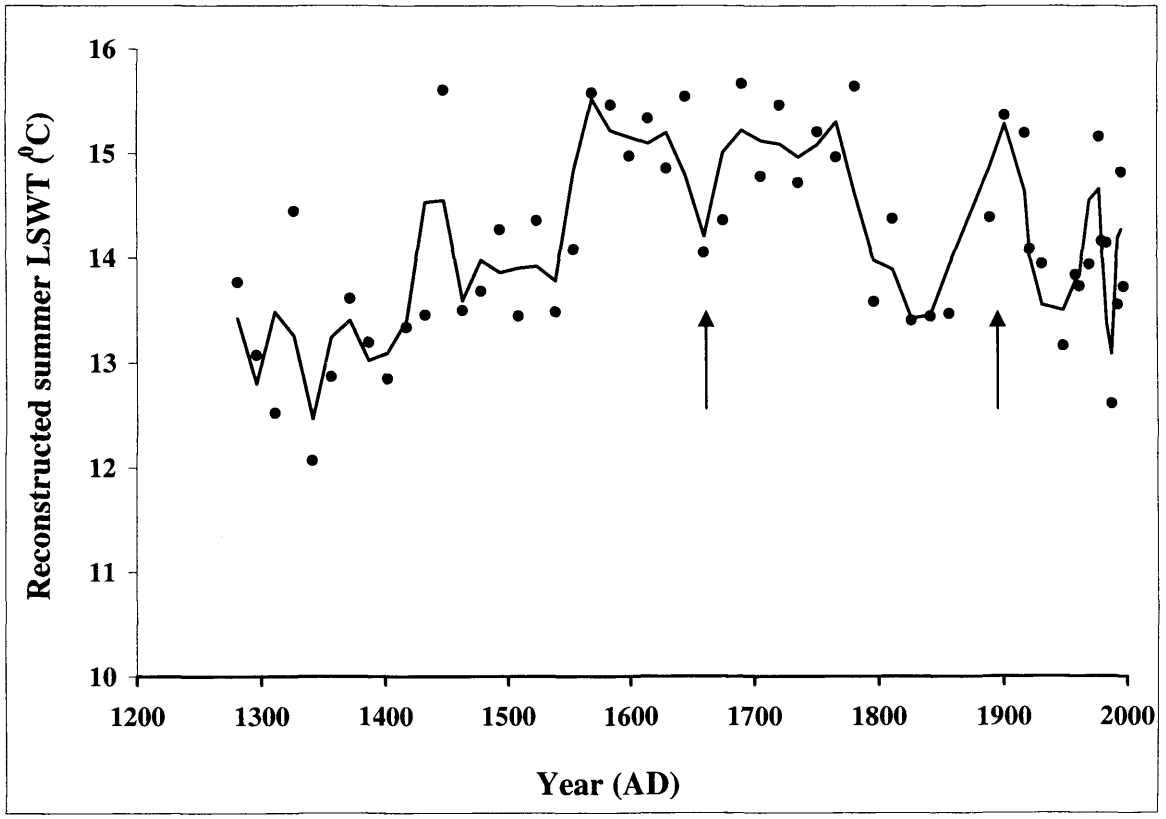


Figure 7.12: The reconstructed summer lake surface water temperature (LSWT) of the Loch Coire Fionnaraich, Scotland for the last 800 years. The ^{210}Pb dating of the core extends to about 1890 AD. The left and right arrows shows the time (1659 AD) back to the availability of the Hadley Centre instrumental temperature records (also see Figure 7.13) and the limit of the ^{210}Pb dating respectively. Data for older sediments are based on extrapolation of the basal ^{210}Pb sediment accumulation rates. For detail see Table 7.2. Smoothing of curve = 2 units moving average.

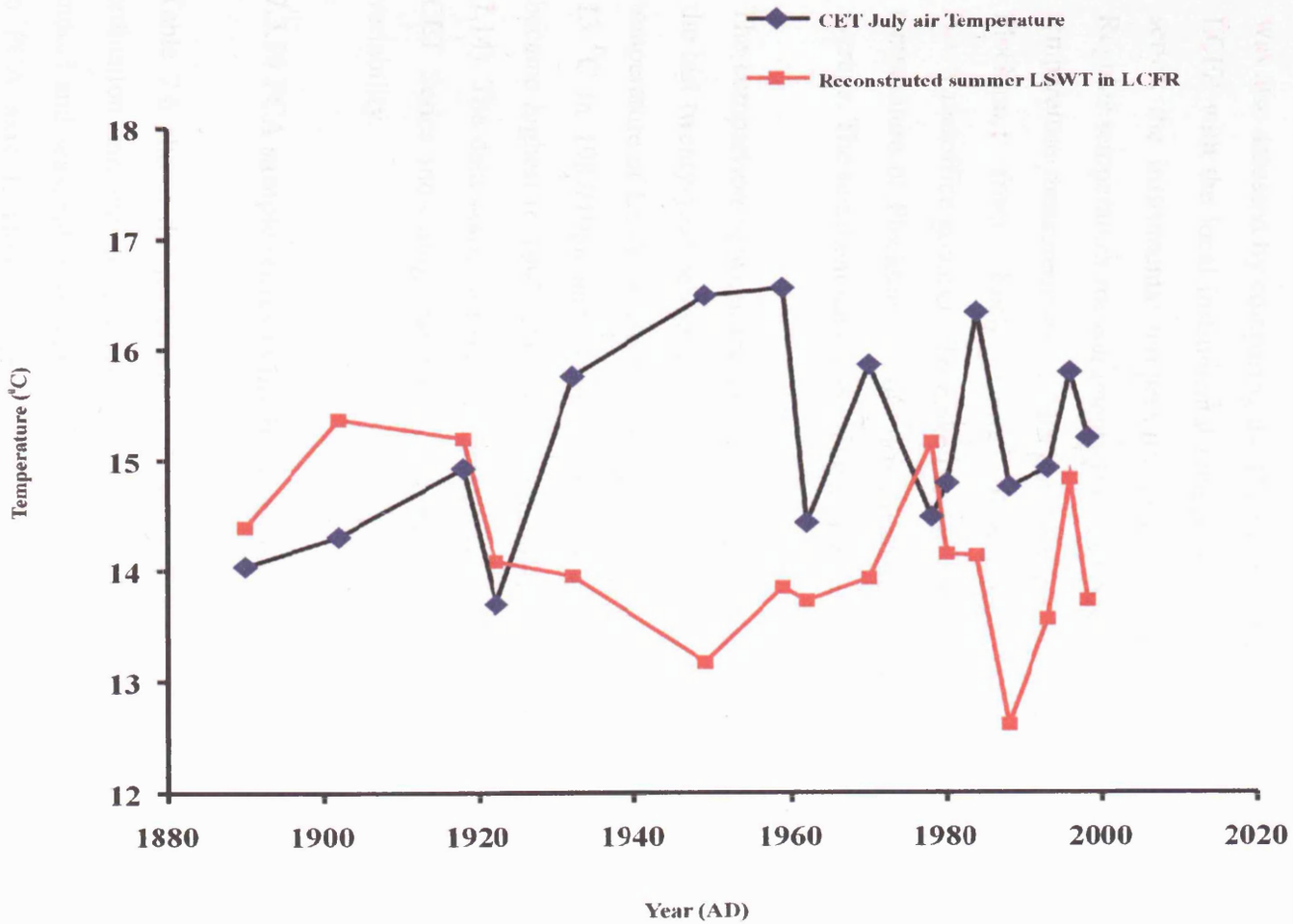


Figure 7.13: Comparison between Central England Temperature (CET) data series (www.met-office.gov.uk) and Cladocera-inferred reconstructed summer lakesurface water temperature (LSWT) in Loch Coire Fionnaraich (LCFR), Scotland. Comparison is made only for the date when Cladocera-inferred summer LSWT was available. The date for the Cladocera-inferred reconstructed LSWT is based on 210Pb dating from 1890 AD. CET data series are not adjusted for latitude and altitudes.

1980 AD, the Cladocera-inferred reconstructed summer LSWT (c. 15 ^{0}C) showed a slightly similar trend with the CET profile but this lasted only for a short period (Figure 7.13).

Since the comparison with the CET was poor, the performance of the inference model was also assessed by comparing the Cladocera-inferred reconstructed summer LSWT in LCFR with the local instrumental temperature records. However, unlike the CET data series, the instrumental temperature record for most Scottish sites are rather short. Regular temperature measurements for most Scottish sites only last 20-30 years. The temperature measurements for the last 20 years of the nearest meteorological station, Plockton, from Loch Coire Fionnaraich, was used in this study (www.metoffice.gov.uk). To make the data-set comparable, the instrumental mean air temperature of Plockton for July was calculated and smoothed using a 3 year moving average. The sediment data were treated in the same way (Figure 7.14).

The comparison between the instrumental and reconstructed temperature data-sets for the last twenty-year period showed a relatively good match (Figure 7.14). The inferred temperature of LCFR in 1984 in summer was about 14 ^{0}C. It then declined to less than 13 ^{0}C in 1987/1988 and again started to rise gradually throughout the 1990s, and became highest in 1997 AD, following the measured temperature quite closely (Figure 7.14). The data output for only the last 20 years match the local record better than the CET Series indicating that the local factors can play a strong role on temperature variability.

7.3.10 PCA sample scores vs instrumental climatic parameters

Table 7.6 shows the regression between four PCA axes of Cladocera derived after ordination and various climatic parameters in Loch Coire Fionnaraich. None of the annual and seasonal instrumental air temperature records were significantly correlated to PCA axis 1. However, the summer atmospheric temperature had a significant relationship with PCA axis 3 while the winter air temperature was significantly associated with PCA axis 2 of littoral Cladocera (Table 7.6).

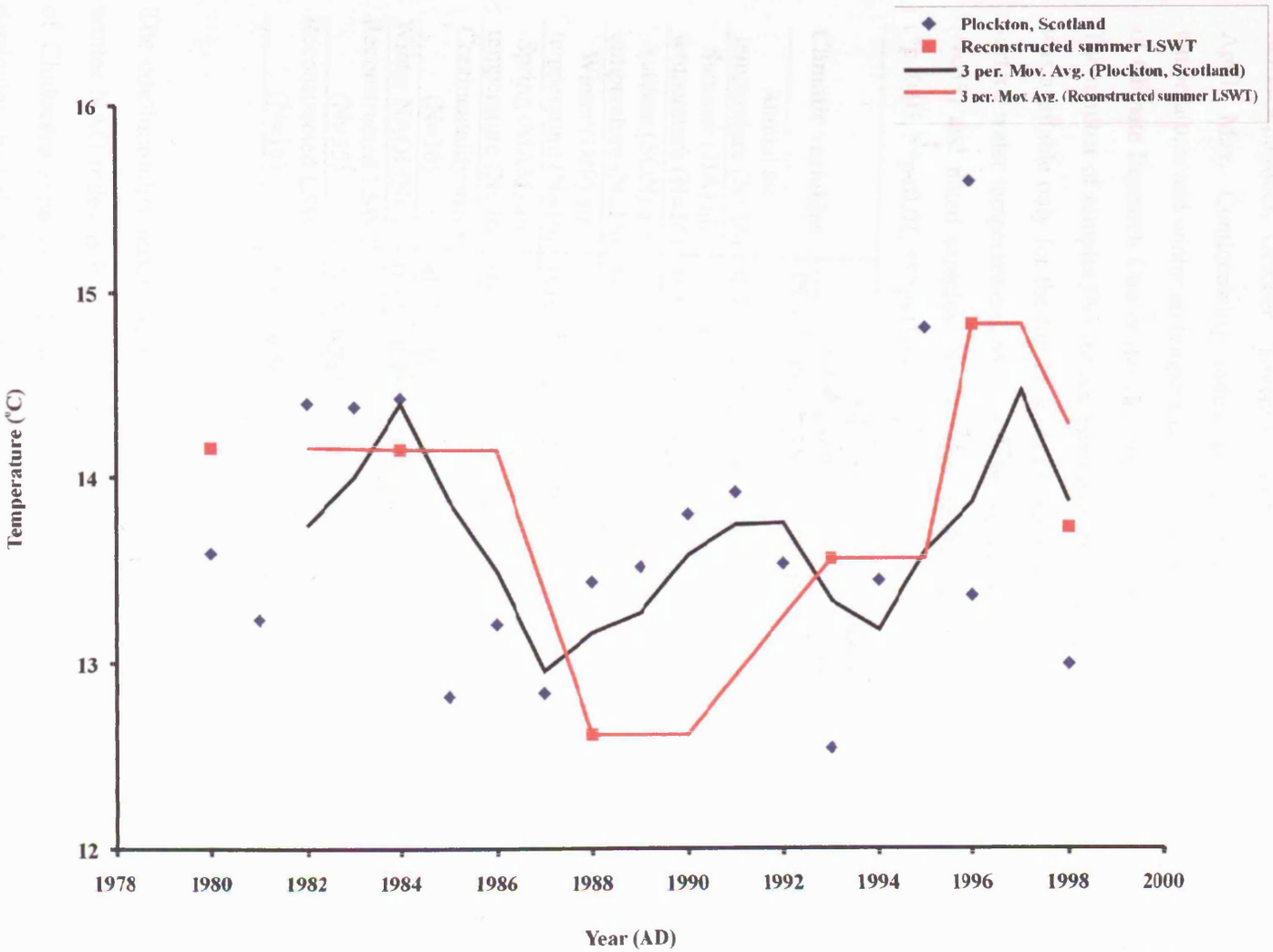


Figure 7.14: Comparison between the Cladocera-inferred reconstructed summer LSWT of LCFR and the instrumental temperature records of Plockton,one of the most closest meteorological station from LCFR. Instrumental temperature records of Plockton were available from 1980 to 1999 AD. The date for the Cladocera-inferred reconstructed summer LSWT of LCFR is based on ^{210}Pb dating. The Plockton temperatures were not adjusted for latitude and altitudes.

Table 7.6: Fraction of variation explained (R^2-squared) for regression between various climatic parameters and principal component axes of Cladocera. Air temperature measurements are Hadley Centre instrumental data for North Scotland (Appendix 7.2). JJA= June, July, August; SON=September, October, November; DJF=December, January, February; MAM= March, April, May. Continentality index is the difference between summer atmospheric air temperatures and winter air temperatures. The winter NAOI was downloaded from the web page of Climate Research Unit of the University of East Anglia (www.uea.ac.uk/cri, Appendix 7.3). The number of samples (N=16) correspond to the dated samples of the core LCFR2. The NAOI was available only for the top 11 samples. Regression between the reconstructed summer lake surface water temperature (LSWT) and PC axes of Cladocera were carried out for all samples (N=55) and dated samples (N=16). The significant variables are highlighted with asterisks (*p<0.05, **p<0.01, ***p<001).

Climatic variables	All Cladocera				Planktonic Cladocera			Littoral Cladocera			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC1	PC2	PC3	PC4
Annual air temperature (N=16)	0.37	-0.23	-0.14	0.04	0.36	0.18	-0.13	0.36	0.24	0.41	-0.09
Summer (JJA) air temperature (N=16)	0.22	-0.30	-0.46	-0.43	0.45	0.03	-0.29	0.07	0.33	**0.55***	-0.49
Autumn (SON) air temperature (N=16)	0.25	0.32	-0.01	0.09	0.22	-0.13	-0.34	0.28	-0.7	0.25	0.002
Winter (DJF) air temperature (N=16)	0.16	-0.46	-0.19	0.01	0.14	0.33	0.24	0.16	**0.50***	0.24	-0.13
Spring (MAM) air temperature (N=16)	0.06	-0.12	0.27	0.21	-0.04	0.13	0.08	0.09	0.11	0.25	0.29
Continentality index (N=16)	-0.02	0.25	0.05	0.23	-0.09	-0.11	-0.03	0.02	-0.28	0.10	0.18
Winter NAOI (N=11)	0.33	**-0.75****	0.55	0.21	0.30	**0.82*****	-0.21	**0.63***	**0.69***	-0.42	0.35
Reconstructed LSWT (N=55)	-0.08	**0.71*****	-0.01	0.24	-0.09	**-0.63*****	-0.18	0.03	**-0.66*****	0.11	0.23
Reconstructed LSWT (N=16)	**-0.44***	**0.58****	-0.13	0.06	**-0.45****	**-0.63****	0.28	-0.40	**-0.51***	-0.15	0.04

The continentality index did not show a relationship with any PCA axes. However, the winter NAO index is highly significant with PCA axis 2 for all, as well as both groups of Cladocera separately (Table 7.6). The planktonic Cladocera and winter NAOI, in particular, had the highest r^2 values (Table 7.6). However, the results presented here should be treated cautiously due to the small sample size (n=11).

7.3.11 PCA sample scores vs reconstructed summer LSWT

The correlations between the reconstructed summer LSWT and PCA sample scores of 55 subfossil assemblage of Cladocera show significant relationships with PCA axes 2 of all Cladocera (Table 7.7). Similarly, the correlation between the reconstructed LSWT and PCA sample scores of 16 dated samples also shows a significant positive correlation. However, the results need to be taken with caution since the eigenvalue for PCA axis 2 was rather small (Table 7.5).

Table 7.7: PCA eigenvalues of all, littoral and planktonic Cladocera in LCFR (N=55).

PCA Eigenvalue	All Cladocera	Littoral Cladocera	Planktonic Cladocera
Axis 1	0.44	0.41	0.62
Axis 2	0.13	0.12	0.22
Axis 3	0.07	0.07	0.14
Axis 4	0.05	0.06	0.00

7.3.12 Major response variables potentially associated with recent environmental change in Loch Coire Fionnaraich

Figure 7.15 shows the major indices of Cladoceran response to recent environmental change in Loch Coire Fionnaraich. These include the Shannon-Wiener species diversity index, the percentage planktonic and the percentage littoral Cladocera values, the concentration of individuals, the littoral:planktonic (L:P) ratio of Cladocera, LOI and the multi-proxy comparison of PCA axes 1 of Cladocera, diatoms and chrysophytes. Since the sampling depths and the resolution of LCFR1 and LCFR2 were different, the ^{210}Pb dating was modified slightly for samples with 0.5 cm resolution to the 18 cm depth while merging the two cores (Figure 7.15).

The results show that the Shannon-Wiener species diversity index of Cladocera in Loch Coire Fionnaraich has declined over time. Meantime, the population of planktonic Cladocera has increased while the population of littoral Cladocera has decreased (Figure 7.15). During the last decade the Cladoceran concentration shows major whilst the littoral:planktonic ratio of the Cladocera has declined significantly (Figure 7.15).

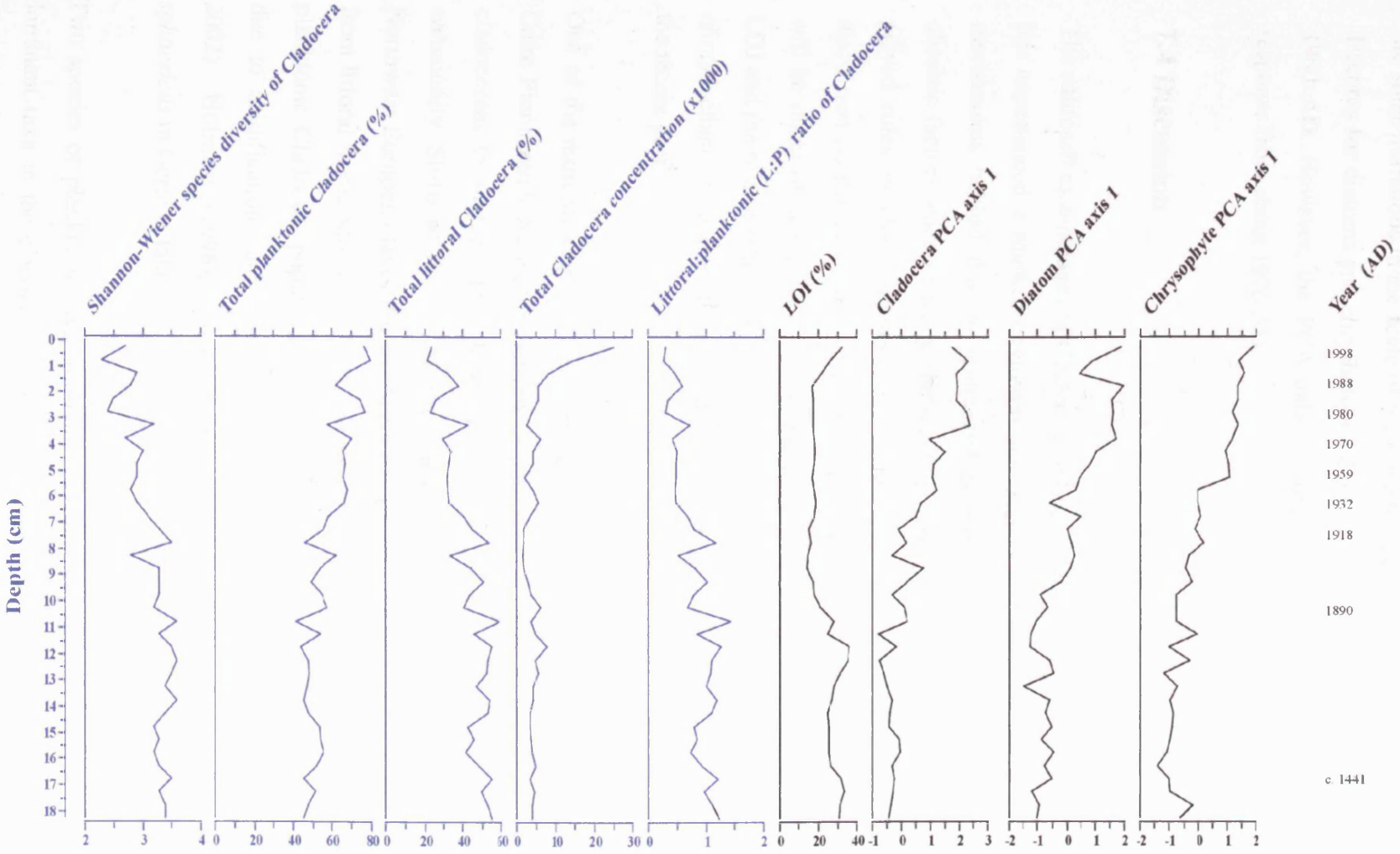


Figure 7.15: Most potential indicators (diversity, subfossil assemblage and L:P ratio) of Cladocera; LOI and the multi-proxy comparison of the PCA axis 1 of Cladocera, diatoms and chrysophytes to recent environmental change in Loch Coire Fionnaraich,Scotland.

The PCA axis 1 score of Cladocera, diatoms and Chrysophytes, all indicate that there has been a rapid rate of ecosystem change in recent years (Figure 7.15). However, there are some variations in the scale of response for the different proxy indicators. PCA axis 1 scores for diatoms and chrysophytes show that the main change occurred after about 1960 AD. However, the PCA axis 1 scores for Cladocera show a somewhat later response from about 1970 AD.

7.4 Discussion

The subfossil assemblages of Cladocera in Loch Coire Fionnaraich suggest that the loch has experienced a marked environmental change during its recent history. However, mechanisms behind this environmental change are complex and concern whether climatic factors alone or many confounding variables including climate, together have played roles in changing the loch. In the following paragraphs, a comprehensive discussion on the succession of Cladocera in LCFR over time will be presented. Use will be made of indicators, such as changes in the diversity of Cladocera, changes in LOI and the role of other proxies. In addition, a comparison will be made with observed climate change from the CET and with the instrumental local air temperature records for the recent past.

One of the most striking features of the Cladoceran community development in Loch Coire Fionnaraich during the last few centuries was a marked shift from one group of cladocerans to another. The planktonic Cladocera has gradually replaced the littoral community. Shifts of littoral and planktonic Cladocera have occurred in the past in Northwest European lakes due to changes in environmental conditions but not always from littoral to planktonic. Sarmaja-Korjonen (2002) argued that in 1800-1700 BP, the planktonic Cladocera populations in a Finnish lake, Lake Kaksoislammi, disappeared due to acidification, and changes in predator-prey interactions (Sarmaja-Korjonen, 2002). Hofmann (1996) also observed a shift from *Bosmina coregoni* to *Chydorus sphaericus* in German lakes.

Two species of planktonic taxa, *Bosmina coregoni* and *Bosmina longispina* were the dominant taxa in the cladoceran zooplankton community in Loch Coire Fionnaraich. The abundance of *B. longispina* was almost constant throughout the period, but *B. coregoni* increased indicating that changes were occurring in the loch and its ecosystem

well before the 20th century. This change in species was also accompanied by a gradual decline of species diversity over time.

Even though the taxonomy of *Eubosmina* sp. is not yet clear (Frey, 1986), the ecology of both *B. coregoni* and *B. longispina* is very similar. They co-occur in most European oligotrophic mountain lakes (Korhola, 1999). However, unlike *B. longispina*, which can withstand sub-Arctic environments (Hann & Karrow 1993), *B. coregoni* prefers somewhat warmer conditions (Megard, 1964). The abundance of this taxon in Loch Coire Fionnaraich suggests that the climate of the loch has been favourable for *B. coregoni* during the last few centuries.

However, most taxa preserved in the sediments of Loch Coire Fionnaraich are littoral forms indicating that the lake has a high habitat diversity. The assemblage composition in zone Lcf-1 (ca.1281 –1327 AD) is dominated by *Chydorus piger*. The ecology of *C. piger* is not yet clear since many authors have described this taxon from different environments. It is recorded in abundance from temperate, deep, clear, oligotrophic to shallow, warm-water lakes of both Europe and North America (Harmsworth, 1968; Whiteside, 1970; Fryer, 1974; Hofmann, 1986; Korhola, 1999). In the training set, the RDA ordination in Chapter 6 (Figure 6.7) suggests that this taxon prefers rather cold water. Its habitat preferences also vary, though it is most often found in muddy substrata (Whiteside et al., 1978) in lakes with a circumneutral pH (Krause-Dellin and Steinberg, 1986).

The higher abundance of *Graptoleberis testudinaria*, *Acroperus harpae, Alona intermedia*, *A. affinis*, *Alonella excisa* and *Sida crystallina* in Lcf-1 also suggests moderately cold conditions. *A. intermedia* in particular, is associated with nutrient poor, oligotrophic, often acidic conditions, and has a predominantly northern and boreo-alpine distribution (Fryer, 1993). In this period, the loch appeared to have more macrophyte beds along its shoreline for cladoceran habitats than the present day as indicated by the presence of *G. testudinaria* and *Sida crystallina*, taxa that prefer dense macrophyte habitats (Lotter & Boucherle, 1984, Frey, 1993).

The succession of Cladocera from Lcf-1 to Lcf-2 (ca.1327 – 1439 AD) is based on an increased abundance of *Alona quadrangularis,* a littoral chydorid taxon. Whiteside (1970) reported that *A. quadrangularis* has a distribution in northern regions of Europe

being dominant in clear water lakes. Similarly the low abundance of *G. testudinaria* and *S. crystallina* in this zone suggests there were changes in habitats within the loch, possibly a decline of the macrophyte-associated habitat (e.g. Frey, 1993).

Zone Lcf-3 (ca.1439-1919 AD) is a zone in which the loch environment was quite stable over time. One of the most interesting features in this zone, however, is the presence of *Daphnia*. The appearance of *Daphnia* in this zone may be due to at least three reasons. First, there may have been changes in the trophic dynamics of the loch due to a loss of planktivorous fish. Second, increased lake productivity could have supported *Daphnia* populations. Korhola et al. (2002a) reported that the increased abundance of *Daphnia* in the Finnish lake, Lake Saanajärvi was induced by climatically-driven lake productivity. And third, a change in the preservation environment, such as an increase in the sediment accumulation rate may have favoured the preservation of *Daphnia* claws in the sediments. Littoral taxa associated with a cold-water climate such as *Alona rustica, Alonella nana, Acroperus elongatus, Chydorus sphaericus*, and *Rhynchotalona falcata*, were also predominant in this zone. For example, Whiteside (1970) described that *A. rustica* is predominant in low alkalinity ponds and bogs. Hofmann (2000) discovered changes from higher to lower abundance of *A. nana* from the Alleröd to the Younger Dryas period suggesting its affinity for cold water. *Chydorus sphaericus* is a cosmopolitan species and occurs across a wide range of latitudes and altitudes from the Arctic to the tropics and from high altitudes to lowland habitats (Megard, 1967; Harmsworth, 1968; Frey, 1980; Tartari et al., 1998).

The cladoceran community in zone Lcf-4 (1919 –1998 AD) is very different from that of other zones. In this zone, the abundance and diversity of most littoral taxa, mainly *C. piger* declines and there is a reciprocal increase in the abundance of *B. coregoni.* Species such as *A. affinis* and *R. falcata* disappear, and a new species of littoral Cladocera, *M. dispar* appears and became dominant among the littoral community. Whiteside (1970) and Hofmann (1986) reported that *M. dispar* prefers clear water lakes in the alpine region of Europe. Fryer (1993) argued that it might also occur in shallow ponds and lakes with muddy bottoms. However, this taxon is often collected from sites with sand and gravel substrata (Frey, 1986; Dole-Oliver et al., 2000). Thus Frey (1986) has categorized *M. dispar*, an 'indicator' species for sediment dwelling species. The affinity of *M. dispar* to sandy substrata in Loch Coire Fionnaraich may reflect an increase in the importance of this habitat (Figure 4.4, Chapter 4). *B. coregoni* and *M.*

dispar has shown a reciprocal relationships in the Cladocera stratigraphy suggesting that climatic variability and annual and inter-annual variations in the seasonality and weather patterns in the region may be playing significant roles. The abundance of a littoral chydorid, *A. rectangula*, was also found to be relatively high compared to other zones. This is a temperate species and occurs mostly on littoral and marginal emergent macrophytes (Harmsworth, 1968; Hofmann, 1978; Fryer, 1993) and is often regarded as an alkaliphilous species (Krause-Dellin & Steinberg, 1986). Reason for the disappearance of *Rhynchotalona falcata* and *Alona affinis* in this zone are unknown, though these taxa do not occur very frequently in Northwest European mountain lakes (Sandøy and Nilssen, 1986). Unlike other chydorids, only the head-shield of *R. falcata* is preserved well in lake sediments (Frey, 1986).

The most striking features of the changes in the sediment sequence of LCFR were indicated by the species diversity, total concentration and the L:P ratio of Cladocera; the PCA axis 1 of the assemblages of Cladocera, diatoms and chrysophytes and the LOI profile. The Shannon-Wiener species diversity of Cladocera has declined and the PCA axis 1 scores of Cladocera, diatoms and chrysophytes all have increased significantly after the 1950s. The total cladoceran concentration and LOI has increased sharply after 1990 AD. Potential explanation for these changes includes catchment disturbances, atmospheric pollution and climate change interaction between these drivers.

Loch Coire Fionnaraich is a remote oligotrophic loch with limited disturbance by people. The catchment is grazed by sheep and reindeer and there has been some minor use of the lake for aquaculture in the recent past. These are not considered significant in explaining the changes in the sediment record, although the increase in *B. coregoni*, may be partly related to increased nutrient loading.

Like many remote sites, LCFR also receives long-range transported atmospheric S and N deposition (Rose and Rippey, 2002). However, the loch has not shown any sign of acidification. One of the closest sites to LCFR, Loch Coire nan Arr, has been closely monitored in the UK Acid Monitoring Network (Monteith and Evans, 2000). It has a pH value 6.9 and low levels of aluminum and calcium (Patrick et al., 1995) indicating a lack of acidification of sites sensitive to acid deposition in this area. However, there is more debate about the potential role of N deposition as a nutrient (Korhola et al.,

2002a). However, nitrate-nitrogen in LCFR is very low (1.59 μeql^{-1}) and primary productivity at this site is more likely to be limited by P.

During the 19th and 20th centuries, particularly after the Little Ice Age, most Northern Hemisphere lakes have undergone climate warming as shown by a variety of proxy records (Overpeck et al., 1997). A comprehensive study of mountain lakes (MOLAR) suggests that Northwest European mountain lakes have undergone significant warming (1-2 ^{0}C) during the last 200 years as revealed both by sediment records of these lakes and the instrumental temperature records (Battarbee et al., 2002a). Agusti-Panareda and Thompson (2002) showed that there were two distinct air temperature trends for the 19th and 20th centuries with general warming during the 20th century, but not during the previous century. Long-term monitoring of contemporary Cladocera in lakes of Northwest Europe has also shown a significant response of these lakes to recent climate change (e.g. George et al., 2004). Thus, unlike catchment disturbance and pollution, the impacts of climate change on the recent ecosystem change of LCFR can be hypothesised more strongly.

Hughes (2000) summarised the effects of climate change on ecosystems in a variety of ways: (i) effects on physiology where climate variables directly affect the metabolic activities and growth rates of organisms; (ii) effects on species distribution where species can shift from lower to higher latitude or altitude during warming; (iii) effects on phenology where the life cycle of organisms is modified significantly, and (iv) effects on species adaptations, particularly where organisms with shorter generation time can undergo micro-evolutionary change, *in situ*. From these categories, it can be argued that significant loss of species diversity of Cladocera, the increase in the abundance of planktonic Cladocera, the reciprocal decrease on the littoral Cladocera, and the increase in the PCA axis 1 scores of Cladocera, diatoms and chrysophytes in LCFR are the result of changes in species distribution during the late 20th century (e.g. Robertson, 1988; Hairston, 1996). Lotter et al. (1997) argued that most Chydorids show a response to the mean annual temperature while the planktonic Cladocera are associated with spring temperature. Sorvari et al., (2000, 2002) have also argued that recent changes in the biota of a sub-Arctic Finnish lake, Lake Saanajärvi, was related to temperature increase through the role of temperature on reproduction (also see Rautio, 1998; Korhola, 1999).

In recent decades not only has average temperature increased in the North Atlantic region, but also it has become more variable (Hurrel, 1995). Winters, in particular, have become more stormy mainly from the mid-1960s (Cooper et al., 2000; Parsons and Lear, 2001). These changes are related to the North Atlantic Oscillation (NAO), measured by the NAO index (NAOI) and changes in the NAO can have ecological impacts on freshwaters (George et al., 2000). In this study, although there are only 11 samples in the data-set, there is a significant positive relationship between Cladocera PCA axis 2 and the winter NAOI (Table 7.6) suggesting that the NAO is also likely to be an important environment influence on the loch in regulating the cladoceran community in recent years. For example, positive values of NAOI associated with mild winters and westerly winds were reported to have a significant positive correlation with the abundance of the planktonic zooplankton, *Eudiaptomus* in the English Lake District (George, 2000).

In addition to this, the increase in LOI in LCFR during the 1990s could be related to warming. LOI is a measure of the organic matter content in the sediment. As it is expressed as a percentage, LOI values can be influenced by inorganic matter (silts, carbonates) from the catchments and from the lake itself, resulting in changes that are often difficult to explain (Battarbee et al., 2002a). However, because of its oligotrophic nature and limited disturbances from human activity, it could be argued that the LOI increase in LCFR is associated with increase primary productivity related to warming (Catalan et al., 2002b).

7.4.1.1 Direct impacts

One of the potentially most important approaches to understand the direct impacts of climate change on past lake ecosystems is the transfer function approach (Battarbee, 2000). The Cladocera-inferred summer LSWT transfer function developed in Chapter 6 was used here to reconstruct the past summer LSWT of Loch Coire Fionnaraich. A number of promising biological transfer function approaches have been used for direct temperature reconstruction in many European mountain lakes (Lotter et al., 1997; Olander et al., 1999; Brooks and Birks, 2001; Larocque et al., 2001; Larocque and Hall, 2003). Recently, Lotter et al. (1997) developed a powerful Cladocera-inferrred transfer function for July air temperature of the Swiss Alps, and later Korhola (1999) also developed a relatively powerful Cladocera-inferred transfer function for July lake water temperature for Finnish mountain lakes. However, the Cladocera-inferred transfer

function developed here was not as statistically strong as the transfer functions developed from other calibration data-sets in Europe. A powerful biological transfer function for temperature requires certain criteria to be met. Sites in the calibration data-set need to be distributed across a wide eco-climatic gradient, and the study sites should be free from human disturbance as well as atmospheric deposition. In addition, the aquatic organisms studied in the calibration data-set should well be distributed and sensitive to climate change (Birks, 1995), and the lake, which is to be used for climate reconstruction should contain biota that are well represented by the calibration data-set and needs to be sensitive to climate change (Birks, 1995). Whilst all these criteria were employed to achieve the most reliable temperature reconstruction of summer LSWT of LCFR using the Cladocera-inferred transfer function approach, the reconstructed summer LSWT did not appear to be as reliable as expected when compared with instrumental and other data. Application of a two-component PLS transfer function model to the core assemblages, did not show a twentieth century warming. The cooler conditions indicated by the transfer function at the base of the core (23-27cm) might indicate the cooling at the start of the Little Ice Age in the 14th century (Figure 7.12). But it is difficult to match the temperature reconstruction after this time with those expected during following centuries, as the temperatures indicated by the model remain fairly constant at about 14 ^{0}C. According to the results, the twentieth century climate appears to be highly changeable (Figure 7.12).

This poor result of the Cladocera-inferred summer LSWT reconstruction in LCFR over this period has posed several questions on the use of the transfer function. The first important question: was the transfer function powerful enough to reconstruct the summer LSWT of LCFR? Compared to other Cladocera-inferred transfer function models, the summer LSWT inference model developed here was indeed less powerful (e.g. Lotter et al., 1997, Korhola, 1999) with a relatively high root mean square error of prediction (RMSEP = 1.8 ^{0}C). However, it was ecologically meaningful to use this model for reconstruction of summer LSWT in LCFR due to its relatively high r^2 values (Chapter 6). A weakness of the model may be its reliance on only a single point measurement of water temperature (e.g. Livingstone and Lotter, 1998; Livingstone et al., 1999). At some sites, e.g. with glacial-fed waters or with shading effects, water temperature may not be in equilibrium with air temperature (Battarbee pers. com.). However, the instrumental air temperature records for the last 30 years used in the calibration data-set were modelled on the basis of the nearest meteorological station to

the lake and on altitudinal lapse rates (Odland & Birks, 1999). Such interpolations may sometimes bias the data. Finally, although Agustì-Panareda and Thompson (2002) reported that air temperatures in most European mountain lakes have very similar long-term trends, this similarity does not always apply to the decadal variability, which can show a more local signal.

Another important question, could taphonomic processes in LCFR bias the water temperature reconstruction? Lotter et al. (2002a) argued that air temperature cannot alone account for the degree of variation observed in the palaeolimnogical record. It is important that taxa sensitive to climate change should be represented in the core, which is used for reconstruction. The taphonomic study in Chapter 5 showed that at least five taxa were not well represented in the core-top sample in LCFR (Figure 5.20). The study on the niche species response in Chapter 6 suggests that at least 2 of these 5 taxa, *Camptocercus rectirostris* and *Pleuroxus aduncus* showed significant responses to mean July air temperature in the calibration data-set (Figure 6.16 & Figure 6.29) indicating that they are good indicators of climate change.

As described above, global warming is apparent for the last twenty years and most Northwest European mountain lakes have already shown a significant response to this warming (e.g. Battarbee et al., 2002a; Sorvari et al., 2002). In order to assess whether the Cladocera-inferred reconstructed summer LSWT in LCFR has responded to the measured air temperature records in Northwest Scotland for the last two decades, comparison between the CET time series and the Plockton data-set with reconstructed summer LSWT was made. The July CET is poorly correlated with the reconstructed LSWT but the correlation with Plockton, Scotland was found to be very good (Figure 7.13). However, because of the limited number of data points, a regression between Plockton and Cladocera-inferred reconstructed temperature profiles is not statistically significant and this result should be taken with caution. The poor performance with the CET, but rather strong relationship between Plockton and Cladocera-inferred summer LSWT indicates that variation in the local weather conditions in Northwest Scotland may be important in driving the lake ecosystem of LCFR.

7.4.1.2 Indirect impacts

Whilst Cladocera may be directly influenced by summer LSWT, indirect effects are also likely to be important. Previous studies show that changes in temperature in mountain

lakes mediate lake level (Korhola, 2000), trophic state/nutrients (Brodersen et al., 1998), ice cover, pH, catchment hydrology, water column stratification (Bradbury et al., 1993; Rioual, 2000) and mixing (Smol & Boucherle 1985; Battarbee, 2000; Smol & Cumming, 2000; Battarbee et al., 2002b). As a result, chemical processes such as nutrient recycling, hypolimnetic O_2 consumption, alkalinity generation and water column pH of the lake can change, and such variables often have a strong influence on habitat characteristics, and the abundance, composition and distribution of Cladocera. LCFR does not show a prolonged stratification during summer and neither is it covered by ice during winter. Thus unlike high mountain lakes, the indirect mechanisms of climate change on the ecosystem of LCFR are considered differently, possibly, via nutrient generation, primary productivity, catchment hydrology and the modification of habitat architecture.

Changes in trophic state

The LOI of LCFR decreased from the end of the 19th century and reached a minimum (<20%) before 1990 AD, it then increased rapidly. During this period two important changes in the cladoceran zooplankton took place. The abundance of the total Cladocera populations in the loch, particularly, the smaller planktonic taxa, *Bosmina coregoni*, increased coincidentally with the LOI curve and the composition of larger Cladocera such as *Daphnia* declined (Figure.7.7). The PCA Axis 1 scores of Cladocera also coincide with the LOI curve, suggesting that the lake trophic state could be the principal driver of Cladoceran community structure at this time, probably influenced by climate and possibly acting together with direct effects as described above. Prior to this recent change, the low LOI values during the earlier part of the 20th century may have been the result of other factors such as catchment erosion related to higher precipitation, but this has not been verified yet. The historical and palaeolimnological data in a nearby loch indicate that no severe physical disturbances have occurred in the region in recent years (Patrick et al., 1995). The absence of *Daphnia* in LCFR in the early stages of the Little Ice Age (14th century) may, however, be associated with a cold climate either directly because temperatures were too low for *Daphnia* ephippia to be hatched or indirectly as a result of decreased production. Whilst changes in lake productivity may have been driven by climate change over the last few hundred years as represented by the core, anthropogenic impacts on trophic states cannot be ruled out to explain the most recent cladoceran changes when some species such as *Daphnia*, *Alona affinis*, *Rhychotalona falcata* disappeared from the loch, while the abundance of other species such as

Monospilus dispar and *Bosmina coregoni* increased significantly. Anthropogenic impacts on the ecosystems of LCFR could gradually have occurred in various ways during the last decade. Some aquacultural activities in the loch have taken place (pers. com. local farmer), and sheep grazing in the catchment may have increased. Consequently, eutrophication independent of factors associated with climate change may account for some of the recent increase in *B. coregoni*, a typical mesotrophic taxon in Loch Coire Fionnaraich (e.g. Hofmann, 1986, Hofmann, 1998b).

Habitat changes

Another possible explanation for some of the recent changes in the lake biota could be due to habitat change also related to climate forcing. Whilst the change in the littoral:planktonic ratio of the cladocerans may be related to changes in trophic state, it may also have been influenced by changing water level and related factors that could have caused changes in the availability and architecture of cladoceran habitats in the loch. Rainfall in the region has been higher than the national average (Hurrel, 1995, also see Mayes, 2000). Hurrel (1995) argued that north Europe and Scandinavia have generally experienced wetter than normal conditions due to the influence of the NAO. There has been a decrease in most typical littoral macrophyte dwelling species such as *C. piger*, *G. testudinaria* and *A. rustica* suggesting that the macrophyte dominant zone of the loch may have contracted over time (e.g. Hofmann, 1996). Similarly, Sarmaja-Korjonen & Alhonen (1999) described an increased lake level in Finland associated with an enlargement of the pelagic zone and a reciprocal shrinkage of littoral habitats and a distinct variation in the populations of planktonic and littoral Cladocera.

7.5 Conclusions

Being located in a sensitive zone to climate change in the North Atlantic region, Loch Coire Fionnaraich is considered to be a good site for studying recent climatic variability in northwest Scotland using Cladocera as an indicator. However, although there is a relatively good agreement between the local instrumental air temperature records and the Cladocera-inferred reconstructed summer LSWT of LCFR for the last two decades, the inconsistent results of the reconstruction of the summer lake surface water temperature of LCFR based on transfer function and CET instrumental data series raises the question whether the transfer function for climate reconstruction is reliable over the entire time period covered by the core. The decline of species diversity of Cladocera

and the increase in LOI, total Cladocera concentration and the PCA axis scores of Cladocera, diatoms and chrysophytes in the sediments of LCFR in the recent past provide strong evidence of recent environmental change in the region, possibly more as a result of indirect impacts, such as changes in trophic state, and habitat architecture related to climatic change rather than as a direct result of temperature change. Although the loch is considered to be free from major anthropogenic influence, the recent apparent eutrophication could also in part be attributed to the influence of nutrient addition from aquaculture or from anthropogenic N deposition. Thus extreme caution is needed in interpreting these results since multiple factors other than climate appear to have driven the community dynamics of Cladocera.

Chapter 8

Conclusions and Recommendations

8.1 Introduction

This study has contributed to the understanding of the structuring and functioning of mountain lake ecosystems and their response to climate change in Northwest Europe. However, the mechanisms behind the impact of climate change on mountain lake ecosystems are not simple. Climate change influences changes in species diversity, composition and distribution in a variety of ways. On one hand, changes in solar output, in volcanic aerosols and in thermo-haline circulation are considered to have caused natural variability in the climate, and ecosystems of Northwest Europe. On the other hand, human-induced greenhouse gas emissions are thought to be the most important factor causing rapid climate change in the region in recent times. These anthropogenic impacts may now be greater than natural climate variability in causing changes in lake ecosystems. In principle, both the effects of natural climate variability and additional effects of greenhouse gas forcing should be recorded by the sub-fossil assemblages of Cladocera used as indicators in lake sediments. However, there are many factors that need to be considered for this approach to be successful.

8.1.1 Ecological complexity

This study has revealed that the mountain lake ecosystems in Northwest Scotland and Norway are complex and their response to climate change in the region can be difficult to understand. Even though a significant response of the assemblage structure of Cladocera to summer lake surface water temperature (LSWT) in the calibration data-set indicating the importance of the role of temperature in lake ecosystems, the mechanisms behind the relationships are far from being resolved. Of the niche species response of 22 taxa in the calibration data-set, only 8 cladocerans showed a significant response to summer LSWT indicating that only a few number of species are highly sensitive to temperature. Surprisingly, one of the climatically sensitive Cladocera, *Acroperus harpae* (e.g. Harmsworth, 1968) failed to show a significant response to summer LSWT

in the calibration data-set indicating that the ecosystem at population level is more complex than expected. The effects of temperature are mediated via changes in habitat, especially macrophyte abundance and distribution of littoral Cladocera (Whiteside et al., 1978) and by physico-chemical changes including conductivity, pH/alkalinity and nutrient status (e.g. Nilssen and Sandøy, 1990).

The complexity in these mountain lakes is also increased due to year-to-year variability in physical, chemical and biological variables related to changing weather patterns, e.g. North Atlantic Oscillation (NAO), and the Gulf Stream (George and Harris, 1985; George and Taylor, 1995; George et al., 2000; Gerten and Adrian, 2000; George et al., 2004). The pronounced effects of NAO on climate of Northwest Europe have been observed during winter (Hurrel, 1995; Rodwell et al., 1999). The surface and bottom water temperatures of lakes of Northwest Europe have also been significantly positively correlated with the winter NAO index (George et al., 2004). As a result, significant variations in timing of ice-cover and thereby phytoplankton blooms and the dynamics of zooplankton in the pelagic zone have been observed (e.g. Gerten and Adrian, 2000, George, 2000). The NAO also has profound impacts on mixing and nutrient cycling of many dimictic lakes in Northwest Europe. Because of the rapid warming, most of these dimictic lakes are reported to have shown monomictic characteristics in recent years. Loch Coire Fionnaraich does not have a history of regular and strong thermal stratification. The wind-induced mixing associated with the NAO appears to have weakened the patterns of stratification of LCFR.

8.1.2 Transfer function

Because of the sensitivity of mountain lake ecosystems to climate change and the potential of Cladocera as fossil indicators, a Cladocera-inferred transfer function model was developed for summer LSWT across a calibration data-set from Scotland and Norway. However, in many respects, the inference model developed here (RMSEP = 1.8 ^{0}C, r^2 = 0.71) for predicting summer LSWT performed poorly when compared to the Central England temperature (CET) series.

This outcome was unexpected since measures were applied to maximise the temperature gradients while developing the training set and minimise the role of confounding variables. As variations in alkalinity in the region are considered one of the major

factors to control, using a 'constant' alkalinity range in the calibration data-set was designed to resolve this problem (Birks pers. com.). It was also thought that the temperature gradient selected would minimise the problems of truncation (e.g. Lotter et al., 1997; Korhola, 1999). However, there are clearly additional secondary gradients in the calibration data-set, which have significant roles in driving the cladoceran community. The low DCCA:DCA ratio to summer LSWT and unusually high residuals of a low-altitude site in the screened calibration data-set indicates the higher influence of secondary gradients in the PLS inference model for water temperature (e.g. Korhola, 1999). These could include physical (e.g. lake perimeter, area), chemical (e.g. TP, TN) and biological factors (e.g. fish, Chl_a) other than temperature (Nilssen and Sandøy, 1990; Aladin, 1991; Lotter et al. 1997; Korhola, 1999; Battarbee, 2000; Jeppesen et al., 1996, 2001a, 2003; Koinig et al., 2002).

Despite attempts to lengthen the gradient the 5^0C range in the calibration data-set may be too short. Only a small number (N = 8) of taxa from the calibration data-set appears to show a significant response to summer LSWT. Taxa, such as *Acroperus harpae* and *Chydorus sphaericus*, which have large range of temperature optima and tolerances (e.g. Harmsworth, 1968) failed to show a significant response to summer LSWT indicating that an enlargement of the calibration set towards the lower temperature gradient is needed to improve the model (cf. Lotter et al., 1997, Korhola, 1999).

Also since most summer LSWTs in the training-set sites were measured on different days and derived from single points, this may have resulted in some biases in the data. It has, however, been argued that single point measurements are not the major problems in many mountain lakes unless water temperatures are influenced by glacial melt waters or shading (e.g. Battarbee et al., 2002a & b). Livingstone et al. (1999) argued that the lake surface water temperature can vary depending on the time and weather conditions of the lake on the day of sampling. Biases in the measurement of water temperature can also occur due to changes in depth and stratification of lakes. For example, variations in niche species response of Cladocera to summer LSWT due to changes in depth and water column stratification have been reported earlier by various authors (e.g. Prâzáková and Fott, 1994; Korhola et al., 2000; Meriläinen et al., 2000). Recently attempts have been made to take direct measurements of water column temperature from different depths from remote mountain lakes on a diel and seasonal basis to improve summer LSWT inference models (Battarbee et al., 2002a & b).

8.1.3 Taxonomy

All palaeoclimate reconstruction requires a detailed knowledge on the taxonomy of biological proxies and the construction of training sets especially requires attention to taxonomy. In this respect, still some taxonomic issues on Cladocera remain to be resolved. In particular, the head pores of *Bosmina coregoni* and *Bosmina longispina* were not distinguished satisfactorily due to variations in the amount of thickening (cf. Goulden and Frey, 1963; Kořínek, 1971). Similarly, the carapaces of *B. coregoni* and *B. longispina* also differed significantly among the calibration sites. Individuals with narrow and long mucros are classified as *B. longispina* while those with a wide carapace with relatively short, gently curved mucros are grouped into *B. coregoni* (cf. Hofmann, 1998b). However, it has been recently suggested that *Bosmina* with exceptionally long mucro should be grouped into *Bosmina reflexa* (Hofmann, 1978). In addition, many species of *Bosmina* show seasonal morphological variations or phenotypic plasticity (Frey, 1960; De Costa, 1968; Nilssen et al., 1980) that have not yet been recognised in fossil assemblages. Moreover, Sarmaja-Korjonen (2001) provides a different key for *Bosmina longispina* from that of Kořínek (1971) and Frey (1976). Fryer (1993) , on the other hand, argued that *B. coregoni* has been incorrectly used and that taxa of the *B. coregoni* group should be known as *B. longispina.*

Similarly, the identification of small *Alona* such as *Alona guttata, Alona rectangula* and *Alona costata* was not very easy due to the similarity in the size and shapes of their carapaces and head shields (cf. Korhola and Rautio, 2001). The postabdomen and the postabdomenal claws were used to identify these taxa more accurately (see Appendix 3.1 for details). However, the identification of postabdomen and postabdominal claws may have been further complicated by the presence of remains from instars (e.g. Frey, 1986). Exoskeletons, particularly from instars, are highly fragile and easily destroyed during transportation and deposition (cf. Korhola & Rautio, 2001).

8.1.4 Taphonomy

The usefulness of Cladocera as indicators of past climate change also depends on how well the sediment assemblages represent the living communities. This study has made a significant contribution to the understanding of the taphonomy of Cladocera, and the Loch Coire Fionnaraich has identified biases in Cladocera-inferred palaeoclimate

reconstruction as a result of taphonomic processes. A variety of approaches were used to understand these processes in LCFR, some of which are considered to be highly useful for studying the taphonomy of other aquatic biota.

Taphonomy is the mechanism, by which an organism undergoes a series of postmortem processes, which extend through the preburial exposure in the sediment-water interface and final burial and diagenesis (Behrensmeyer & Kdiwell, 1985). Transportation of the remains of the individual Cladocera from littoral habitats to the lake centre is especially important. In LCFR, remains of most chydorid Cladocera (e.g. *Chydorus piger*, *Graptoleberis testudinaria*) and *Sida crystallina,* which predominantly inhabit shoreline vegetation beds, are deposited close to their source habitat (e.g. Mueller, 1964). However, the remains of the large chydorids, *Eurycercus lamellatus, Alona affinis* and *Alona quadrangularis* were deposited higher at the lake centre than close to their source habitats indicating that they are effectively transported by water currents and sediment focusing (e.g. Lehman, 1975). The distribution pattern of the remains, especially the ratio between littoral and planktonic (L:P) Cladocera indicates the significance of lake morphometry on habitat structure and on fossil transport and deposition. High concentrations of the remains of the chydorid species, *Alonella nana* and *Acroperus harpae* are deposited in sandy substrata at the eastern end of LCFR. These taxa normally do not prefer sandy substrata (e.g Whiteside et al., 1978) indicating that they are transported by wind-induced currents. These results are counter to Frey (1988), who argued that the deepest basin of the lake integrates most lake biota.

Even though only small numbers of remains were recovered from the sediment traps, the trap approach provided useful taphonomic information. In this respect, a majority of the taxa that were present in the trap assemblages was also found in the core assemblages. However, there was evidence for a significant loss of fossil remains of a few number of taxa such as *Camptocercus rectirostris* and *Pleuroxus aduncus* indicating that these taxa may be poorly represented (e.g. Kato et al., 2003).

Overall, the taphonomic studies suggest that there are significant differences between the composition of the fossil assemblages in the core sample and the cladoceran communities in the lake, and that this may influence palaeoclimate reconstructions significantly. However, accounting for these differences is quantitatively difficult unless

the seasonal production rate of individual Cladocera with respect to specific areas of the littoral and planktonic habitats available are fully known.

8.1.5 Climate reconstruction

Ideally if problems of ecology, taxonomy and taphonomy of Cladocera are taken into account, Cladocera assemblages in lake sediments can be used as indicators of climate change. The sediments of Loch Coire Fionnaraich have very well preserved assemblages of Cladocera and with a few exceptions, for example, the absence of remains of *Alona costata* and *Alonella exigua* in the sediment core, the fossil remains of Cladocera preserved in LCFR are well represented in the training set. Moreover, LCFR is a suitable site for climate reconstruction as it is located in a remote region and has limited human disturbance. The sediment cores from LCFR have a relatively high and constant rate of sediment accumulation that allow high-resolution studies to be carried out.

However, despite these characteristics, it has not been possible to reconstruct climate variability from the cladoceran record in a reliable way. One of the problems is the location of the site at low altitude with relatively mild surface water temperatures in all seasons. Unlike high-altitude lakes, LCFR does not freeze during winter. As described earlier, climate change has significant impacts on the duration of ice-cover, which in turn can influence light penetration, the length of the growing season and the water column stratification (Battarbee, 2000). LCFR does not lie on this environmental threshold and is therefore less sensitive to changes than colder sites. LCFR may be more sensitive to water column turbulence. As a result, nutrient dynamics and the primary productivity of the pelagic systems may be influenced by weather pattern variability and the increased concentration of the planktonic taxa *Bosmina coregoni* and *B. longispina* in the sediment of LCFR could be the result of such processes.

A test of the methodology developed here is the extent to which cladoceran-based temperature transfer-function agrees with relatively well understood periods of climate change in the past (e.g. the LIA) and with the measured temperature from instrumental record. In this case, the Central England temperature series was used as the longest available instrumental records in particular. Although the core chronology has its own

uncertainties it is clear that the reconstructed summer LSWT during the most part of the late Little Ice Age (c. 1550 – 1750 AD) is over-estimated (i.e. >15 ^{0}C) by the model.

For the last 200 years, a comparison between the Cladocera-inferred reconstructed summer LSWT for LCFR and the instrumental Central England Temperature (CET) series is also very poor. The CET shows a rapid warming episode during this period (Jones, 2002) and it has been argued that Scotland's annual mean temperature between 1900 and 1950 AD was more than 0.4^{0}C higher than the temperature during the 15th century and a further 0.4^{0}C higher by 1996 AD (Price, 1983; Harrison, 1997). The lack of a good agreement during this period can not be accounted for by poor chronology as reliable ^{210}Pb dating is available for this time period. One of the reasons for the poor outcome could be the insensitivity of LCFR to small change in climate. Alternatively, the transfer function model, despite its relatively high r^2 values, may contain errors associated with the estimated temperatrue optima of species in the model. However, despite the overall mismatch with the CET, there is a relatively close agreement between the Cladocera-inferred reconstructed summer LSWT and the instrumental temperature records of the local meteorological station at Plockton, Scotland for the last 20 years, suggesting that the lake is responding to local climate change, and indicating that the use of the CET series may not be warranted. The rate of rising global temperature is unprecedented during the late 20th century (Mann, 2000), particularly in the North Atlantic region, which was especially warm in the 1990s (Harrison, 1997; Bradley et al., 2003) suggesting that the transfer function may be performing relatively well over this very recent time period.

The sediment record from Loch Coire Fionnaraich shows that there has been a significant change in the ecosystem of the loch over the last four decades and the evidence suggests the changes were to some degree mediated by climate. However, the mechanisms that explain a potentially direct relationship between Cladocera and climate are unclear although ecosystem changes such as the species diversity and composition of Cladocera appear to be related with temperature, which has a role in controlling growth and reproduction (e.g. Yurista, 1999). Indirect mechanisms through productivity and habitat architecture may also be important.

In most remote oligotrophic mountain lakes, the loss-on-ignition (LOI) record can be regarded as a powerful proxy indicator of productivity, and in lakes with minimal

catchment disturbance or anthropogenic eutrophication, this can be related to climate change (Dalton et al., 2000; Battarbee et al., 2001a; Nesje and Dahl, 2001), as an increase in temperature might be expected to increase the length of the growing season (Battarbee, 2000). The increase in the LOI of LCFR during the 1990s is consistent with this idea, as is the increase in the concentration of total Cladocera, particularly the planktonic taxon, *B. coregoni* (cf. Hofmann (1986).

Global warming may also cause shift in habitat architecture that have significant consequences on species diversity (e.g. Shindler, 1997). The sharp decline of species diversity and reciprocal relationships between littoral and planktonic Cladocera, as revealed by a low littoral: planktonic (L:P) ratio may be related to increased rainfall and lake water levels in LCFR in recent years. In addition, the increased abundance of *Monospilus dispar* during the last decade may reflect an increase in the availability of sandy substrata created by hydrological change.

Finally the coincidental increase in the PCA axis 1 scores of all three biological proxies, Cladocera, diatoms and chrysophytes, also indicates a common cause for the changes in ecosystem of the loch related to nutrient status, possibly caused by recent climate change. Sorvari et al. (2000) and Korhola et al. (2002b) have also reported similar evidence from changes in Finnish lakes.

8.2 Recommendations

The results of this dissertation has highlighted both the potential of Cladocera as indicators of climate change, but also the difficulties. Of central importance is an improved understanding of ecological processes in remote lakes, improved taxonomy for some cladoceran groups, further development of training sets and more thorough studies of taphonomy.

Climate change acts upon the planktonic and littoral groups of Cladocera in mountain lakes quite differently. Planktonic Cladocera are likely to be driven directly via changes in temperature, ice-cover, thermal stratification, nutrient cycling and fish predation (e.g. Battarbee, 2000; George, 2000; Jeppesen et al., 2001b; Mckee et al., 2002), while the littoral Cladocera are regulated more indirectly via changes in substrate quality and micro-habitat structures (e.g. Whiteside, 1974; Whiteside et al., 1978). Understanding

the ecology of littoral Cladocera is most important as there are many taxa, they are well preserved in sediments, and have significantly high indicator value for past environmental change (Frey, 1986; Korhola and Rautio, 2001).

Long-term monitoring programme would be especially useful to understand the interaction between climate change, Cladocera composition and food web dynamics of mountain lakes. Considering the significant effects of the North Atlantic Oscillation on these lakes via changes in storminess, winter water temperature, precipitation and nutrients (e.g. Monteith et al., 2000; George et al., 2004), such a programme should be focused on the seasonal and year-to-year variation of the biological communities.

For a small number of genera of planktonic Cladocera (*Bosmina* and *Daphnia*) that are preserved in lacustrine sediments it is necessary to improve the identification of the remains (Frey, 1986). In particular, the identification of the headshield of *Bosmina coregoni* and *Bosmina longispina*, has not been resolved yet. It needs to take place alongside a continued effort on studies of the geographic speciation of these taxa and their morphological expression (e.g. Haney and Taylor, 2003; Sacherova and Hebert, 2003).

A greater understanding of Cladoceran taphonomy is also essential where fossil assemblages of Cladocera are used for palaeoclimate reconstruction. In particular, the sediment trap approach is needed to quantify the relationships between production in the water column and in the littoral zone, and fluxes to the sediment and the fossil representation at the sediment-water interface. The study here could have been enhanced by the use of sequential trapping to relate production and deposition on a seasonal basis. The sediment accumulation rate, which influences the concentration of remains in a sample, is partly a function of climate (Harmsworth and Whiteside, 1968), and should be understood before any palaeoclimate reconstruction being carried out.

The use of Cladocera to reconstruct summer temperature has great potential revealed by the low RMSEP and high r^2 values in the PLS and WA-PLS inference models (e.g. Lotter et al., 1997, Korhola, 1999). However, improvements are clearly needed by extending the calibration data-set along the temperature gradient, and by a fuller exploration in the training set of the influence of other driving variables, such as habitat, that may be also climatically dependent. Verification of reconstructions by comparison

to instrumental time series and other proxy indicators (e.g. stable isotopes) is also most important. This can be extended by comparison to records from other lakes and other natural archives, such as tree rings, peatlands and spleothems (e.g. Baker et al., 1993; D'Arrigo et al., 1997; Brooks and Birks, 2001; Bigler and Hall, 2002; Charman et al., 2001; Proctor et al., 2001 & 2002; Larocque and Hall, 2003).

Finally the impact of climate change has become one of the most significant societal concerns worldwide (IPCC, 2001). Climatic change should be considered holistically and palaeolimnological and palaeoclimate studies need to be fully integrated into the science need to understand global change.

References

Abbott, M.B., Wolfe, B.B., Wolfe, A.P., Seltzer, G.O., Aravena, R., Mark, B.G., Polissar, P.J., Rodbell, D.T., Rowe, H.D. & Vuille, M. (2003). Holocene paleohydrology and glacial history of the central Andes using multiproxy lake sediment studies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **194:** 123-138.

Adams, C. E. (1994). The fish community of Loch-Lomond, Scotland-its history and rapidly changing status. *Hydrobiologia*, **290**: 91-102.

Agusti-Panareda, A. & Thompson, R. (2002). Reconstructing air temperature at eleven remote alpine and arctic lakes in Europe from 1781 to 1997 AD. *Journal of Paleolimnology*, **28**: 7-23.

Aladin, N.V. (1991). Salinity tolerance and morphology of the osmoregulation organs in Cladocera with special reference to Cladocera from the Aral Sea. *Hydrobiologia*, **225:** 291-299.

Alhonen, P. (1970). On the significance of the planktonc/littoral ratio in the cladoceran stratigraphy of lake sediments. *Community Biology*, **35:** 1-9.

Allan, J.D. (1976). Life history patterns in zooplankton. *The American Naturalists*, **110:** 165-180.

Ammann, B., Birks, H.J.B., Brooks, S.J., Eicher, U., von Grafenstein, U., Hofmann, W., Lemdahl, G., Schwander, J., Tobolski, K. & Wick, L. (2000). Quantification of biotic responses to rapid climatic changes around the Younger Dryas - a synthesis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **159:** 313-347.

Anderson, N.J. & Battarbee, R.W. (1992). Aquatic community persistence and variability: a paleolimnological perspective. In: *Aquatic Ecology, Scale, Pattern and Process*, Giller, P. S., Hildrew, P. S., and Raffaelli, D. G. (Eds.), Blackwell Science, Oxford, pp. 233-259.

Appleby P G, (2001). Chronostratigraphic techniques in recent sediments, In: Last, W.M. & Smol, J.P. (eds.), *Tracking Environmental Change Using Lake Sediments Volume 1: Basin Analysis, Coring, and Chronological Techniques*, Kluwer Academic Publishers, Dorrecht, The Netherlands, pp. 171-203.

Appleby, P.G., Nolan, P.J., Gifford, D.W., Godfrey, M.J., Oldfield, F., Anderson, N.J. & Battarbee, R.W. (1986). ^{210}Pb dating by low background gamma counting. *Hydrobiologia*, **141:** 21-27.

Appleby, P.G. & Oldfield, F. (1978). The calculation of ^{210}Pb dates assuming a constant rate of supply of unsupported 210Pb to the sediment. *Catena*, **5:** 1-8.

Appleby, P.G., Richardson, N., Nolan, P.J. & Oldfield, F. (1990). Radiometric dating of the United Kingdom SWAP sites. *Philosophical Transactions of the Royal Society of London*, **B327:** 233-238.

Appleby, P.G., Richardson, N. & Nolan, P.J. (1992). Self-absorption corrections for well-type germanium detectors. *Nuclear Instruments and Methods in Physics Research Section B*, **71:** 228-233.

Baier, J., Lücke, A., Negendank, J.F.W., Schleser, G-H. & Zolischka, B. (2004). Diatom and geochemical evidence of mid- to late Holocene climatic changes at Lake Holzmaar, West-Eifel (Germany). *Quaternary International*, **113:** 81-96.

Baker, A., Smart, P.L., Edwards, R.L. & Richards, D.A. (1993). Annual growth banding in a cave stalagmite. *Nature*, **364:** 518-520.

Battarbee, R.W. (1979). Early algological records: help or hindrance to palaeolimnology? *Nova Hedwigia*, **64:** 379-393.

Battarbee, R.W. (1991). Recent paleolimnology and diatom-based environmental reconstruction. In: Shane, L. C. K. and Chshing, E. J. (eds.), *Quaternary Landscapes*, Minneapolis, University of Minnesota Press, pp. 129-174.

Battarbee, R.W. (2000). Palaeolimnological approaches to climate change, with special regard to the biological record. *Quaternary Science Reviews*, **19:** 107-124.

Battarbee, R.W., Cameron, N.G., Golding, P., Brooks, S.J., Switsur, R., Harkness, D., Appleby, P., Oldfield, F., Thompson, R., Monteith, D.T. & McGovern, A. (2001a). Evidence for Holocene climate variability from the sediments of a Scottish remote mountain lake. *Journal of Quaternary Science*, **16:** 339-346.

Battarbee, R.W., Grytnes, J.-A., Thompson, R., Appleby, P., Catalan, J., Korhola, A., Birks, H.J.B., Heegaard, E. & Lami, A. (2002a). Comparing palaeolimnological and instrumental evidence of climate change for remote mountain lakes over the last 200 years. *Journal of Paleolimnology*, **28:** 161-179.

Battarbee, R.W., Jones, V.J., Flower, R.J., Cameron, N.G., Bennion, H., Carvalho, L. & Juggins, S. (2001b). Diatoms. In: Smol, J. P., Birks, H. J. B., & Last, W. M. (eds.), *Tracking Environmental Change Using Lake Sediments, Volume 3: Terrestrial, Algal, and Siliceous Indicators*, Kluwer Academic Publishers, pp. 155-202.

Battarbee, R.W., Thompson, R., Catalan, J., Grytnes, J.-A. & Birks, H.J.B. (2002b). Climate variability and ecosystem dynamics of remote alpine and arctic lakes: the MOLAR project. *Journal of Paleolimnology*, **28:** 1-6.

Beckett, K.-E. & Wilson, A.L. (1974). The manual determination of ammonia in fresh waters using an ammonia-sensitive membrane-electrode. *Water Research*, **8:** 333-340.

Behrensmeyer, A.K. & Kidwell, S.M. (1985). Taphonomy's contributions to paleobiology. *Paleobiology*, **11:** 105-119.

Bennett, K.D. (1996). Determination of the number of zones in a biostratigraphical sequence. *New Phytologist*, **132:** 961-979.

Berger, A. & Loutre, M.F. (1991). Insolation values for the climate of the last 10 million years. *Quaternary Science Reviews*, **10:** 297-317.

Bigler, C. & Hall, R.I. (2002). Diatoms as indicators of climatic and limnological change in Swedish Lapland: a 100-lake calibration set and its validation for paleoecological reconstructions. *Journal of Paleolimnology*, **27:** 97-115.

Birks, H.H., Whiteside, M.C., Stark, D.M. & Bright, R.C. (1976). Recent paleolimnology of three lakes in Northwestern Minnesota. *Quaternary Research*, **6:** 249-272.

Birks, H.J.B. (1995). Quantitative paleoenvironmental reconstructions. In: *Statistical Modelling of Quaternary Science Data*, Maddy, D. & Brew, J.S. (Eds.), Cambridge University Pres, 254 pp.

Birks, H.J.B. (1996). Great Britain - Scotland. In: *Palaeoecological Events During the Last 15 000 Years: Regional Synthesis of Palaecological Studies of Lakes and Mires in Europe*, Berglund, B.E., Ralska-Jasiewiczowa, M. & Wright, H.E. (Eds.), John Wiley & Sons Ltd., 143 pp.

Birks, H.J.B. (1998). Numerical tools in palaeolimnology-progress, potentialities, and problems. *Journal of Paleolimnology*, **20:** 307-332.

Birks, H.J.B. & Gordon, A.D. (1985). *Numerical methods in Quaternary pollen analysis*. Academic Press, London.

Birks, H.J.B., Line, J.M., Juggins, S., Stevenson, A.C. & ter Braak, C.J.F. (1990). Diatoms and pH reconstruction. *Philosophical Transactions of the Royal Society of London*, **B327**: 263-278

Blais, J.M. & Kalff, J. (1995). The influence of lake morphometry on sediment focusing. *Limnology and Oceanography*, **40:** 582-588.

Borcard, D., Legendre, P. & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, **73:** 1045-1055.

Boucherle, M.M. & Züllig, H. (1983). Cladoceran remains as evidence of change in trophic state in three Swiss lakes. *Hydrobiologia*, **103:** 141-146.

Bradbury, J.P., Dean,W.E. & Anderson, R.Y. (1993). *Elk Lake, Minnesota: Evidence for Rapid Climate Change in the North-Central United States*. Boulder, Colorado: Geological Society of America. 328 pp.

Bradbury, J.P. & Winter, T.C. (1976). Areal distribution and stratigraphy of diatoms in the sediments of Lake Sallie, Minnesota. *Ecology*, **57:** 1005-1014.

Bradley, R.S., Briffa, K.R., Cole, J., Hughes, M.K. & Osborn, T.J. (2003). The climate of the last millennium. In: *Climate Change and Society*, Bradley, R.S. & Law, N.E. (Eds.), Stanley Thornes, Cheltenham, 104pp.

Brancelj, A., Sisko, M. & Kosi, G. (1997). Distribution of algae and crustacean (Copepoda and Cladocera) in mountain lake in Slovenia with different trophic levels. *Periodicum Biologorum*, **99:** 86-87.

Brauer, A., Endres, C. & Negendank, F.W. (1999). Lateglacial calendar year chronology based on annually laminated sediments from Lake Meerfelder Maar, Germany. *Quaternary International*, **61:** 17-25.

Brauer, A. & Negendank, J. F. W. (2002). The value of annually laminated lake sediments in palaeoenvironment reconstruction. *Quaternary International*, **88:** 1-3.

Brimblecombe, P. (2003). Multi-proxy climatic reconstructions. In: *Global Change in the Holocene*, Mackay, A., Battarbee, R., Birks, J. & Oldfield, F. (Eds.), Arnold, London, pp. 159-167.

Brodersen, K.P., Whiteside, M.C. & Lindergaard, C. (1998). Reconstruction of trophic state in Danish lakes using subfossil chydorid (Cladocera) assemblages. *Canadian Journal of Fisheries and Aquatic Sciences*, **55:** 1093-1103.

Broecker, W.S. (1994). Massive iceberg discharge as triggers for global climate change. *Nature*, **372:** 421-424.

Broecker, W.S. (1997). Thermohaline circulation, the Achilles Heel of our climate system: Will man-made CO_2 upset the current balance? *Science*, **278:** 1582-1588.

Broecker,W.S. (1998). The end of the present interglacial: how and when? *Quaternary Science Reviews*, **17:** 689-694.

Broecker, W.S. (1999). Climate change prediction. *Science*, **283:** 175.

Broecker, W.S. (2000). Abrupt climate change: causal constraints provided by the paleoclimate record. *Earth-Science Reviews*, **51:** 137-154.

Broecker, W. S., Sutherland, S. & Peng, T.-H. (1999). A possible 20th century slowdown of Southern Ocean deep-water formation. *Science*, 286: 1132-1135.

Brooks, S.J. & Birks, H.J.B. (2000). Chironomid-inferred late-glacial and early Holocene mean July air temperatures for Kråkenes Lake, western Norway. *Journal of Paleolimnology*, **23:** 77-89.

Brooks, S.J. & Birks, H.J.B. (2001). Chironomid-inferred air temperatures from Lateglacial and Holocene sites in north-west Europe: progress and problems. *Quaternary Science Reviews*, **20:** 1723-1741.

Busuioc, A., Chen, D. & Hellström, C. (2001). Temporal and spatial variability of precipitation in Sweden and its link with the large-scale atmospheric circulation. *Tellus*, **53A:** 348-367.

Cadée G.C., González H. & Schnack-Schiel S.B. (1992). Krill diet affects faecal string settling. *Polar Biology*, **12:** 75-80.

Cameron, N.G. (1990). Representation of diatom communities by fossil assemblages in Loch Fleet, Galloway, Scotland. PhD thesis, Department of Geography, University College London, 290pp.

Cameron, N.G. (1995). The representation of diatom communities by fossil assemblages in a small acid lake. *Journal of Paleolimnology*, **14:** 223.

Cameron, N.G., Schnell, Ø.A., Rautio, M., Livingstone, D.M., Appleby, P., Dearing, J.A. & Rose, N. (2002). High-resolution analyses of recent sediments from a Norwegian mountain lake and comparison with instrumental records of climate. *Journal of Paleolimnology*, **28:** 79-93.

Cammarano, P. & Manca, M. (1997). Studies on zooplankton in two acidified high mountain lakes in the Alps. *Hydrobiologia*, **356:** 97-109.

Carl, G.C. (1940). The distribution of some Cladocera and free living copepoda in British Columbia. *Ecological Monographs*, **10:** 5-110.

Caroni, R. & Irvine, K. (2000). Relationships between water chemistry and zooplankton distribution in Irish lakes. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **27:** 768-772.

Carpernter, S.R., Fisher, S.G., Grimm, N.B. & Kitchell, J.F. (1992). Global change and freshwater ecosystems. *Annual Review of Ecology and Systematics*, **23:** 119-139.

Carter, J.C.H., Dadswell, M.J., Rolf, J.C. & Sprules, W.G. (1980). Distribution and zoogeography of planktonic crustaceans and dipterans in glaciated eastern North America. *Canadian Journal of Zoology*, **58:** 1355-1387.

Catalan, J., Pla, S., Rieradevall, M., Felip, M., Ventura, M., Buchaca, T., Camarero, L., Brancelj, A., Appleby, P.G., Lami, A., Grytnes, J.A., Agusti-Panareda, A. & Thompson, R. (2002a). Lake Redó ecosystem response to an increasing warming in the Pyrenees during the twentieth century. *Journal of Paleolimnology*, **28:** 129-145.

Catalan, J., Ventura, M., Brancelj, A., Granados, I., Thies, H., Nickus, U., Korhola, A., Lotter, A., Barbieri, A., Stuchlik, E., Lien, L., Bitušik, P., Buchaca, T., Camarero, L., Goudsmit, G.H., Kopácek, J., Lemcke, G., Livingstone, D.M., Müller, B., Rautio, M., Siško, M., Sorvari, S., Šporka, F., Strunecký, O. & Toro, M. (2002b). Seasonal ecosystem variability in remote mountain lakes: implications for detecting climatic signals in sediment records. *Journal of Paleolimnology*, **28:** 25-46.

Cattaneo, A., Asioli, A., Comili, P. & Manca, M. (1998). Organisms' response in a chronically polluted lake supports hypothesized link between stress and size. *Limnology and Oceanography*, **43:** 1938-1943.

Charles, D.F. (1985). Relationships between surface sediment diatom assemblages and lakewater characteristics in Adirondack Lakes. *Ecology*, **66:** 994-1011.

Charles, D.F., Smol, J.P., & Engstrom, D.R. (1994). Paleolimnological approaches to biological monitoring. In: *Biological Monitoring of Aquatic Systems*, Loeb, S.L. & Spacie, A. (Eds.), pp. 233-293, CRC Press, Boca Raton, Florida,

Charman, D.J., Caseldine, C.J., Baker, A., Gearey, B. & Hatton, J. (2001). Palaeohydrological records from peat profiles and spleothems in Sutherland, NW Scotland. *Quaternary Research*, **55:** 223-234.

Chen, C.Y. & Folt, C.L. (1996). Consequences of fall warming for zooplankton overwintering success. *Limnology and Oceanography*, **41:** 1077-1086.

Chumra, G.L., Smirnov, A. & Campbell, I.D. (1999). Pollen transport through distributaries and depositional patterns in coastal waters. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **149:** 257-270.

Cladocera (http://www.cladocera.uoguelph.ca)

Clair, T.A. & Ehrman, J.M. (1996). Variations in discharge and dissolved organic carbon and nitrogen export from terrestrial basins with changes in climate: A neural network approach. *Limnology and Oceanography*, **41:** 921-927.

Clark, P.U., Pisias, N.G., Stocker, T.F. & Weaver, A.J. (2002). The role of the thermohaline circulation in abrupt climate change. *Nature*, **415:** 863-868.

Cliff, N. (1987). *Analysing Multivariate Data.* San Diego, California: Harcourt Brace Jovanovich Publishers.

Colbourne, J. & Hebert, P.D.N. 1996. The systematic of North American *Daphnia* (Crustacea: Anomopoda): a molecular phylogenetic approach. *Philosophical Transactions of the Royal Society of London*, **B351:** 349-360.

Colman, S.M., Jones, G.A., Rubin, M., King, J.W., Peck, J.A. & Orem, W.H. (1996). AMS radiocarbon analyses from Lake Baikal, Siberia Challenges of dating sediments from a large, oligotrophic lake. *Quaternary Science Reviews*, **15:** 669-684.

Cooper, M.C., O'Sullivan, P.E. & Shine, A.J. (2000). Climate and solar variability recorded in Holocene laminated sediments – a preliminary assessment. *Quaternary International*, **68-71**: 363-371.

Crawley, M.J. (1993). *GLIM for Ecologists.* Blackwell Scientific Publications, Oxford.

Crowley, T.J. (1993). Geological assessment of the greenhouse effect. *Bulletin of the American Meteorological Society*, **74:** 2363-2373.

Cumming, B.F., Wilson, S.E., Hall, R. I. & Smol, J.P. (1995). *Diatoms from British Columbia (Canada) Lakes and Relationships to Salinity, Nutrients and Other Limnological Varaibles.* Bibliotheca Diatomologica, J. Cramer, Stuttgart, Germany, 207pp.

Dal-Hansen, G.A.P. (1995) Long term chnages in crustacean zooplankton – the effects of mass removal of Arctic charr, *Salvelinus alpinus* (L.), from an oligotrophic lake. *Journal of Plankton Research*, **17:** 1819-1833.

Dalton, C.P.D., Battarbee, R.W., Birks, H.J.B., Brooks, S.J., Cameron, N.G., Derrick, S., Evershed, R.P., McGovern, A., Peglar, S.M., Scott, J.A. & Thompson, R. (2001). Climate history through the Holocene at Lochnagar, Scotland. *Biology and Environment: Proceedings of the Royal Irish Academy*, **101B:** 159.

D'Arrigo, R.D., Cook, E.R. & Cullen, H. (1997). North Atlantic sector tree-ring records and SST variability. *ACCP Notes, the Newletter of the Atlantic Climate Change Progrmme,* **4:** 2-2.

De Costa, J. (1964). Latitudinal distribution of chydorid Cladocera in the Mississippi valley, based on their remains in surficial lake sediments. *Investigations Indiana Lakes Streams*, **6:** 65-101.

De Costa, J. (1968). Species diversity of chydorid fossil communities in the Mississippi Valley. *Hydrobiologia*, **32:** 497-512.

de Eyto E. & Irvine K (2001). The response of three chydorid species to temperature, pH and food. *Hydrobiologia*, **459:** 165-172.

De Nicola, D.M. (1986). The representation of living diatom communities in deep-water sedimentatry diatom assemblages in two Maine (USA) lakes. In: *Diatoms and lake acidity,* Smol, J. P., Battarbee, R. W., Davis, R. B. and Meriläinen, J. (Eds.), Dr. W. Junk Publisher, Dordrecht.

Dean, W. (2002). A 1500-year record of climatic and environmental change in Elk Lake, Clear Water County, Minnesota II: geochemistry, mineralogy, and stable isotopes. *Journal of Paleolimnology*, **27:** 301-319.

Deevey, E.S. (1964). Preliminary account of fossilization of zooplankton in Rogers Lake. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **115:** 981-992.

Delworth, T.L. & Dixon, K.W. (2000). Implications of the recent trend in the Arctic/North Atlantic oscillation for the North Atlantic thermohaline circulation. *Journal of Climate*, **13:** 3721-3727.

Delworth, T.L. & Knutson,T.R. (2000). Simulation of early 20th century global warming. *Science*, **287:** 2246-2250.

Dillon, P.J. & Lazerte, B.D. (1992). Response of the Plastic Lake catchement, Ontario, to reduced Sulfur deposition. *Environmental Pollution*, **77:** 211-217.

Dixit, S.S., Dixit, A.S. & Smol, J.P. (1991). Multivariable environmental inferences based on diatom assemblages from Sudbury (Canada) lakes. *Freshwater Biology*, **26:** 251-266.

Dole-Olivier, M., Galassi, D.M.P. & des Châtelliers, M.C. (2000). The biology and ecology of logic microcrustaceans. *Freshwater Biology*, **44:** 63-91.

Duigan, C.A. (1992). The ecology and distribution of the littoral freshwater Chydoridae (Branchiopoda, Anomopoda) of Ireland, with taxonomic comments on some species. *Hydrobiologia*, **241:** 1-70.

Duigan, C.A. (1996). The environmental history of a late-glacial site at Kråkenes, Western Norway, based on Cladoceran microfossil assemblages: preliminary results and interpretation. *Quaternary Newsletter*, **80**:2-9

Duigan, C. (2001). *Cladocera Short course*. (http://www.cladocera.fsnet.co.uk).

Duigan, C. & Birks, H.H. (2000). The late-glacial and early-Holocene palaeoecology of cladoceran microfossil assemblages at Kråkenes, western Norway, with a quantitative reconstruction of temperature changes. *Journal of Paleolimnology*, **23**: 67-76.

Efremov, J.A. (1940). Taphonomy: new branch of paleontology. *Pan American Geologist*, **74:** 81-93.

Eimers, M.C. & Dillon, P.J. (2002). Climate effects on sulphate flux from forested catchments in south-central Ontario. *Biogeochemistry*, **61:** 337-355.

EMERGE (1999). European Mountain lake Ecosystems: Regionalisation, diagnostics & socio-economic Evaluation protocol, ECRC, UCL, London, 53p.

Eriksson, L., Hermens. J.L.M., Johansson, E., Verhaar, H.J.M., Wold, S. (1995). Multivariate-Analysis of Aquatic Toxicity: Data with PLS. *Aquatic Sciences* **57**: 217-241.

Fairchild, G. W. (1981). Movement and microdistribution of *Sida crystallina* and other littoral microcrustacea. *Ecology*, **62:** 1341-1352.

Fee, E.J., Hecky, R.E., Kasian, S.E.M. & Cruikshank, D.R. (1996). Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. *Limnology and Oceanography*, **41:** 912-920.

Figuerola, J. & Green, A.J. (2002). Dispersal of aquatic organisms by waterbirds; a review of past research and priorities for future studies. *Freshwater Biology*, **47:** 483-494.

Filter, R. & Manuel, R. (1995). *Lakes, Rivers, Streams and Ponds of Britain and North West Europe*. Hongkong: HarperCollins Publishers. 382 pp.

Flower, R.J. (1993). Diatom preservation: experiments and observations on dissolution and breakage in modern and fossil material. *Hydrobiologia*, **269/270:** 473-484.

Flower, R.J., Cameron, N.G., Rose, N., Fritz, S.C., Harriman, R. & Stevenson, A.C. (1990). Post-1970 water-chemistry changes and palaeolimnology of several acidified upland lakes in the UK. *Philosophical Transactions of the Royal Society of London*, **B327:** 427-433.

Flössner, D. (1972). Krebstiere, Crustacea. In: *Kiemen-und Blattfusser, Branchiopoda, Fischläuse, Branchiura.* Fisher, G. (Ed.). Die Tierwelt Deutschlands, 501pp.

Folland, C.K., Karl, T. R., Christy, J. R., Clarke, R. A., Gruza, G. V., Jouzel, J., Mann, M. E., Oerlemans, J., Salinger, M.J. & Wang, S.-W. (2001). *Observed climate variability and Change. In: Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change.* Houghton, J. T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P. J., Dai, X., Makell, K. & Johnson, C. A. (Eds.), Cambridge: Cambridge University Press, pp. 99-192.

Fott, J. (1996). Zooplankton - Protocol for WP1 - Sampling large zooplankton (ZOOL) with nets. In: *A programme of mountain lake research (MOLAR)*, Charles University, Prague.

Fott, J., Prazáková, M., Stuchlík, E. & Stuchlícovà, Z. (1994). Acidification of lakes in Šumava (Bohemia) and in the High Tatra Mountains (Slovakia). *Hydrobiologia*, **274:** 37-47.

Fott, J., Stuchlík, E., Stuchlíkova, Z., Straškrabova, V., Kopácek, J. & Šimek, K. (1992). Acidifications of lakes in Tatra Mountains (Czechoslovakia) and its ecological significance. In: Mosello, R., Wathne, B. and Giussani, G. (eds.), *Documenta Ist. ital. Idrobiol. Limnology on groups of remote mountain lakes: ongoing and planned activities*, 69-81pp.

Fowler, H.J. & Kilsby, C.G. (2002). Precipitation and the North Atlantic Oscillation: a study of climatic variability in Northern England. *International Journal of Climatology*, **22:** 843-866.

Frey, D.G. (1958). The late-glacial cladoceran fauna of a small lake? *Archiv für Hydrobiologie*, **54:** 209-275.

Frey, D.G. (1959). The taxonomic and phylogenetic significance of the headpores of the Chydoridae (Cladocera). *Internationale Revue der Gesamten Hydrobiologie*, **44:** 27-50.

Frey, D.G. (1960). The ecological significance of cladoceran remains in lake sediments. *Ecology*, **41:** 684-699.

Frey, D.G. (1964). Remains of animals in Quaternary lake and bog sediments and their interpretation. *Arch.Hydrobiol.Suppl. Ergebon. Limnol.*, 2:1-114.

Frey, D.G. (1975). Subgeneric differentiation within Eurycercus (Cladocera, Chydoridae) and a new species from Northern Sweden. *Hydrobiologia*, **46:**2-3.

Frey, D.G. (1976). Interpretation of Quaternary paleoecology from Cladocera and midges, and prognosis regarding usability of other organisms. *Canadian Journal of Zoology*, **54:** 2208-2226.

Frey, D.G. (1980). On the plurality of *Chydorus sphaericus* (O. F. Müller) (Cladocera, Chydoridae), and designation of neotype from Sjaelsø, Denmark. *Hydrobilogia*, 69: 83-123.

Frey, D.G. (1982). Contrasting strategies of Gamogenesis in northern and southern populations of Cladocera. *Ecology*, **63:** 223-241.

Frey, D.G. (1986). Cladocera analysis. In: *Handbook of Holocene Palaeoecology and Palaeohydrology*, Berglund, B.E. (Ed.), pp. 667-692, John Wiley & Sons Ltd.

Frey, D.G. (1988). Littoral and offshore communities of diatoms, cladocerans and dipterous larvae, and their interpretation in paleolimnology. *Journal of Paleolimnology*, **1:** 179-191.

Frey, D. G. (1993). Subdivision of the genus Pleuroxus (Anomopoda, Chydoridae) into subgenera worldwide.Hydrobiologia. 224: 11-48. **Frey, DG 1993**. *Hydrobiologia,* **262:** 133-144

Fritz, S.C. (1996). Paleolimnological records of climatic change in North America. *Limnology and Oceanography*, **41:** 882-889.

Fryer, G. (1974). Evolution and adaptive radiation in the chydoridae (Crustacea: Cladocera): A study in comparative functional morphology and ecology. *Philosophical Transactions of the Royal Society of London*, **B254:** 226-385.

Fryer, G. (1993). *The Freshwater Crustacea of Yorkshire A Faunistic and Ecological Survey.* Yorkshire Naturalists' Union and Leeds Philosophical and Literary Society.

Gauch, H.G. Jr. (1982). *Multivariate Analysis and Community Structure.* Cambridge: Cambridge University Press.

Geladi, P. & Kowalski, B.R. (1986). Partial least-squares regression: A tutorial. *Analytica Chimica Acta*, **185:** 1-17.

George, D.G. (2000). The impact of regional-scale changes in the weather on the long-term dynamics of *Eudiaptomus* and *Daphnia* in Esthwaite Water, Cumbria. *Freshwater Biology*, **45:** 111-121.

George, D.G. & Harris, G.P. (1985). The effect of climate on long-term changes in the crustacean zooplankton biomass of Lake Windermere, UK. *Nature*, **316:** 536-539.

George, D.G., Maberly, S.C. & Hewitt, D.P. (2004). The influence of the North Atlantic Oscillation on the physical, chemical and biological characteristics of four lakes in the English Lake District. *Freshwater Biology*, **49:** 760-774.

George, D.G., Talling, J.F. & Rigg, E. (2000). Factors influencing the temporal coherence of five lakes in the English Lake District. *Freshwater Biology*, **43:** 449-461.

George, D.G. & Taylor, A. H. (1995). UK lake plankton and the Gulf Stream. *Nature*, **378:** 139-139.

George, D.G. & Winfield, I.J. (2000). Factors influencing the spatial distribution of zooplankton and fish in Loch Ness, UK. *Freshwater Biology*, **43:** 557-570.

Gerten, D. & Adrian, R. (2000). Climate driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic Oscillation. *Limnology Oceanography*, **45:** 1058-1056.

Glew, J.R. (1991). Miniature gravity corer for recovering short sediment cores. *Journal of Paleolimnology*, **5:** 285-287.

Glew, J.R. (1995). Conversion of shallow water gravity coring equipment for deep-water operation. *Journal of Paleolimnology*, **14:** 83-88.

Glew, J.R. & Last, W.M. (2001). Chrysophytes. In: Last, W.M., & Smol, J.P. (eds.), *Tracking Environmental Change Using Lake Sediments: Basin Analysis, Coring, and Chronological Techniques, Volume 1*, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 73-105.

Gliwicz, Z.M. (1986). Predation and evolution of vertical migration in zooplankton. *Nature*, **320:** 746-748.

Gordon, A.D. & Birks, H.J.B. (1972). Numerical methods in Quaternary palaeoecology. I. Zonation of pollen diagrams. *New Phytologist*, **71:** 961-979.

Goulden, C.E. (1964). The history of the cladoceran fauna of Esthwaite Water (England) and its limnological significance. *Archiv für Hydrobiologie,* **60:** 1-52.

Goulden, C.E. (1969). Interpretative studies of cladoceran microfossils in lake sediments. *Mitteilungen Internationale Vereinigung für theoretische und angewandte Limnologie*, **17:** 43-55.

Goulden, C.E. (1971). Environmental control of the abundance and distribution of the Chydorid Cladocera. *Limnology and Oceanography*, **16:** 320-331.

Goulden, C.E. & Frey, D.G. (1963). The occurrence and significance of lateral headpores in the genus *Bosmina* (Cladocera). *Internationale Revue der Gesamten Hydrobiologie*, **48:** 513-522.

Gran, G. (1950). Determination of the equivalence point in potentiometric titration. *Acta Chemica Scandinavica*, **4:** 577.

Grimm, E.C. (1987). CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers Geosciences*, **13:** 13-35.

Guilizzoni, P., Marchetto, A., Lami, A., Cameron, N.G., Appleby, P.G., Rose, N.L., Scnell, O.A., Belis, C.A., Giorgis, A. & Guzzi, L. (1996). The environmental history of a mountain lake (Lago Paione Superiore, Central Alps, Italy) for the last c. 100 years: a multidisciplinary palaeolimnological study. *Journal of Paleolimnology*, **15:** 245-264.

Hairston, N.G.Jr. (1996). Zooplankton egg banks as biotic reservoirs in changing environments. *Limnology and Oceanography,* **41:** 1087-1092.

Haney, R.A. & Taylor, D.J. (2003). Testing paleolimnological predictions with molecular data: the origins of Holarctic *Eubosmina*. *Journal of Evolutionary Biology*, **16:** 871-882.

Hann, B. & Karrow, P.F. (1993). Comparative analysis of cladocerarn microfossils in the Don and Scarborough Formations, Toronto, Canada. *Journal of Paleolimnology*, **9:** 223-241.

Hann, B.J. & Turner, M.A. (2000). Littoral microcrustacea in Lake 302S in experimental area of Canada: acidification and recovery. *Freshwater Biology*, **43:** 133-146.

Hanner, R.H. (1997). Taxonomic problems with phylogenetic solutions derived from integration of biochemical, morphological and molecular data. Unpublished PhD thesis, University of Oregon, USA.

Harmsworth, R.V. (1968). The developmental history of Blelham Tarn (England) as shown by animal microfossils, with special reference to the Cladocera. *Ecological Monographs*, **38:** 223-241.

Harmsworth, R.V. & Whiteside, M.C. (1968). Relation of cladoceran remains in Lake sediments to primary productivity of lakes. *Ecology*, **49:** 998-1000.

Harriman, R., Anderson, H. & Miller, J.D. (1995). The role of sea-salts in enhancing and mitigating surface water acidity. *Water Air and Soil Pollution*, **85:** 553-558.

Harriman, R. & Morrison, B.R.S. (1982). The ecology of streams draining forested and non-forested catchments in an area of central Scotland subject to acid precipitation. *Hydrobiologia*, **88:** 251-263.

Harriman, R. & Pugh, K.B. (1994). Water Chemistry. In: *The Freshwaters of Scotland: A National Resource of International Significance*, Maitland, P.S., Boon, P.J. & McLusky, D.S. (eds.), John Willey & Sons Ltd, pp. 89-112.

Harrison, S. J. (1997). Changes in Scottish climate. *Botanical Journal of Scotland*, **49:** 287-300.

Hauer, F.R., Baron, J.S., Campbell, D.H., Fausch, K.D., Hostetler, S.W., Leavesley, G.H., Leavitt, P.R., McKnight, D.M. & Stanford, J.A. (1997). Assessment of climate change and freshwater ecosystems of the Rocky Mountains, USA and Canada. *Hydrological Processes*, **11:** 903-924.

Hays, J.D., Imbrie, J. & Shackleton, N.J. (1976). Variations in the Earth's Orbit: Pacemaker of the Ice Ages. *Science*, **194:** 1121-1132.

Hedberg, H. D. (1976). *International Stratigraphic Guide*. Willey, New York.

Henriksen, A., Skjelvåle, B.L., Mannio, J., Wilander, A., Harriman, R., Curtis, C., Jensen, J.P., Fjeld, E. & Moiseenko, T. (1998). Northern European lake survey. *Ambio*, **27:** 80-91.

Hill, M.O. (1973). Reciprocal averaging: an eigenvector method of ordination. *Journal of Ecology*, **61:** 237-254.

Hill, M.O. (1979). *TWINSPAN - A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes.* Ithaca, N.Y.: Cornell University, 90p.

Hill, M.O. & Gauch, H.G.Jr. (1980). Detrended correspondence analysis: an improved ordination technique. *Vegetatio*, **42:** 47-58.

Hofmann, W. (1978). Analysis of animal microfossils from the Groβer Segeberger (F. R. G.). *Archiv für Hydrobiologie*, **82:** 316-346.

Hofmann, W. (1986). Developmental history of the Groβer Plöner See and the Schöhsee (north Germany): cladoceran analysis, with special reference to eutrophication. *Archiv für Hydrobiologie Supplement*, **74:** 259-287.

Hofmann, W. (1987). Cladocera in space and time: analysis of lake sediments. *Hydrobiologia*, **145:** 315-321.

Hofmann, W. (1993). Dynamics of littoral cladocera assemblage under the influence of climatic and water depth changes from Allerod to Sub-boreal. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **25:** 1095-1101.

Hofmann, W. (1996). Empirical relationships between cladoceran fauna and trophic state in thirteen northern German lakes: Analysis of surficial sediments. *Hydrobiologia*, **318:** 195-201.

Hofmann, W. (1998a). Cladocerans and chironomids as indicators of lake level changes in north temperate lakes. *Journal of Paleolimnology*, **19:** 55-62.

Hofmann, W. (1998b). The response of *Bosmina (Eubosmina)* to eutrophication of Upper Lake Constance: the subfossil record. *Archiv für Hydrobiologie Special Issues in Advance Limnology*, **53:** 275-283.

Hofmann, W. (2000). Response of the chydorid faunas to rapid climatic changes in four alpine lakes at different altitudes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **159:** 281-292.

Hofmann,W. (2003). The long-term succession of high-altitude cladoceran assemblages: a 9000-year record from Sägistalsee (Swiss Alps). *Journal of Paleolimnology*, **30:** 291-296.

Horel, J. & Geisler, J. (1997). *Global Environmental Change: An Atmospheric Perspective*. John, Willy & Sons, Inc. 152 pp.

Houghton, J. (1994). *Global Warming the Complete Briefing*. Oxford: Lion Publishing plc. 192 pp.

Hrbácek, J. (1969). On the possibility of estimating predation pressure and nutrition level of populations of *Daphnia* (Crust., Cladoc.) from their remains in sediments. *Mitteilungen Internationale Vereinigung für theoretische und angewandte Limnologie*, **17:** 269-279.

Hu, F.S. & Shemesh, A. (2003). A biogenic-silica $\delta^{18}O$ record of climatic change during the glacial-interglacial transition in southwestern Alaska. *Quaternary Research*, **59**: 379-385.

Hughes, L. (2000). Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15:** 56-61.

Huisman, J., Olff, H. & Fresco, L.F.M. (1993). A hierarchical set of models for species response analysis. *Journal of Vegetation Science*, **4:** 37-46.

Hurrel, J.W. (1995). Decadal trends in the North Atlantic Oscillation: Regional Temperatures and Precipitation. *Science*, **269:** 676-679.

IPCC (1995). *Climate Change: Radiative Forcing of Climate Change and an Evaluation of the IPCC IS92 Emission Scenarios*, Houghton, J. T., Meira, Filho L. G., Bruce, J., Lee, H., Callander, B. A., Haites, E., Harris, N., and Maskell, K. (Eds.), Cambridge University Press, 339pp.

IPCC (2001). *Climate Change and Biodiversity*. Gitay, H., Suárez, A., Watson, R. T., and Dokken, D.J.V. (Eds.), IPCC.

Jenkin, P.M. (1942). Seasonal changes in the temperature of Windermere (English Lake District). *Journal of Animal Ecology*, **11:** 248-269.

Jenniss, S.W., Katz, S.A. & Lynch, R.W. (1997). *Application of atomic spectrometry to regulatory compliance monitoring*. New York: Wiley-VCH.

Jeppesen, E., Christoffersen, K., Landkildehus, F., Lauridsen, T. (2001a). Fish and crutaceans in northeast Greenland lakes with special emphasis on interactions between Arctic charr (*Savelinus alpinus*), *Lepidurus arcticus* and benthic chydorids. *Hydrobiologia*, **442:** 329-337.

Jeppesen, E., Jensen, J.P., Lauridsen, T.L., Amsinck, S.L., Christoffersen, K., Søndergaard, M. & Mitchell, S.F. (2003). Sub-fossils of cladocerans in the surface sediment of 135 lakes as proxies for community structure of zooplankton, fish abundance and lake temperature. *Hydrobiologia*, **491:** 321-330.

Jeppesen,E., Leavitt, P.R., de Meester, L., Jensen, J.P. (2001b). Functional ecology and paleolimnology: using cladoceran remains to reconstruct anthropogenic impact. *Trends in Ecology and Evolution,* **16:** 191-198.

Jeppesen, E., Madsen, E.A., Jensen, J.P. (1996). Reconstructing the past density of planktivorous fish and trophic structure from sedimentary zooplankton fossils: a surface sediment calibrartion data set from shallow lakes. *Freshwater Biology*, **36:** 115-127.

Jones, P.D. (2002). Changes in climate and variability over the last 1000 years. In: *Meteorology at the Millennium,* Pearce, R.P. (Ed.), Academic Press, 133-142pp.

Jones, P.D., Osborn, T. J., Wigley, T.M.L., Kelly, P. M. & Santer, B.D. (1997a). Comparisons between microwave sounding unit temperature record and the surface temperature record over 1979 to 1996: real differences or potential discontinuities? *Journal of Geophysical Research,* **102:** 30135-30145.

Jones, V.J., Battarbee, R.W., Rose, N.L., Curtis, C., Appleby, P.G., Harriman, R. & Shine, A.J. (1997b). Evidence for the pollution of Loch Ness from the analysis of its recent sediments. *The Science of the Total Environment*, **203:** 37-49.

Jones, V.J. & Flower, R.J. (1986). Spatial and temporal variability in periphytic diatom communities: palaeoecological significance in an acidified lake. In*: Diatom and Lake Acidity*, Smol, J. P., Battarbee, R. W., Davis, R. B., Meriläinen, J. Dordrecht, Dr. W. (Eds.), Junk Publisher, 307pp.

Jones, V.J., Flower, R.J., Appleby, P.G., Natkanski, J., Richardson, N., Rippey, B., Stevenson, A.C. & Battarbee, R.W. (1993). Paleolimnological evidence for the acidification and atmospheric contamination of lochs in the Cairngorm and Lochnagar areas of Scotland. *Journal of Ecology*, **81:** 3-24.

Jones, R.I., Fulcher, A.S., Jayakody, J.K.U., Laybournparry, J., Shine, A.J., Walton, M.C. & Young, J.M. (1995) The horizontal distribution of plankton in a deep, oligotrophic lake – Loch Ness, Scotland. *Freshwater Biology*, **33**, 161-170.

Juggins, S. (2003). *C^2 User Guide. Software for ecological and palaeoecological data analysis and visualisation.* University of Newcastle-upon-Tyne, UK. 69pp.

Juggins, S. (1991). ZONE Version 1.2 – A cluster analysis technique. University of Newcastle upon Tyne, Unpublished computer program.

Juggins, S. & ter Braak, C.J.F. (1997). CALIBRATE Version 0.81 – A Computer Program for Species-Environmental Calibration by WA (Weighted Averaging) Partial Least Squares Regression. University of Newcastle upon Tyne, Unpublished computer program.

Kato, M., Tanimura, Y., Matsuoka, K. & Fukusawa, H. (2003). Planktonic diatoms from sediment traps in Omura Bay, western Japan with implications for ecological implications for ecological and taphonomic studies of coastal marine environments. *Quaternary International*, **105:** 25-31.

Keen, R. (1973). A probabilistic approach to the dynamics of natural populations of the Chydoridae (Cladocera, Crustacea). *Ecology*, **54:** 524-534.

Keller, A.A., Oviatt, C.A., Walker, H.A. & Hawk, J.D. (1999). Predicted impacts of elevated temperature on the magnitude of the winter-spring phytoplankton bloom in temperate coastal waters: A mesocosm study. *Limnology and Oceanography*, **44:** 344-356.

Kerfoot, W.C. (1974). Net accumulation rates and the history of Cladoceran communities. *Ecology*, **55:** 51-61.

Kirchhefer, A.J. (2001). Reconstruction of summer temperatures from tree-rings of Scots pine (*Pinus sylvestris* L.) in coastal northern Norway. *Holocene*, **11:** 41-52.

Koinig, K.A., Kamenik, C., Schmidt,R., Agusti-Panareda,A., Appleby,P., Lami,A., Miroslava, P., Rose, N., Schnell, Ø.A., Tessadri, R., Thompson, R. & Psenner, R. (2002). Environmental changes in an alpine lake (Gossenköllesee, Austria) over the last two centuries - the influence of air temperature on biological parameters. *Journal of Paleolimnology*, **28:** 147-160.

Kopácek, J., Stuchlík, E., Blažka, P., Vyhnálek, V. & Závodský (1996a). Concentration of nutrients in selected lakes in the high Tatra Mountains, Slovakia: effect of season and watershed. *Hydrobiologia*, **319:** 47.

Kopácek, J., Stuchlík, E., Straškarabová, V. & Pšenáková, P. (1996b). Factors governing nutrient status of mountain lakes in the Tatra Mountains. *Freshwater Biology*, **43:** 369-383.

Kopácek, J., Stuchlík, E., Straškarabová, V.F.J., Veselý, J. & Pšenáková, P. (2000). Factors governing nutrient status of mountain lakes in the Tatra Mountains. *Freshwater Biology*, **43:** 369-383.

Korhola, A. (1990). Paleolimnology and hydroseral development of the Kotasuo Bog, Southern Finland, with special reference to the Cladocera. *Ann.Acad.Sci.Fenn.A.III*, **155:** 1-40.

Korhola, A. (1992). The early Holocene hydrosere in a small acid hill-top basin studied using crustacean sedimentary remains. *Journal of Paleolimnology*, **7:** 1-22.

Korhola, A. (1999). Distribution patterns of Cladocera in subarctic Fennoscandian lakes and their potential in environmental reconstruction. *Ecography*, **22:** 357-373.

Korhola, A., Olander, H. & Blom, T. (2000). Cladoceran and chironomid assemblages as quantitative indicators of water depth in subarctic Fennoscandian lakes. *Journal of Paleolimnology*, **24:** 43-54.

Korhola, A.A. & Rautio, M. (2001). Cladocera and other branchipod crustaceans. In: Smol, J. P., Birks, H. J. B., and Last, W. M., *Tracking Environmental Change Using Lake Sediments, Volume 4: Zoological Indicators*, Kluwer Academic Publishers, Dordrecht, The Netherlands, 240pp.

Korhola, A., Sorvari, S., Rautio, M., Appleby, P.G., Dearing, J.A., Hu, Y., Rose, N., Lami, A. & Cameron, N.G. (2002a). A multi-proxy analysis of climate impacts on the recent development of subarctic Lake Saanajärvi in Finnish Lapland. *Journal of Paleolimnology*, **28:** 59-77.

Korhola, A., Weckström, J. & Blom, T. (2002b). Relationships between lake and land-cover features along latitudinal vegetation ecotones in arctic Fennoscandia. *Archiv fur Hydrobiologie Supplement.*, **139:** 203-235.

Korínek, V. (1971). Comparative study of the head pores in the genus *Bosmina* Baird (Crustacea, Cladocera). *Vestnik Ceskoslovenske Spolecnosti Zoologicke*, **35:** 275-207.

Kotov, A.A. (1996). Morphology and postembryonic development of males and females of *Bosmina longispina* Leydig (Crustacea, Anomopoda) from a North Iceland population. *Hydrobiologia*, **341:** 187-196.

Krause-Dellin, D. & Steinberg, C. (1986). Cladoceran remains as indicators of lake acidification. *Hydrobiologia*, **143:** 129-134.

Krause, H.R. (1959). Beitrage zur Kenntnis des Chitinabbaues im toten Zooplankton. *Archiv für Hydrobiologie Supplement*, **25:** 67-82.

Lami, A., Guilizzoni, P., Bettinetti, R., Belis, C.A., Manca, M., Comoli, P., Marcheto, A., Ariztegui, D. & Chondrogianni, C. (1996). Biological records of late Pleistocene and Holocene environmental changes from two Italian Crater Lake sediments: Results from a European interdisciplinary research project (PALICLAS). *II Quarternario Italian Journal of Quaternary Sciences*, **9:** 711-720.

Lami, A., Guilizzoni, P., Ryves, D.B., Jones, V.J., Marchetto, A., Battarbee, R.W., Belis, C.A., Bettinetti, R., Manca, M., Comoli, P., Nocentini, A. & Langone, L. (1997). A late glacial and Holocene record of biological and environmental changes from the Crater Lake Albano, central Italy: an interdisciplinary European project (PALICLAS). *Water, Air and Soil Pollution*, **99:** 601-613.

Lapse rate calculation (http://farside.ph.utexas.edu/teaching/sm1/lectures/node55.html)

Larocque, I., Hall, R.I. & Grahn, E. (2001). Chironomids as indicators of climate change: a 100-lake training set from a subarctic region of northern Sweden (Lapland). *Journal of Paleolimnology*, **26:** 307-322.

Larocque, I. & Hall, R.I. (2003). Chironomids as quantitative indicators of mean July air temperature: validation by comparison with century-long meteorological records from northern Sweden. *Journal of Paleolimnology*, **29:** 475-493.

Lehman, J.T. (1975). Reconstructing the rate of accumulation of Lake Sediment: The effect of sediment focusing. *Quaternary Research*, **5:** 541-550.

Leibold, M. A. (1990) Resources and predators can affect the vertical distribution of zooplankton. *Limnology and Oceanography*, **35**, 938-944.

Leps, J. & Smilauer, P. (2003). *Multivariate Analysis using CANOCO*. Cambridge University Press.

Levesque, A.J., Cwynar, L.C. & Walker, I.R. (1996). Richness, diversity and succession of lake-glacial chironomid assemblages in New Brunswick, Canada. *Journal of Paleolimnology*, **16:** 257-274.

Lieder, U. (1991). The *Bosmina kessleri-* like morphotype of *Eubosmina* in Lake Muskoka, Ontario, Canada, as putative inter-specific hybrids. *Hydrobiologia*, **225:** 71-80.

Line, J.M., ter Braak, C.J.F., & Briks, H.J.B. (1994). WACALIB version 3.3 – a computer program to reconstruct environmental variables from fossil assemblages by weighted averaging and to derive sample-specific errors of prediction. *Journal of Paleolimnology*, **10:** 147-152.

Livingstone, D.M. & Dokulil, M.T. (2001). Eighty years of spatially coherent Austrian lake surface temperature and their relationship to regional air temperature and the North Atlantic Oscillation. *Limnology and Oceanography,* **46:** 1220-1227.

Livingstone, D.M. & Lotter, A.F. (1998). The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palaeolimnological implications. *Journal of Paleolimnology*, **19:** 181-198.

Livingstone, D.M., Lotter, A.F. & Walker, I.R. (1999). The decrease in summer surface water temperature with altitude in Swiss Alpine Lakes: A comparison with air, temperature lapse rates. *Arctic, Antarctic and Alpine Research*, **31:** 341-352.

Loose, C.J. & Dawidoxicz, P. (1994). Trade-off in diel vertical migration by zooplankton: the costs of predator avoidance. *Ecology*, **75:** 2255-2263.

Lotter, A. (2003). Multi-proxy climatic reconstructions. In: *Global Change in the Holocene*, Mackay, A., Battarbee, R., Birks, J. & Oldfield, F. (Eds.), Arnold, London, pp. 373-38.

Lotter, A.F., Birks, H.J.B., Eicher, U., Hofmann,W. & Marchetto, A. (1997). Modern diatom, Cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. *Journal of Paleolimnology*, **18:** 395-420.

Lotter, A.F., Birks, H.J.B., Eicher, U., Hofmann, W., Schwander, J. & Wick, L. (2000a). Younger Dryas and Allerod summer temperatures at Gerzensee (Switzerland) inferred from fossil pollen and cladoceran assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **159:** 349-361.

Lotter, A.F., Eicher, U., Siegenthaler, U. & Birks, H.J.B. (1992). Late-glacial climatic oscillations as recorded in Swiss lake sediments. *Journal of Quaternary Science*, **7:** 187-204.

Lotter, A. & Boucherle, M.M. (1984). A late-glacial and post-glacial history of Amsoldingersee and vicinity, Switzerland. *Schweizerische Zeitschrift für Hydrologie*, **46:** 193-209.

Lotter, A.F., Hofmann, W., Kamenik, C., Lami, A., Ohlendorf, C., Sturm, M., Van Der Knaap & W.O. Van Leeuwen, J.F.N. (2000b): Sedimentological and biostratigraphical analyses of short sediment cores from Hagelseewli (2339 m a. s. l.) in the Swiss Alps. *Journal of Limnology*, **59 (Suppl.):**53-64.

Lotter, A.F. & Lemcke, G. (1999). Methods for preparing and counting biochemical varves. *Boreas*, **28:** 243-252.

Lucassen, E.C.H.E.T., Bobbink, R., Oonk, M.M.A., Brandrud, T.-E. & Roelofs, J.G.M. (1999). The effects of liming and reacidification on the growth of *Juncus bulbosus*: a mesocosm experiment. *Aquatic Botany*, **64:** 95-103.

Maguire, B.J. (1963). The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. *Ecological Monographs*, **33:** 161-185.

Maitland, P.S., Smith, B. D. & Dennis, G.M. (1981) The crustacean zooplankton. In: *The ecology of Scotland's largest lochs* (Ed. P. Maitland), pp. 135-154, Dr. W. Junk Publishers, The Hague, 135-154.

Manca, M. & Comoli, P. (1995). Temporal variations of fossil Cladocera in the sediments of Lake Orta (N. Italy) over the last 400 years. *Journal of Paleolimnology*, **14:** 113-122.

Manca, M., Comoli, P. & Lencioni, V. (1999). Population dynamics and production of crustacean zooplankton in two mountain lakes in the Italian Alps (Lake Paione Superiore and Lake Malghette). *Journal of Limnology*, **58:** 25-28.

Manly, B.F.J. (1991). *Randomization and Monte Carlo Methods in Biology*. London: Chapman and Hall.

Manly, B.F.J. (2000). *Multivariate Statistical Methods: A Primer.* Chapman and Hall/CRC.

Mann, M.E. (2000). Lessons for a new millennium. *Science*, **289:**253-254

Mann, M.E. (2002). The value of multiple proxies. *Science*, **297:** 1481-1482.

Mann, M.E., Bradley, R.S. & Hughes, M.K. (1998). Global-scale temperature patterns and climate forcing over the past six centuries. *Nature*, **392:** 779-787.

Marcheto, A. (1997). Performances of analytical methods for freshwater analysis assessed through intercomparison exercises. I. Total alkalinity. *Memorie dell'Istituto Italiano di Idrobiologia*, **56:** 1-13.

Marcheto, A. (1998). The study of high mountain lakes in the activity of the Istituto Italiano di Hydrobiologia. In: Lami, A. and Giussani, G. (Eds.), 1-10. 1998. Verbania Pallanza, (Nepal).

Marotzke, J. (2000). Abrupt climate change and thermohaline circulation: Mechanisms and predictability. *Proceedings of the National Academy of the Sciences of the United States of America*, **97:** 1347-1350.

Maslin, M.A. & Berger, A. (1997). A European view of the future of the palaeoclimate research. *Quaternary Science Reviews*, **16:** 501-504.

Maslin, M. A., Pike, J., Stickley, C. & Ettwein, V. (2003). Evidence of Holocene climate variability in marine sediments. In: *Global Change in the Holocene,* Mackay, A., Battarbee, R.W., Birks, H.J. B. & Oldfield, F. (Eds.), Arnold, London, pp.185-209.

Matsumara-Tundisi, T., Tundisi, J.G. & Tavares, L.S. (1984). Diel migration and vertical distribution of Cladocera in Lake D. Helvecio (Minas Gerais, Brazil). *Hydrobiologia*, **113:** 299-306.

Mayes, J. (2000). Changing regional climatic gradients in the United Kingdom. *The Geographical Journal*, **166:** 125-138.

McCullagh, P. & Nelder, J.A. (1989). *Genralised Linear Models*. London: Chapman & Hall.

Mckee, D., Atkinson, D., Collings, S., Eaton, J. Harvey, I. Heyes, T., Hatton, K., Wilson, D. & Moss, B. (2002). Macro-zooplankter responses to simulated climate warming in experimental freshwater microcosms. *Freshwater Biology*, **47:** 1557-1570.

Megard, R.O. (1964). Biostratigraphic history of Dead Man Lake, Chuska Mountains, New Mexico. *Ecology*, **45:** 529-546.

Megard, R.O. (1967). Late Quaternary Cladocera of Lake Zeribar, Western Iran. *Ecology*, **48:** 179-189.

Meriläinen, J.J., Veijola, H. & Hynynen, J. (2000). Zoobenthic communities in relation to the depth zone in a large boreal lake in Finland. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **27:** 985-988.

Meyers, P.A. & Teranes, J.L. (2001). Sediment organic matter. In: Last, W.M. & Smol, J.P. (eds.), *Tracking Environmental Change Using Lake Sediments, Volume 2: Physical and Geochemical Methods*, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp.139-269.

Mezquita, F. & Miracle, M.R. (1997). Chydorid assemblages in the sedimentary sequence of Lake La Cruz (Spain) subject to water level changes. *Hydrobiologia*, **360:** 277-285.

Milly, P.C.D., Wetherrald, R.T., Dunne, K.A. & Delworth, T.L. (2002). Increasing risk of great risk of great floods in a changing climate. *Nature*, **415:** 514-517

Monteith, D.T. & Evans, C. (2000). *UK Acid Water Monitoring Network: 10-year report*. London, ENSIS Ltd. 364pp.

Monteith, D.T., Evans, C.D. & Reynolds, B. (2000). Are temporal variationis in the nitrate content of UK upland freshwaters linked to the North Atlantic Oscillation? *Hydrological Processes*, **14:** 1745-1749.

Moore, J.J., Hughen, K.A., Miller, G.H. & Overpeck, J.T. (2001). Little Ice Age recorded in summer temperature reconstruction from varved sediments of Donard Lake, Baffin Island, Canada. *Journal of Paleolimnology*, **25:** 503-517.

Moritz, R.E., Bitz, C.M. & Steig, E.J. (2002). Dynamics of recent climate change in the Arctic. *Science*, **297:** 1497-1502.

Mueller, W.P. (1964). The distribution of cladoceran remains in surficial sediments from three Northern Indiana Lakes. *Investigations Indiana Lakes Streams*, **6:** 1-63.

Muguel, S., Bolívar, J.P. & García-Tenorio, R. (2003). Mixing, sediment accumulation and focusing using 210Pb and 137Cs. *Journal of Paleolimnology*, **29:** 1-11.

NERC Report No. 114 (2003) The influence of the North Atlantic Oscillation on the acidity status of upland Scottish lochs (Award No.: NER/B/S/2000/00752).

Nesje, A. & Dahl, S.O. (2001). The Greenland 8200 cal. Yr BP event detected in loss-on-ignition profiles in Norwegian lacustrine sediment sequences. *Journal of Quaternary Science*, **16:** 155-156.

Nilssen, J.P., Halvorsen, G. & Melåen, J. (1980). Seasonal divergence of *Bosmina* morphs. *Internationale Revue der Gesamten Hydrobiologie*, **65:** 507-516.

Nilssen, J.P. & Sandøy, S. (1990). Recent lake acidification and cladoceran dynamics: surface sediment and core analyses from lakes in Norway, Scotland and Sweden. *Philosophical Transactions of the Royal Society of London*, **B327:** 299-309.

North Atlantic Drift (http://www.metoffice.com/weather/europe/uk/nwscotland.html)

Odland, A., Birks, H.J.B. & Line, J.M. (1995). Ecological optima and tolerances of *Thelypteris limbosperma*, *Athyrium disterntifolium*, and *Matteuccia struthiopteris* along environmental gradients in Western Norway. *Vegetatio*, **120:** 115-129.

Odland, A. & Birks, H.J.B. (1999). The altitudinal gradient of vascular plant richness in Aurland, western Norway. *Ecography*, **22:** 548-566.

Oksanen, J. & Minchin, P.R. (2002). Continuum theory revisited: what shape are species responses along ecological gradients? *Ecological Modelling*, **157:** 119-129.

Olander, H., Birks, H.J.B., Korhola, A. & Blom, T. (1999). An expanded calibration model for inferring lakewater and air temperatures from fossil chironomid assemblages in northern Fennoscandia. *The Holocene* , **9:** 279-294.

Olsen, L-H., Sunesen, J. & Pedersen, B.V. (2001). *Small Freshwater Creatures.* Oxford: Oxford University Press. 228 pp.

Økland, R.H. (1999) On the variation explained by ordination and constrained ordination axes. *Journal of Vegetation Science*, **5:** 117-126.

Overpeck, J. K., Hughen, D., Hardy, R., Bradley, R., Case, M., Douglas, M., Finny, B., Gajewski, K., Jacoby, G., Jennings, A., Lamoureux, S., Lasca, A., MacDonal, G., Moore, J., Retelle, M., Smith, S., Wolfe, A. & Zielinski, G. (1997). Arctic environmental changes of the last four centuries. *Science*, **278:**1251-1256.

Parsons, L.S. & Lear, W.H. (2001). Climate variability and marine ecosystem impacts: A North Atlantic perspective. *Progress in Oceanography*, **49**: 167-188.

Patalas, K. (1990). Diversity of the zooplankton communities in Canadian lakes as a function of climate. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **24:** 360-368.

Patrick, S., Monteith, D. T. & Jenkins, A. (1995). *UK Acid Water Monitoring Network: The Five Yeas Report.* London, ENSIS Ltd. 320pp.

Peck, J.A., Khosbayar, P., Fowell, S., Pearce, R.B., Ariunbileg, S., Hansen, C.S.H. & Soninkhishig, N. (2002). Mid to Late Holocene climate change in north central Mongolia as recorded in the sediments of Lake Telmen. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **183:** 135-153.

Peglar, S. (1979). A radiocarbon dated pollen diagram from Loch of Winless, Caithness. *New Phytology*, **82:** 245-263.

Petit, J.R., Basile, I., Leruyuet, A., Raynaud, D., Lorius, C., Jouzel, J., Stievenard, M., Lipenkov, V. Y., Barkov, N. I., Kudryashov, B. B., Davis, M., Saltzman, E. & Kotlyakov, V. (1997). Four climate cycles in Vostok ice core. *Nature*, **387:** 359-360.

Pla, S. (2001). *Chrysophycean Cysts from the Pyrenees.* J. Cramer, Berlin. 179 pp.

Pla, S., Camarero, L. & Catalan, J. (2003). Chrysophyte cyst relationships to water chemistry in Pyrenean lakes (NE Spain) and their potential for environmental reconstruction. *Journal of Paleolimnology*, **30:** 21-34.

Pompilio, L., Ambrosetti, W. & Barbanti, L. (1996). Morphometry and thermal stratification in Italian lakes. 1. Predictive models. *Memorie dell'Istituto Italiano di Idrobiologia*, **54:** 1-29.

Porinchu, D.F. & Cwynar, L.C. (2002). Late-Quaternary history of midge communities and climate from a tundra site near the lower Lena River, Northeast Siberia. *Journal of Paleolimnology*, **27:** 59-69.

Porinchu, D.F., MacDonald, G.M., Bloom, A.M. & Moser, K.A. (2002). The modern distribution of chironomid sub-fossils (Insecta: Diptera) in the Sierra Nevada, California: Potential for paleoclimatic reconstructions. *Journal of Paleolimnology*, **28:** 355-375.

Powell, E.N., Parsons-Hubbard, K.M., Callender, W. R., Staff, G.M., Rowe, G.T., Brett, C.E., Walker, S.E., Raymond, A., Carlson, D.D., White, S. & Heise, E.A. (2002). Taphonomy on the continental shelf and slope: two-year trends – Gulf of Mexico and Bahamas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **184**: 1-35.

Prâzáková, M. and Fott, J. (1994). Zooplankton decline in the Cerné Lake (Šumava Mountains, Bohemia) as reflected in the stratification of cladoceran remains in the sediment. *Hodrobiologia*, **274:** 11-126.

Price, R. J. (1983). *Scotland Environments during the last 30,000 years.* Edinburgh: Scottish Academic Press.

Proctor, C.J., Baker, A. & Barnes, W.L. (2002). A three thousand year record of North Atlantic climate. *Climate Dynamics*, **19:** 449-454.

Proctor, C.J., Baker, A., Barnes, W.L. & Gilmour, M.A. (2000). A thousand year speleothem proxy record of North Atlantic Climate from Scotland. *Climate Dynamics,* **16:** 815-820.

Psenner, R. (1988). Alkalinity generation in a soft-water lake: watershed and in-lake processes. *Limnology and Oceanography*, **33:** 1463-1475.

Psenner, R. & Schmidt, R. (1992). Climate-driven pH control of remote alpine lakes and effects of acid deposition. *Nature*, **356:** 781-783.

Qinghong, H. & Bråkenhielm, S. (1995). A statistical approach to decompose ecological variation. *Water, Air and Soil Pollution*, **85:** 1587-1592.

Quade, H.W. (1969). Cladoceran faunas associated with aquatic macrophytes in some lakes in northwestern Minnesota. *Ecology*, **50:** 170-179.

Ramdani, M., Flower, R.J., Elkhiati, N., Birks, H., Kraiem, M. & Fathi, A. A. (2001). Zooplankton (Cladocera, Ostracoda), Chironomidae and other benthic faunal remains in sediment cores from nine African wetland lakes: ther CASSARINA Project. Aquatic Ecology, 35: 389-403.

Rasmussen, J.B. (1988). Littoral zoobenthic biomass in lakes, and its relationship to physical, chemical, and trophic factors. *Canadian Journal of Fisheries and Aquatic Sciences*, **45:** 1436-1447.

Rautio, M. (1998). Community structure of crustacean zooplankton in subarctic ponds-effects of altitude and physical heterogeneity. *Ecography*, **21:** 327-335.

Rautio, M., Sorvari, S. & Korhola, A. (2000). Diatom and crustacean zooplankton communities, their seasonal variability and representation in the sediments of subarctic Lake Saanajarvi. *Journal of Limnology*, **59:** 81-96.

Raynaud, D., Barnola, J.M., Chappellaz, J., Delmas, R.J. & Lorius, C. (1993). The ice record of greenhouse gases. *Science*, 259: 926.

Renberg, I. (1991). The HON-Kajak sediment corer. *Journal of Paleolimnology*, **6:** 167-170.

Reed, J. M. (1998). A diatom-conductivity transfer function for Spanish salt lakes. *Journal of Paleolimnology*, **19:** 399-416.

Rioual, P. (2000). Diatom assemblages and water chemistry of lakes in the French Massif Central: A methodology for reconstruction of past limnological and climate fluctuations during the Eemian Period. Unpublished PhD thesis, University of London, 520pp.

Rioual, P., Andrieu-Ponel, V., Rietti-Shati, M., Battarbee, R.W., de Beaulieu, J.L., Reille, M., Svobodova, H. & Shemesh, A. (2001). High-resolution record of climate stability in France during the last interglacial period. *Nature*, **413:** 293-296.

Roberstson, A.L., Rundle, S.D. & Schmid-Araya, J.M. (2000). Putting the meio-into stream ecology: current findings and future directions for lotic meiofaunal research. *Freshwater Biology*, **44:** 177-183.

Robock, A. (1981). The Mount St. Helens volcanic eruptions of 18 May 1980: Minimal climatic effect. *Science*, **212:** 1383-1384.

Rodwell, M.J., Rowell, D.P. & Folland, C.K. (1999). Oceanic forcing of the wintertime North Atlantic Oscillation and European climate. *Nature*, **398:** 320-323.

Rose, N. L., Harlock, S., Appleby, P.G. & Battarbee, R.W. (1995). Dating of recent lake sediments in the United Kingdom and Ireland using spheroidal carboneous particle (SCP) concentration profiles. *The Holocene*, **5:** 328-335.

Rose, N. & Rippey, B. (2002). The historical record of PAH, PCB, trace metal and fly-ash particle deposition at a remote lake in north-west Scotland. *Environmental Pollution*, **17:** 121-132.

Røen, U. (1981). The Branchipoda (Crustacea) of three high-arctic areas: Ellesmere Island, N. W. T., Canada; Greenland north of 74 ^{0} N; and Svalbard. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **21:** 1541-1544.

Rouse, W.R., Douglas, M.V., Hecky, R.E., Hershey, A.E., Kling,G.W., Lesack,L., Marsh, P., McDonald, M., Nicholson, B.J., Roulet, N.T. & Smol, J.P. (1997). Effects of climate change on the freshwaters of arctic and subarctic north America. *Hydrological Processes*, **11:** 873-902

Ryves, D.B., Jewson, D.H., Sturm, M., Battarbee, R.W., Flower, R.J., Mackay, A.W., Granin, N.G. (2003). Quantitative and qualitative relationships between planktonic diatom communities and diatom assemblages in sedimenting material and surface sediments in Lake Baikal, Siberia. *Limnology and Oceanography*, **48:** 1643-1661.

Sacherova V. & Hebert, P.D.N. (2003). The evolutionary history of the Chydoridae (Crustacea: Cladocera). *Biological Journal of the Linnean Society*, **79**: 629-643.

Sandøy, S. & Nilssen, J.P. (1986). A geographical survey of littoral crustacea in Norway and their use in paleolimnology. *Hydrobiologia*, **143:** 277-286.

Sarmaja-Korjonen, K. (2001). Correlation of fluctuations in cladoceran planktonic:littoral ratio between three cores from a small lake in southern Finland: Holocene water-level changes.*The Holocene*, **11:** 53-63.

Sarmaja-Korjonen, K. (2002). Multi-proxy data from Kaksoislammi Lake in Finland: dramatic change of the late Holocene cladoceran assemblages. *Journal of Paleolimnology,* **28:** 287-296.

Sarmaja-Korjonen, K. (2003). Chydorid ephippia as indicators of environmental change - biostratigraphical evidence from two lakes in southern Finland. *The Holocene*, **13:** 691-700.

Sarmaja-Korjonen, K. & Alhonen, P. (1999). Cladoceran and diatom evidence of lake-level fluctuations from a Finnish lake and the effect of aquatic-moss layers on microfossil assemblages. *Journal of Paleolimnology*, **22:** 277-290.

Sarvala, J. & Halsinaho, S. (1990). Crustacean zooplankton of Finnish forest lakes in relation to acidity and other environmental factors. In: Kauppi, P.; Anttila, P. & Kenttämies, K. (Eds.), *Acidification in Finland*, Springer-Verlag, 1009-1027.

Scheffer, M. (1998). *Ecology of Shallow Lakes*. Population and Community Biology Series 22, Chapman and Hall, pp. 1-346.

Schindler, D.W. (1997). Widespread effects of climatic warming on freshwater ecosystems in North America. *Hydrological Processes*, **11:** 1043-1067.

Schindler, D.W. (1998). A dim future for Boreal Waters and Landscapes. Cumulative effects of climate warming, stratospheric ozone depletion, acid precipitation and other human activities. *Bioscience*, **48:** 157-164.

Schindler, D.W., Beaty, K.G., Fee, E.J., Cruikshank, D.R., DeBruyn, E.R., Findlay, D.L., Linsey, G.A., Shearer, J.A., Stainton, M.P. & Turner, M.A. (1990). Effects of climatic warming on lakes of the Central Boreal Forest. *Science*, **250:** 967-970.

Schmidt, R., Müller, J., Drescher-Schneider, R., Krisai, R., Szeroczynska, K. & Baric, A. (2000). Changes in lake level and trophy at Lake Vrana, a large karstic lake on the Island of Cres (Croatia), with respect to palaeoclimate and anthropogenic impacts during the last approx. 16000 years. *Journal of Limnology*, **59:** 113-130.

Schneider, S.H. (1994). Detecting climatic change signals: Are there any 'fingerprints?'. *Science*, **263:** 341-347.

Schwalb, A. & Dean, W.E. (2002). Reconstruction of hydrological changes and response to effective moisture variations from North-Central USA lake sediments. *Quaternary Science Reviews,* **21:** 1541-1554.

Scottish Weather (http://www.metoffice.com/weather/europe/uk/nwscotland.html).

Scourfield, D.J. & Harding, J.P. (1958). *A key to the British Freshwater Cladocera with notes on their ecology.* Freshwater Biological Association, Scientific Publication.

Scourfiled, D.J. & Harding, J. P. (1958). *A key to the British Freshwater Cladocera with notes on their ecology.* Freshwater Biological Association, Scientific Publication.

Shannon-Wiener Diversity Index-http://math.hws.edu/javamath/ryan/DiversityTest.

Sherrod, B.L. (1999). Gradient analysis of diatom assemblages in a Puget Sound salt marsh: can such assemblages be used for quantitative paleoecological reconstructions? *Palaeogeography, Palaeoclimatology, Palaeoecology*, **149:** 213-226.

Shindell, D.T, Rind, D. & Balachandran, N. (1999). Interannual variability of the Antarctic ozone hole in a GCM. Part II: A comparison of unforced and QBO-induced variability. *Journal of The Atmospheric Sciences*, **56**: 1873-1884.

Shuter, B.J. & Ing, K.K. (1996). Factors affecting the production of zooplankton in lakes. *Canadian Journal of Fisheries and Aquatic Sciencies*, **54:** 359-377.

Sinha, A. (1995). Relative influence of lapse rate and water vapor on the greenhouse effect. *Journal of Geophysical Research*, **100:** 5095-5103.

Sissons, J.B. (1976). *The geomorphology of the British Isles.* London : Methuen & Co., 150p.

Smayda, T. J. (1969). Some measurements of the sinking rate of fecal pellets. *Limnology and Oceanography*, **14:** 621-625.

Smiley, E.A. & Tessier, A.J. (1998). Environmental gradients and horizontal distribution of microcrustaceans in lakes. *Freshwater Biology*, **39:** 397-409.

Smirnov, N.N. (1998). A revision of the genus *Camptocercus* (Anomopoda, Chydoridae, Aloninae). *Hydrobiologia*, **386:** 63-83.

Smol, J.P. & Cumming, B.F. (2000). Tracking long-term changes in climate using algal indicators in lake sediments. *Journal of Phycology*, **36:** 986-1011.

Smol, J.P., Walker, I.R. & Leavitt, P.R. (1991). Paleolimnology and hindcasting climatic trends. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **24:** 1240-1246.

Smol, J.P. & Boucherle, M.M. (1985). Post-glacial changes in algal and cladoceran assemblages in Little Round Lake, Ontario. *Archiv für Hydrobiologie*, **103:** 25-49.

Smyly, W. J. P. (1958). The Cladocera and copepoda (Crustacea) of the tarns of the English Lake District. *Journal of Animal Ecology*, **27:** 87-103.

Soden, B.J., Wetherald, R.T., Stenchikov, G.L. & Robock, A. (2002). Global cooling after the eruption of Mount Pinatubo: A test of climate feedback by water vapor. *Science*, **296:** 727-730.

Sommaruga-Wögrath, S., Koing, K.A., Schmidt, R. & Psenner, R. (1997). Temperature effects on the acidity of remote alpine lakes. *Nature*, **387:** 64-67.

Sommaruga, R. & Psenner, R. (1997). Ultraviolet radiation in high mountain lake of the Austrian Alps: air and underwater measurements. *Photochemistry and Photobiology*, **65:** 957-963.

Sorvari, S., Korhola, A. & Thompson, R. (2002). Lake diatom response to recent Arctic warming in Finnish Lapland. *Global Change Biology*, **8:** 171-181.

Sorvari, S., Rautio, M. & Korhola, A. (2000). Seasonal dynamics of subarctic Lake Saanjärvi in Finnish Lapland. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **27:** 507-512.

Soulsby, C., Gibbins, C., Wade, A.J., Smart, R. & Helliwell, R. (2002). Water quality in Scottish uplands: a hydrological perspective on catchment hydrochemistry. *The Science of the Total Environment*, **294:** 73-94.

Stefanova, I., Ognjanova-Rumenova, N., Hofmann, W. & Ammann, B. (2003). Late Glacial and Holocene environmental history of the Pirin Mountains (SW Bulgaria): a paleolimnological study of Lake Daloto (2310 m). *Journal of Paleolimnology*, **30:** 95-111.

Stemberger, R.S., Herlihy, A.T., Kgler, D.L. & Paulsen, S.G. (1996). Climatic forcing on zooplankton richness in lakes of the northeastern United States. *Limnology and Oceanography*, **41:** 1093-1101.

Stoermer, E.F. & Ladewski, T.B. (1976). *Apperant optimal temperatures for the occurrence of some common phytoplankton species in southern Lake Michigan*. An Arbor, The University of Michigan: 49 pp.

Straškrabová,V., Callieri, C., Carrillo, P., Cruz-Pizarro, L., Fott, J., Hartman, P., Macek, M., Medina-Sánchez, J.M., Nedoma, J. & Šimek, K. (1999). Investigation on pelagic food webs in mountain lakes – aims and methods. *Journal of Limnology*, **58:** 77-87.

Synerholm, C.C. (1979). The chydorid cladocera from surface lake sediments in Minnesota and North Dakota. *Archiv für Hydrobiologie,* **86:** 137-151.

Takashi, K., Billings, J.D.& Morgan, J.K. (1990). Oceanic province: Assessment from the time series diatom fluxes in the northeastern Pacific. *Limnology & Oceanography,* **35:** 165.

Tartari, G.A., Marcheto, A. & Moselleo, R. (1995). Precision and linearity of inorganic analyses by ion chromatography. *Journal of Chromatography*, **706**: 21-30.

Tartari, G.A., Tartari, G. & Mosello, R. (1998). Water chemistry of high altitude lakes in the Khumbu and Imja Kola valleys (Nepalese Himalayas). *Memorie dell'Istituto Italiano di Idrobiologia*, **59:** 51-76.

ter Braak, C.J.F. (1987). Unimodal models to relate species to environment. University of Wageningen, 152pp.

ter Braak, C.J.F. (1990). Interpreting canonical correlation analysis through biplots of structural correlations and weights. *Psychometrika*, **55**: 519-531.

ter Braak, C.J.F. (1994). Canonical Community Ordination, Part I: Basic theory and linear methods. *Ecoscience*, **1**: 127-140

ter Braak, C.J.F. (1995). *Ordination*, Cambridge University Press. 169 pp.

ter Braak, C. J. F. & Juggins, S. (1993). Weighted averaging partial least squares regression (WA-PLS) an improved method for reconstructing environmental variables from species assemblages. *Hydrobiologia*, **269:** 485-502.

ter Braak, C.J.F., Juggins, S., Birks, H.J.B. & van der Voet, H. (1993). Weighted averaging partial least squares regression (WA-PLS). In: *Definition and comparison with other methods for species-environment calibration. Multivariate Environmental Statistics*, Patil, G. P. & Rao, C. R (Eds.), pp. 529-560, Elsevier Science Publications.

ter Braak, C.J.F. & Prentice, I.C. (1988). A theory of gradient analysis. *Advances in Ecological Research*, **18:** 271-317.

ter Braak, C. J. F. & Smilauer, P. (2002). *CANOCO reference manual and CanoDraw for Window's User's guide: Software for Canonical Community Ordination (Version 4.5).* Microcomputer Power (Ithaca, NY, USA), 500pp.

ter Braak, C.J.F. & Van Dam, H. (1989). Inferring pH from diatoms: a comparison from old and new calibration methods. *Hydrobiologia*, **178:** 209-223.

ter Braak, C.J.F. & Verdonschot, P.F.M. (1995). Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences*, **57**: 255-289.

Tremel, B., Frey (Libby), S.E., Yan, N.D. & Somers, K.M. (2000). Habitat specificity of littoral Chydoridae (Crustacea, Branchiopoda, Anomopoda) in Plastic Lake, Ontario, Canada. *Hydrobiologia*, **432:** 195-205.

University of East Anglia, Climate Research Institute (www.uea.ac.uk/cri).

Van Tongeren, O.F.R. (1995). Cluster Analysis. In: Data Analysis Community and Landscape Ecology (Eds.)

Ventura, M., Camarero, L., Buchaca, T., Bartumeus, F., Livingstone, D.M. & Catalan, J. (2000). The main features of seasonal variability in the external forcing and dynamics of a deep mountain lake (Redó, Pyrenees). *Journal of Limnology*, **59:** 97-108.

Walker, I.R. (2001). Midges: Chironomidae and related Diptera. In: Smol, J. P., Birks, H. J. B., and Last, W. M., *Tracking Environmental Change Using Lake Sediments, Volume 4: Zoological Indicators*, Kluwer Academic Publishers, Dordrecht, The Netherlands, 240pp.

Walker, I.R., Smol, J.P., Engstrom, D.R. & Birks, H.J.B. (1991). As assessment of chironomidae as quantitative indicators of past climatic change. *Canadian Journal of Fisheries and Aquatic Sciences*, **48:** 975-987.

Webster, K.E., Kratz, T.K., Bowser, C.J. & Magnuson, J.J. (1996). The influence of landscape position on lake chemical responses to drought in northern Wisconsin. *Limnology and Oceanography*, **41:** 977-984.

Werritty, A. & Acreman, M. C. (1985). The flood hazard in Scotland. In: *Climatic Hazards in Scotland*, Harrison, S.J. (Ed.), Norwich: Geobooks, pp. 25-40.

Wetzel, R.G. & Likens, G.E. (2000). *Limnological Analyses*. Springer.

White, M.D. (1998). Horizontal distribution of pelagic zooplankton in relation to predation gradients. *Ecography*, **21:** 44-62.

Whiteside, M.C. (1970). Danish Chydorid Cladocera: Modern ecology and core studies. *Ecological Monographs*, **40:** 79-118.

Whiteside, M.C. (1974). Chydorid (Cladocera) ecology: seasonal patterns and abundance of populations in Elk Lake, Minnesota. *Ecology*, **55:** 538-550.

Whiteside, M.C. & Harmsworth, R.V. (1967). Species diversity in Chydorid (Cladocera) communities. *Ecology*, **48:** 664-667.

Whiteside, M.C. & Swindoll, M.R. (1988). Guidelines and limitations to cladoceran paleoecological interpretations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **62:** 405-412.

Whiteside, M.C., Williams, J.B. & White, C.P. (1978). Seasonal abundance and pattern of chydorid, Cladocera in mud and vegetative habitats. *Ecology*, **59:** 1177-1188.

Williams, J.B. (1982). Temporal and spatial patterns of abundance of the Chydoridae (Cladocera) in Lake Itasca, Minnesota. *Ecology*, **63:** 345-353.

Wolfe, B.B., Aravena, R., Abbott, M.B., Seltzer, G.O. & Gibson, J.J. (2001). Reconstruction of paleohydrology and paleohumidity from oxygen isotope records in the Bolivian Andes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **176:** 177-192.

Wood, R.A., Keen, A.B., Mitchell, J.F.B. & Gregory, M. (1999). Changing spatial structure of the thermohaline circulation in response to atmospheric CO_2 forcing in climate model. *Nature*, **399:** 572-575.

Wooldridge, J. M. (2000). *Introductory Econometrics: A Modern Approach*, South Western, USA.

Wright, R. F. & Cosby, B. J. (2003). Future recovery of acidified lakes in southern Norway predicted by the MAGIC model. Hydrology and Earth System Sciences **7:** 467-483.

Yan, N.D., Keller, W., Somers, K.M., Pawson, T.W. & Girard, R.E. (1996). Recovery of crustacean zooplankton communities from acid and metal contamination: comparing manipulated and reference lakes. *Canadian Journal of Fisheries and Aquatic Sciences,* **53:** 1301-1327.

Yurista, P.M. (1999). Temperature-dependent energy budget of an Arctic Cladoceran, *Daphnia middendorffiana. Freshwater Biology*, **42:** 21-34.

Zeeb, B. & Smol, J.P. (2001). Chrysophytes. In: Smol, J. P., Birks, H. J. B. & Last, W. M., *Tracking Environmental Change Using Lake Sediments, Volume 3: Terrestrial, Algal, and Siliceous Indicators*, Kluwer Academic Publishers, Dordrecht, The Netherlands, 400pp.

Zillen, L.M., Wastegard, S. & Snowball, I.F. (2002). Calendar year ages of three mid-Holocene tephra layers identified in varved lake sediments in west central Sweden. *Quaternary Science Reviews*, **21:** 1583-1591.

Zolitschka, B. (2003). Dating based on freshwater-and marine-laminated sediments. In: *Global change in the Holocene*, Mackay, A. Battarbee, R., Birks, J. & Oldfield, F. (Eds.), Arnold, London, 92-106pp.

Zolitschka, B. & Negendank, J.F.W. (1999). High-resolution records from European Lakes. *Quaternary Science Reviews*, **18:** 885-888.

APPENDICES

Appendix 1

Appendix 1.1: Systematics of Cladocera (http://www.cladocera.uoguelph.ca; http://www.funet.fi/pub/sci/bio/life/crustacea/cladocera/index.html), and the attribution and the authorities of cladoceran taxa recorded in the study sites in Scotland and Norway. NA = attribution and authorities are not available; TS = Taxa recorded in the training set sites; TP = Taxa recorded in the taphonomic samples; CO = Taxa recorded in the core samples; CS = Taxa recorded in the contemporary samples. Blank space shows no species was recorded under this genus in the study sites. Appendix 3.1 further gives a detailed description of each taxon recorded in the study sites.

Class: **Branchiopoda Latreille, 1817**

Subclass: **Diplostraca Gerstaecker, 1866**

Order: **Cladocera Latreille, 1829**

I. Suborder: **Anomopoda**

(i) Family: **Daphnidae Straus 1820**

Genera worldwide	Taxa recorded in the study sites
Ceriodaphnia Dana 1853	*Ceriodaphnia dubia* Richards, 1894 (CS)
Daphnia Müller 1785	*Daphnia culcullata* Sars, 1862 (CS)
	Daphnia magna Straus, 1820 (CS)
	Daphnia galeata Sars, 1865 (CS)
	Daphnia hyalina Leydig, 1860 (CS)
	Daphnia longispina Müler, 1776 (CS)
	Daphnia ambigua NA (CS)
Daphniopsis Sars 1903	-
Megafenestra Dumont & Pensaert 1983	-
Simocephalus Schödler 1858	-
Scapholeberis Schödler 1858	-

(ii) Family: **Moinidae Goulden 1968**

Genera worldwide	Taxa recorded in the study sites
Moina Baird 1850	-
Moinodaphnia Herrick 1887	-

(iii) Family: Bosminidae Baird 1846

Genera worldwide	Taxa recorded in the study sites
Bosmina Baird 1846	*Bosmina coregoni* Baird, 1857 (TS, TP, CO, CS)
	Bosmina longispina Leydig, 1860 (TS, TP, CO,CS)
	Bosmina longirostris O. F. Müller, 1785 (TP, CS)
Bosminopsis Richard 1895	-

(iv) Family: Macrothricidae Norman & Brady 1867

Genera worldwide	Taxa recorded in the study sites
Acantholeberis	-
Bunops Binge 1893	-
Drepanothrix Sars 1862	-
Echinisca Liévin 1848	-
Grimaldina Richard 1892	-
Guernella Richard 1892	-
Iheringula Sars 1900	-
Ilyocryptus Sars 1862	-
Lathonura Lilljeborg 1853	*Lathonura rectirostris* Müller, 1776 (CS)
Macrothrix Baird 1843	*Macrothrix* sp. NA (CS)
Neothrix Gurney 1927	-
Ophryoxus Sars 1862	-
Parophryoxus Doolittle 1909	-
Pseudomoina Sars 1912	-
Streblocerus Sars 1862	*Streblocerus serricaudatus* Fischer, 1849 (CS)
Wlassisca Daday 1904	-

(v) Family: Chydoridae Stebbing 1902

Genera worldwide	Taxa recorded in the study sites
Acroperus Baird 1843	*Acroperus harpae* Baird, 1835 (TS, TP, CO, CS)
	Acroperus elongatus Sars, 1862 (TS, TP, CO, CS)
Alona Baird 1843	*Alona affinis* Leydig, 1886 (TS, TP, CO, CS)
	Alona quadrangularis O. F. Müller, 1785 (TS, TP, CO, CO, CS)
	Alona rustica Scot, 1895 (TS, TP, CO, CS)
	Alona guttata Sars, 1862 (TS, TP, CO, CS)
	Alona guttata tuberculata NA (TP)

	Alona intermedia Sars, 1862 (TS, TP, CO, CS)
	Alona rectangula Sars, 1861 (TS, TP, CO, CS)
	Alona costata Sars, 1862 (TS, TP)
Alonella Sars 1862	*Alonella excisa* Fischer, 1854 (TS, TP, CO, CS)
	Alonella exigua Lilijeborg, 1853 (TS, TP, CS)
	Alonella nana Baird, 1850 (TS, TP, CO, CS)
Alonopsis Sars 1862	-
Anchistropus Sars 1862	*Anchistropus emarginatus* Sars 1862 (TS, CO)
Archepleuroxus Smirnov & Timms 1983	-
Australochydorus Smirnov & Timms 1983	-
Biapertura Smirnov 1971	-
Bryospilus	-
Camptocercus Baird 1843	*Camptocercus rectirostris* Schödler, 1862 (TS, TP, CO, CS)
Celsinotum	-
Chydorus Leach 1816	*Chydorus sphaericus* O. F. Müller, 1785 (TS, TP, CO, CS)
	Chydorus piger Sars, 1862 (TS, TP, CO, CS)
	Chydorus globosus NA (TP)
Dadaya Sars 1901	-
Disparalona Sars 1862	*Disparolana* (*Alonella*) *rostrata* Koch, 1841 (TS, CO)
Dunhevedia King 1853	-
Ephemeroporus Frey 1982	-
Euryalona Sars 1901	-
Eurycercus Baird 1843	*Eurycercus lamellatus* O. F. Müller, 1785 (TS, TP, CO, CS)
Graptolebris Sars 1862	*Graptoleberis testudinaria* Fischer, 1848 (TS, TP, CO, CS)
Kurzia Dybowski & Grochowski 1894	*Kurzia latissima* Kurz, 1875 (TP, CO, CS)
Leberis	-
Leydigia Kurz 1875	-
Monope Smirnov & Timms 1983	-
Monospilus Sars 1862	*Monospilus dispar* Sars, 1862 (TS, TP, CO, CS)

Notalona	-
Oxyurella Dybowski & Grochowski 1894	*Oxyurella tenuicaudis* NA (TS, CO, CS)
Paralona Šráhek-Hušek 1962	-
Phrixura P.E. Müller 1867	-
Planicirclus	-
Pleuroxus Baird 1843	*Pleuroxus aduncus* Jurine, 1820 (TS, CO, TP) *Pleuroxus trigonellus* Müller, 1785 (TS) *Pleuroxus truncatus* Müller, 1785 (CS)
Plurispina	-
Pseudochydorus Fryer 1968	-
Rak Smirnov & Timms 1983	-
Rhynchotalona Norman 1903	*Rhynchotalona falcata* Sars, 1861 (TS, TP, CO, CS)
Saycia Sars 1904	-
Spinalona	-
Tretocephala Frey 1965	-

II. Suborder: Ctenopoda

(i) Family: Sididae Baird 1850

Genera worldwide	Taxa recorded in the study sites
Diaphanosoma Fischer 1850	*Diaphanosoma brachyurum* Liévin, 1848 (CS)
Latona Straus 1820	-
Latonopsis Sars 1888	-
Penilia Dana 1849	-
Pseudosida Herrick 1884	-
Sarsilatona Korovchinsky 1985	-
Sida Straus 1820	*Sida crystallina* Müller, 1776 (TS, TP, CO)

(ii) Family: Holopedidae Sars 1865

Genera worldwide	Taxa recorded in the study sites
Holopedium Zaddach 1855	-

III. Suborder: Onychopoda

(i) Family: Polyphemidae Baird 1845

Genera worldwide	Taxa recorded in the study sites
Polyphemus Linnaeus 1758	*Polyphemus pediculus* Linnaues, 1761 (TP, CS)

(ii) Family: Cercopagidae Mordukhai-Boltovskoi 1966

Genera worldwide	Taxa recorded in the study sites
Bythotrephes Leydig 1860	*Bythotrephes longimanus* Leydig, 1860 (CS)
Cercopagis Sars 1897	-

(iii) Family: Podonidae Mordukhai-Boltovskoi 1968

Genera worldwide	Taxa recorded in the study sites
Caspievadne Behning 1941	-
Cornigerius Mordukhai-Boltovskoi 1967	-
Evadne Lovén 1836	-
Pleopsis Dana 1852	-
Podon Lilljeborg 1853	-
Podonevadne Gibitz 1922	-

IV. Suborder: Haplopoda

(i) Family: Leptodoridae Lilljeborg 1861

Genera worldwide	Taxa recorded in the study sites
Leptodora Lilljeborg 1861	*Leptodora kindtii* Focke, 1844 (CS)

Appendix 2

Appendix 2.1: Total number of lakes available for calibration set. Their number, official code, site name, and modified code for this study are presented.

Number	Official Code	Site Name	Modified Code
20001834	SC0366	LOCHAN NAN CAT	L001CAT
20001835	SC0399	LOCHNAGAR	L002GAR
20001836	SC0382	LOCHAN UAINE	L003INE
20001837	SC0386	LOCH NAN EUN	L004EUN
20001838	SC0271	LOCHAN COIRE NAN LOCHAIN	L005AIN
20001839	SC0379	UN NAMED	L006MED
20001867	SC0172	UN-NAMED	L007MED
20001868	SC0330	LOCH COIRE CHOILLE RAIS	L008AIS
20001883	SC0010	LOCHAN BAC AN LOCHAIN	L009AIN
20001884	SC0335	UN-NAMED	L010MED
20001885	SC0191	LOCH CARN A' CHAOCHAIN	L011AIN
20001931	SC0101	LOCH A CHLEIRICH	L012ICH
20001932	SC0029	UN NAMED	L013MED
20001949	SC0002	LOCH COIR A GHRUNNDA	L014NDA
20001950	SC0124	LOCH AN FHRAOICH CHOIRE	L015IRE
20001951	SC0084	UN NAMED	L016MED
20001996	SC0076	FHEARCHAIR	L017AIR
20001997	SC0067	CAIME	L018IME
20002005	SC0165	LOCH A MHADAIDH	L019IDH
20002006	SC0068	LOCH BHUIC MOIR	L020OIR
20002007	SC0180	LOCH TOLL LOCHAN	L021HAN
20002008	SC0204	LOCHAN A CHNAPAICH	L022ICH
20002030	SC0211	LOCH BEALACH NA H-UIDHE	L023DHE
20002031	SC0197	LOCH A CHOIRE DHAIRG	L024IRG
20002070	SC0349	UN-NAMED	L025MED
20002071	SC0190	LOCH GORM	L026ORM
20002072	SC0153	LOCH BEAG	L027EAG
20002073	SC0189	LOCH DU FHUAR THIULL MHOIR	L028OIR
20002074	SC0108	UN-NAMED	L029MED
20002075	SC0140	GORM LOCHAN	L030HAN
96-1	na	Hestretjønn	L031ØNN
96-2	na	UNNAMED	L032MED
96-3	na	Skredvatn	L033ATN
96-4	na	MAURSET vt.	L034TVT
96-5	na	OSDALSÆTER vt.	L035RVT
96-6	na	PAULS vt.	L036SVT
96-7	na	BATA tj.	L037ATJ
96-8	na	BAKKEBERG tj.	L038GTJ
96-9	na	UNNAMED	L039MED
96-10	na	NØGLA vt.	L040AVT
96-11	na	TÅBAKK tj.	L041KTJ
96-12	na	Rindtjønn	L042ØNN
96-13	na	SLOM tj.	L043MTJ
96-14	na	FLOT vt.	L044TVT
96-15	na	STIGEDALS vt.	L045SVT
96-16	na	LANGE vt.	L046EVT
96-17	na	SLETTEBØ vt.	L047ØVT
96-18	na	UNNAMED	L048MED

96-19	na	SKIN vt.	L049NVT
96-20	na	KONSDALS vt.	L050SVT
96-21	na	UNNAMED	L051MED
96-22	na	KUPE vt.	L052EVT
96-23	na	LITLE vt.	L053EVT
96-24	na	LITLE 147	L054147
96-25	na	STØLS vt.	L055SVT
96-26	na	FULLSKJEGG vt.	L056GVT
96-27	na	SLÅTTESTØLS vt.	L057SVT
96-28	na	DALE vt.	L058EVT
96-29	na	LITLE vt.	L059EVT
96-30	na	SKOGSTAD tj.	L060DTJ
96-31	na	DALE vt.	L061EVT
96-32	na	STØL vt.	L062LVT
96-33	na	FAGREDALS vt.	L063SVT
96-34	na	VÅGS vt.	L064SVT
96-35	na	STANGA vt.	L065AVT
96-36	na	UNNAMED	L066MED
96-37	na	Elversvatn	L067ATN
96-38	na	Lontjønn	L068ØNN
96-39	na	Røldalstjønn	L069ØNN
96-40	na	Isbenttjønn	L070ØNN
96-41	na	Lomtjønn	L071ØNN
96-42	na	UNNAMED	L072MED
96-43	na	UNNAMED	L073MED
96-44	na	Kyrkjestøltjønn	L074ØNN
96-45	na	UNNAMED	L075MED
96-46	na	UNNAMED	L076MED
96-47	na	UNNAMED	L077MED
96-48	na	Storemyrstjønn	L078ØNN
96-49	na	UNNAMED	L079MED
96-50	na	Sjølskottjønn	L080ØNN
96-51	na	UNNAMED	L081MED
96-52	na	UNNAMED	L082MED
96-53	na	UNNAMED	L083MED
96-54	na	Hermodholtjørni	L084RNI
96-55	na	Haraldseidvatn	L085ATN
96-56	na	Rådalstjønn	L086ØNN
96-57	na	Eikelandstjønn	L087ØNN
96-58	na	Lintjønn	L088ØNN
96-59	na	UNNAMED	L089MED
96-60	na	Røyrtjønn	L090ØNN
96-61	na	Vatnedalsvatn	L091ATN
96-62	na	Langareidtjønn	L092ØNN
96-63	na	Grastjørni	L093RNI
96-64	na	Rausvatn	L094ATN
96-65	na	Midtre Søyletjønn	L095ØNN
96-66	na	Sæsvasstjønn	L096ØNN
96-67	na	Flotatjønn	L097ØNN
96-68	na	Stokketjønn	L098ØNN
96-69	na	Litle Kjelavatn	L099ATN
96-70	na	Godtholstjønn	L100ØNN
96-71	na	Holebudalen	L101LEN
96-72	na	Isbenttjønn	L102ØNN
96-73	na	Lisletjønn	L103ØNN
96-74	na	Øytjønn	L104ØNN
96-75	na	UNNAMED	L105MED

96-76	na	UNNAMED	L106MED
96-77	na	UNNAMED	L107MED
96-78	na	Reinstjønn	L108ØNN
97-1	na	UNNAMED	L109MED
97-2	na	Ormetjønn	L110ØNN
97-3	na	Øygardstjønn	L11ØNN
97-4	na	Gravdalstjønn	L112ØNN
97-5	na	Trolletjønn	L113ØNN
97-6	na	Gregarstjønn	L114ØNN
97-7	na	Bjørntjønn	L115ØNN
97-8	na	Vassendkilen	L116LEN
97-9	na	UN NAMED	L117MED
97-10	na	Grostjønn	L118ØNN
97-11	na	UN NAMED	L119MED
97-12	na	Espeland	L120AND
97-13	na	Tjovetjønn	L121ØNN
97-14	na	UN NAMED	L122MED
97-15	na	Histøl	L123TØL
97-16	na	Tovetjønna	L124NNA
97-17	na	Jinninstjønn	L125ØNN
97-18	na	UN NAMED	L126MED
97-19	na	Skarpengland	L127AND
97-20	na	Fjellestad	L128TAD
97-21	na	Dalane	L129ANE
97-22	na	UN NAMED	L130MED
97-23	na	Rypestøl	L131TØL
97-24	na	UN NAMED	L132MED
97-25	na	Ormestad	L133TAD
97-26	na	Bærvannet	L134NET
97-27	na	UN NAMED	L135MED
97-28	na	Åmdalstjønn	L136ØNN
97-29	na	Skogenvatn	L137ØNN
97-30	na	Årstøl	L138TØL
97-31	na	Heimretjønn	L139ØNN
97-32	na	Kjostveittjønn	L140ØNN
97-33	na	Stemtjønn	L141ØNN
97-34	na	Hommerkleivtjønn	L142ØNN
97-35	na	Kråkenes	L143NES
B98-1	na	UN NAMED	L144MED
B98-2	na	Hornsvatn	L145ATN
B98-3	na	UN NAMED	L146MED
B98-4	na	Finndalsvatn	L147ATN
B98-5	na	Vargebovatn	L148ATN
B98-6	na	Leirvatn	L149ATN
B98-7	na	UN NAMED	L150MED
B98-8	na	Gryta	L151YTA
B98-9	na	Mefjellsvatn	L152ATM
B98-10	na	Galgebergstjønn	L153ØNN
B98-11	na	Nedre Bakkebergtjønn	L154ØNN
B98-12	na	Øvre Bakkebergtjønn	L155ØNN
B98-13	na	Sjutjørnin	L156NIN
B98-14	na	Vesleguttj	L157TTJ
B98-15	na	Råtasjøen	L158ØEN
B98-16	na	Langsjøen	L159ØEN
B98-17	na	Grønnbakktjønn	L160ØNN
B98-18	na	Hornsjøen	L161ØNN
B98-19	na	Bukkehammarstjønn	L162ØNN

B98-20	na	Rasletjernet	L163NET
B98-21	na	Fisketjerni	L164RNI
B98-22	na	Fisketjerni	L165RNI
B98-23	na	Stavtjern	L166ERN
B98-24	na	Låketjønn	L167ØNN
B98-25	na	Gammelheimen	L168MEN
B98-26	na	Bjørnfjellvatnet	L169NET
B98-27	na	Vuoskojaurasj	L170ASJ
N98-1	na	Nigardsbrevatnet	L171NET
99-1	na	Gammvatn	L172ATN
99-2	na	Eidsvatn	L173ATN
99-3	na	Peder Sørensensvatn	L174ATN
99-4	na	Bukkvatn	L175ATN
99-5	na	Dåfjordvatn	L176ATN
99-6	na	UN NAMED	L177MED
99-7	na	Jansvatn	L178ATN
99-8	na	UN NAMED	L179MED
99-9	na	Rumpetrollvatn	L180ATN
99-10	na	UN NAMED	L181MED
99-11	na	Skarsvågsvatn	L182ATN
99-12	na	UN NAMED	L183MED
99-13	na	UN NAMED	L184MED
99-14	na	UN NAMED	L185MED
99-15	na	UN NAMED	L186MED
99-16	na	Råggejav`ri	L187VRI
99-17	na	UN NAMED	L188MED
99-18	na	Abdersbyvatn	L189ATN
99-19	na	UN NAMED	L190MED
99-20	na	Poas`tagurrajav`ri	L191VRI
99-21	na	UN NAMED	L192MED
99-22	na	UN NAMED	L193MED
99-23	na	UN NAMED	L194MED
99-24	na	Reinkalvvatn	L195ATN
99-25	na	UN NAMED	L196MED
99-26	na	Morttjenn	L197ENN
99-27	na	Abbortjørn	L198ØRN
99-28	na	UN NAMED	L199MED
99-29	na	Guletjenn	L200ENN
99-30	na	Lomtjenn	L201ENN
99-31	na	Kjennertjenn	L202ENN
99-32	na	Lågstjøen	L203ØEN
99-33	na	Skiersjøen	L204ØEN
99-34	na	Vardrunstjern	L205ERN
99-35	na	Raudtjern	L206ERN
99-36	na	Jønsnudtjern	L207ERN
99-37	na	Haugtjern	L208ERN
99-38	na	Kinnshaugen	L209GEN
99-40	na	Auretjern	L210ERN
99-41	na	Måsåtjornet (S)	L211NET
99-42	na	Måsåtjornet (N)	L212NET
99-43	na	Langrumpa	L213MPA
99-44	na	Gututjørn	L214ØRN
99-45	na	Ovre Lundtjern	L215ERN
99-46	na	Veslafstjørna	L216RNA
99-47	na	Afstjørna	L217RNA
99-50	na	Midttjørna	L218RNA
20010668	na	Loch Coire Lair (LCL)	L219AIR

20010669	na	Loch Sail An Ruathair (LSR)	L220IDH
20010670	na	Lochan Bealach Cornaidh (LBC)	L221IDH
20010671	na	Loch Langwell (LL)	L222ELL
20010673	na	Loch Coire Finonaraich (LCFR)	L223ICH

na = Not Available

Appendix 2.2: Measurement of environmental variables in selected training set sits (Source: Botanical Institute, University of Bergen, Norway and EMERGE Scotland).

Code Number	Cond (μScm^{-1})	Na (μeql^{-1})	NH_4 (μeql^{-1})	K (μeql^{-1})	Mg (μeql^{-1})	Ca (μeql^{-1})	Cl (μeql^{-1})	NO_3 (μeql^{-1})	SO_4 (μeql^{-1})	Al-NL (μgl^{-1})	Al-L (μgl^{-1})	Abs-250	TOC mgl^{-1})	SAMDEPTH (m)	JulT (^{0}C)	JanT (^{0}C)	SurT (^{0}C)	PPT (mm)	LOI (%)
L007MED	22.00	101.00	0.00	4.00	30.00	75.00	115.00	0.95	23.00	25.00	1.00	0.06	2.60	8.20	10.91	-0.39	11.20	2699.00	56.17
L008AIS	19.00	92.00	0.00	7.00	31.00	63.00	89.00	0.73	31.00	0.00	0.00	0.02	1.30	26.00	10.45	-0.74	12.75	2095.00	65.20
L009AIN	29.00	172.00	0.00	5.00	48.00	46.00	167.00	0.30	49.00	7.00	6.00	0.08	2.40	4.10	10.17	1.08	11.60	2505.00	57.06
L011AIN	28.00	152.00	0.00	4.00	45.00	67.00	168.00	0.00	22.00	11.00	3.00	0.25	6.70	4.00	9.48	-0.64	12.40	1792.00	20.98
L013MED	19.00	120.00	0.00	3.00	33.00	33.00	109.00	0.00	18.00	34.00	4.00	0.16	5.20	0.70	11.02	1.74	13.50	2161.00	49.56
L015IRE	22.00	118.00	0.00	6.00	38.00	51.00	112.00	0.00	23.00	9.00	0.00	0.07	2.40	5.50	11.13	2.19	13.60	1972.00	50.29
L017AIR	24.00	147.00	0.00	5.00	47.00	34.00	145.00	1.20	30.00	3.00	0.00	0.05	1.50	24.00	11.23	-0.52	10.10	2088.00	52.93
L020OIR	37.00	213.00	0.00	6.00	54.00	78.00	225.00	0.00	27.00	26.00	0.00	0.22	5.60	7.30	10.16	1.44	12.20	2000.00	49.45
L021HAN	32.00	195.00	0.00	8.00	56.00	54.00	199.00	0.73	25.00	41.00	0.00	0.30	6.70	13.00	11.29	-0.48	12.30	1782.00	75.41
L022ICH	19.00	110.00	0.00	4.00	29.00	51.00	94.00	1.70	26.00	7.00	0.00	0.07	2.40	8.50	10.62	0.30	10.80	1513.00	52.42
L023DHE	37.00	222.00	0.00	8.00	71.00	37.00	233.00	3.80	36.00	24.00	1.00	0.16	3.50	3.50	9.55	-0.60	11.30	1561.00	34.99
L026ORM	34.00	205.00	0.00	7.00	54.00	58.00	233.00	2.70	33.00	11.00	2.00	0.08	2.00	3.80	10.74	0.39	13.10	1830.00	32.70
L033ATN	12.00	31.00	0.00	5.00	14.00	74.00	18.00	3.60	42.00	6.00	3.00	0.05	1.60	7.20	13.40	-2.20	9.50	2000.00	15.97
L035RVT	14.00	58.00	0.00	5.00	36.00	40.00	47.00	0.87	26.00	9.00	2.00	0.08	2.00	18.50	12.40	-2.40	11.00	2000.00	23.96
L036SVT	14.00	38.00	0.00	9.00	17.00	70.00	23.00	8.50	44.00	13.00	6.00	0.07	2.20	4.30	13.80	-1.90	10.00	2000.00	23.74
L041KTJ	13.00	21.00	2.00	9.00	18.00	83.00	15.00	0.42	45.00	12.00	1.00	0.13	4.30	3.70	10.90	-9.80	15.00	1022.00	35.37
L044TVT	9.00	16.00	0.00	7.00	16.00	58.00	12.00	0.70	24.00	3.00	0.00	0.01	0.80	2.60	8.10	-8.50	11.50	700.00	7.49
L046EVT	13.00	60.00	0.00	6.00	22.00	33.00	44.00	1.00	22.00	23.00	16.00	0.13	3.50	6.80	11.90	-2.00	13.00	2000.00	38.27
L048MED	34.00	195.00	0.00	9.00	55.00	52.00	162.00	1.90	45.00	82.00	4.00	0.31	7.20	12.00	13.20	0.60	14.50	2000.00	13.31
L050SVT	28.00	155.00	0.00	3.00	44.00	59.00	128.00	0.19	44.00	34.00	4.00	0.18	5.00	6.50	13.20	0.80	13.00	2000.00	31.24
L051MED	24.00	117.00	0.00	3.00	35.00	77.00	121.00	1.40	27.00	29.00	0.00	0.11	3.20	26.00	11.80	-1.00	13.00	1500.00	10.36
L054147	19.00	95.00	0.00	6.00	34.00	57.00	75.00	0.72	33.00	74.00	43.00	0.29	7.20	12.00	13.30	-0.40	16.00	2500.00	44.54
L055SVT	13.00	64.00	4.00	10.00	23.00	35.00	53.00	0.18	22.00	30.00	8.00	0.13	3.90	8.50	11.90	-2.20	15.50	1800.00	58.79
L056GVT	13.00	59.00	0.00	5.00	22.00	48.00	38.00	0.54	28.00	55.00	5.00	0.22	6.10	13.50	12.90	-1.00	16.00	2700.00	24.82
L057SVT	15.00	62.00	0.00	8.00	24.00	48.00	51.00	4.00	22.00	37.00	11.00	0.19	4.70	8.50	13.20	-0.80	15.50	2600.00	31.05
L058EVT	21.00	77.00	0.00	12.00	30.00	63.00	72.00	8.60	31.00	38.00	7.00	0.18	4.80	13.00	13.20	-1.50	16.50	2200.00	36.57
L060DTJ	13.00	72.00	0.00	7.00	24.00	36.00	39.00	2.00	36.00	14.00	12.00	0.10	2.90	8.70	13.40	-1.30	16.50	2200.00	26.99
L063SVT	14.00	57.00	0.00	5.00	21.00	53.00	41.00	0.83	22.00	51.00	14.00	0.25	5.60	21.00	11.60	-2.20	14.00	2200.00	46.21
L065AVT	17.00	77.00	0.00	8.00	30.00	38.00	39.00	0.21	22.00	62.00	6.00	0.39	8.40	11.50	12.50	-1.40	18.60	2200.00	37.50
L066MED	19.00	26.00	2.00	4.00	15.00	95.00	25.00	2.10	39.00	5.00	1.00	0.05	2.40	6.60	9.00	-6.50	12.00	1360.00	25.72
L069ØNN	23.00	67.00	0.00	11.00	31.00	79.00	41.00	0.26	35.00	63.00	10.00	0.41	9.70	6.10	10.90	-4.30	16.40	2000.00	64.71
L078ØNN	16.00	55.00	0.00	6.00	20.00	47.00	27.00	3.90	40.00	25.00	3.00	0.11	2.80	8.50	12.20	-2.50	13.10	2300.00	39.41
L081MED	16.00	47.00	3.00	6.00	19.00	65.00	32.00	9.60	28.00	24.00	12.00	0.12	4.00	18.50	11.20	-3.70	13.20	2500.00	50.61
L082MED	22.00	51.00	3.00	10.00	23.00	60.00	34.00	17.00	29.00	12.00	4.00	0.07	3.00	7.80	10.70	-4.10	14.30	2500.00	33.19
L084RNI	14.00	22.00	3.00	6.00	19.00	81.00	17.00	0.69	54.00	0.00	1.00	0.02	2.80	5.00	8.60	-7.40	12.60	900.00	33.25
L088ØNN	37.00	171.00	0.00	10.00	56.00	68.00	142.00	18.00	70.00	37.00	4.00	0.10	3.30	7.50	13.30	0.00	16.50	2000.00	29.34
L091ATN	38.00	187.00	0.00	12.00	41.00	97.00	169.00	28.00	53.00	7.00	1.00	0.07	2.70	15.00	13.00	-1.30	16.70	2300.00	28.31
L092ØNN	40.00	163.00	4.00	14.00	47.00	125.00	152.00	45.00	56.00	2.00	1.00	0.03	2.30	12.50	13.30	-1.10	17.30	2400.00	35.47
L093RNI	17.00	62.00	0.00	17.00	27.00	54.00	47.00	3.90	39.00	20.00	6.00	0.11	3.40	10.20	12.10	-3.30	17.70	2400.00	20.22
L095ØNN	18.00	63.00	0.00	13.00	23.00	61.00	37.00	0.76	35.00	70.00	4.00	0.24	6.70	13.00	11.90	-3.30	18.30	2300.00	43.63
L096ØNN	15.00	45.00	2.00	9.00	21.00	70.00	29.00	0.31	30.00	6.00	0.00	0.08	3.80	12.00	10.50	-7.70	16.00	990.00	34.40
L097ØNN	18.00	50.00	0.00	10.00	22.00	74.00	38.00	0.00	26.00	4.00	2.00	0.08	4.10	8.10	10.40	-7.60	16.00	990.00	31.12
L098ØNN	18.00	46.00	0.00	7.00	26.00	54.00	34.00	0.00	20.00	1.00	1.00	0.06	4.00	4.50	10.50	-7.70	17.00	990.00	44.69
L103ØNN	25.00	96.00	0.00	12.00	33.00	90.00	71.00	0.00	67.00	11.00	4.00	0.10	4.80	7.10	12.90	-5.00	18.00	900.00	44.72
L107MED	20.00	65.00	0.00	17.00	30.00	76.00	52.00	0.23	57.00	4.00	0.00	0.04	3.70	12.00	14.10	-4.10	17.00	1000.00	37.05
L109MED	16.00	56.00	2.00	3.00	23.00	96.00	28.00	0.00	21.00	34.00	11.00	0.32	7.50	4.10	12.70	-6.00	18.00	1000.00	40.98
L113ØNN	10.00	23.00	0.00	6.00	13.00	72.00	20.00	0.00	10.00	14.00	4.00	0.16	4.20	3.30	11.90	-6.70	19.00	842.00	56.92
L114ØNN	14.00	36.00	2.00	2.00	26.00	95.00	21.00	0.43	20.00	83.00	34.00	0.51	12.50	8.10	12.20	-6.40	20.00	910.00	47.98
L123TØL	40.00	154.00	0.00	17.00	53.00	136.00	166.00	0.00	79.00	26.00	1.00	0.14	3.90	9.20	14.30	-3.20	19.00	1310.00	48.55
L125ØNN	36.00	163.00	0.00	12.00	50.00	99.00	173.00	0.64	68.00	33.00	20.00	0.15	5.00	6.30	14.80	-2.70	20.50	1310.00	37.42
L131TØL	77.00	322.00	9.00	23.00	90.00	231.00	446.00	0.00	94.00	10.00	0.00	0.09	3.40	11.00	14.30	-1.90	20.50	1380.00	44.56
L134NET	30.00	126.00	4.00	12.00	43.00	109.00	124.00	0.00	70.00	23.00	3.00	0.13	5.10	17.00	14.10	-3.40	20.00	1310.00	67.62

L135MED	42.00	168.00	3.00	15.00	67.00	124.00	193.00	0.70	97.00	13.00	26.00	0.07	3.30	8.70	15.00	-2.40	20.00	1310.00	53.57
L138TØL	55.00	231.00	0.00	16.00	75.00	173.00	293.00	0.00	90.00	23.00	3.00	0.14	5.60	12.50	13.90	-2.20	20.50	1380.00	61.82
L144MED	9.00	12.00	1.00	0.00	21.00	68.00	7.00	0.35	35.00	0.00	29.00	0.01	0.90	3.00	7.60	-8.00	9.20	700.00	6.61
L145ATN	7.00	14.00	0.00	3.00	13.00	52.00	8.00	1.10	17.00	0.00	0.00	0.01	0.90	12.50	7.60	-8.00	8.90	700.00	19.52
L146MED	8.00	15.00	0.00	0.00	24.00	54.00	6.00	0.00	28.00	0.00	0.00	0.01	0.70	4.80	7.80	-7.80	8.00	700.00	5.94
L148ATN	8.00	12.00	0.00	2.00	24.00	57.00	6.00	3.80	22.00	0.00	0.00	0.02	0.80	10.50	5.90	-11.00	7.50	1039.00	8.25
L162ØNN	7.00	11.00	0.00	2.00	25.00	53.00	3.00	4.80	18.00	4.00	0.00	0.00	0.70	13.00	7.10	-12.70	6.00	540.00	7.83
L163NET	8.00	18.00	0.00	8.00	14.00	50.00	4.00	0.34	24.00	5.00	0.00	0.01	0.70	4.50	7.90	-12.20	8.50	540.00	13.72
L166ERN	10.00	24.00	1.00	3.00	23.00	67.00	7.00	0.00	22.00	9.00	0.00	0.07	2.30	6.50	10.20	-10.40	9.80	540.00	20.21
L169NET	13.00	45.00	0.00	7.00	17.00	71.00	27.00	0.00	40.00	24.00	4.00	0.09	2.80	12.90	10.50	-12.00	9.00	940.00	29.94
L171NET	11.00	31.00	0.00	7.00	11.00	77.00	17.00	1.70	40.00	8.00	1.00	0.02	1.10	12.20	13.60	-4.70	5.00	1380.00	0.78
L184MED	49.00	225.00	0.00	14.00	69.00	75.00	233.00	0.00	75.00	3.00	0.00	0.02	1.30	10.50	9.60	-4.00	11.00	796.00	19.36
L186MED	29.00	176.00	0.00	12.00	43.00	56.00	181.00	0.00	29.00	4.00	1.00	0.03	1.80	1.30	8.80	-4.70	7.50	796.00	20.82
L188MED	26.00	114.00	0.00	4.00	62.00	63.00	106.00	0.00	49.00	3.00	4.00	0.05	3.00	1.00	10.30	-13.70	9.00	455.00	27.06
L190MED	76.00	435.00	0.00	10.00	163.00	93.00	518.00	1.00	57.00	12.00	4.00	0.17	6.00	0.60	8.60	-5.90	11.80	563.00	27.89
L193MED	34.00	171.00	0.00	3.00	75.00	79.00	160.00	0.00	69.00	3.00	2.00	0.05	2.90	0.50	9.00	-6.90	9.80	660.00	14.03
L198ØRN	21.00	64.00	0.00	9.00	45.00	83.00	41.00	0.00	60.00	151.00	41.00	0.44	11.70	11.50	15.90	-7.50	15.00	830.00	57.18
L204ØEN	21.00	58.00	9.00	10.00	37.00	111.00	29.00	0.00	37.00	227.00	52.00	1.26	23.00	18.50	14.70	-7.70	19.00	790.00	60.92
L221IDH	44.00	266.00	3.00	10.00	83.00	44.00	308.00	0.38	45.00	2.00	0.00	0.06	3.00	13.40	11.72	1.06	14.50	1830.00	37.80
L223ICH	24.00	144.00	1.20	6.75	40.80	38.00	143.00	1.59	24.00	32.20	3.00	0.19	4.28	14.00	12.97	0.81	14.75	2256.00	32.16

Appendix 3

Appendix 3.1: Taxonomic notes of most common species of fossil Cladocera recorded from the Scottish and Norwegian training set sites and the core sequence of Loch Coire Fionnaraich, Scotland.

Appendix 3.1.1 Daphnidae

In spite of recent developments on identification, the family Daphnidae still has taxonomic uncertainties (Colbourne and Herbert, 1996). Most palaeolimnologists do not make an attempt to identify the species involved in this family (Frey, 1976). The identification for the genus is based on ephippial eggs and to a lesser extent on the post-abdominal claws, mandibles and sometimes on adjacent post-abdominal teeth whre these are still attached (Frey, 1958; Frey, 1976). Since ephippia were not always frequent, the post-abdominal claws and the adjacent remains were used for identification.

The claws of *Daphnia* have two crescents of minute spinules on the convex or ventral surface. Particularly, the claws of *D. longispina* are distinctly double ciliated from the base almost to the apex (e.g. Frey, 1958). Frey (1960) reported that *Daphnia* with postabdominal claws, sometimes with post abdominal teeth attached are in the quantitative remains. Two distinct types of postabdominal claws were common in the sediments. Quite large claws were easily identified but those with differential destruction during early instar phases are a difficult to recover quantitatively (e.g. Frey, 1960). Hrbáček (1969) reported that the correlation between the length of the claws and the number of teeth on the post-abdomen could be somewhat different in species such as *D. culculata*, *D. hyalina* and *D. pulicaria*. For example, the strains with smaller full-grown individuals and smaller neonates have somewhat lower number of teeth. However, this evidence was not sufficient in identifying the individual species in the study area.

Appendix 3.1.2 Bosminidae

The taxonomy of Bosminidae is also still uncertain (Frey, 1986; Korhola and Rautio, 2001) because many species of *Bosmina* show seasonal morphological variations, phenotypic plasticity or cyclomorphosis (Frey, 1960; De Costa, 1968; Nilssen et al., 1980).

Two species, *(Eu)Bosmina coregoni* and *(Eu)Bosmina longispina* were widely recorded in the training set and Loch Coire Fionnaraich but *Bosmina longirostris* was rare, so was not included for quantitative analysis in the training set. A few *B. longirostris* remains were recovered in surficial sediments of Loch Coire Fionnaraich. The shells and the head shields of these taxa are common in the sediment (e.g. Frey, 1958; 1960). Post-abdominal claws, sometimes with the post-abdomens attached, occurred to a much lesser extent. The headshields were identified from the positions and morphology of the headpores. With a few exceptions, *B. longirostris*, *B.*

coregoni and *B. longispina* have very similar morphological characteristics making their identification complicated.

Appendix 3.1.2.1 *(Eu)Bosmina coregoni* (Baird, 1857)

Locations of the lateral headpores were the most distinguishing features for identifying the head-shields of *Bosmina*. The lateral headpores of *B. coregoni* were generally exhibited circular and surrounded by a pear-shaped thickening. However, it is not equally pronounced in all populations (e.g. Kořínek, 1971; Frey, 1976). Megard (1964) noted that the pores in head-shields of *Bosmina* of the Dead Man Lake, New Mexico, were rather far from the edge of the head-shileds, and reported to be typical of *B. coregoni* (Figure-appendix 3.1.2.1).

The shells of *B. coregoni* were large with a sizeable, often gently curved, mucrone, and sometimes it could be seen with serrated dorsal margins (e.g. Megard, 1964). The shells were usually reticulated. Hofmann (1998b) argues that *Bosmina* sp. (e.g. *B. coregoni kessleri*) with intermediate mucrones (approximately 60-100μm), are due to hybridization between species with long (*B. longispina*) and short (*B. c. coregoni*) mucrones. The claws of *B. coregoni*, on the other hand, had a row of stouter and shorter spines at the base, increasing in length distally (e.g. Frey, 1958).

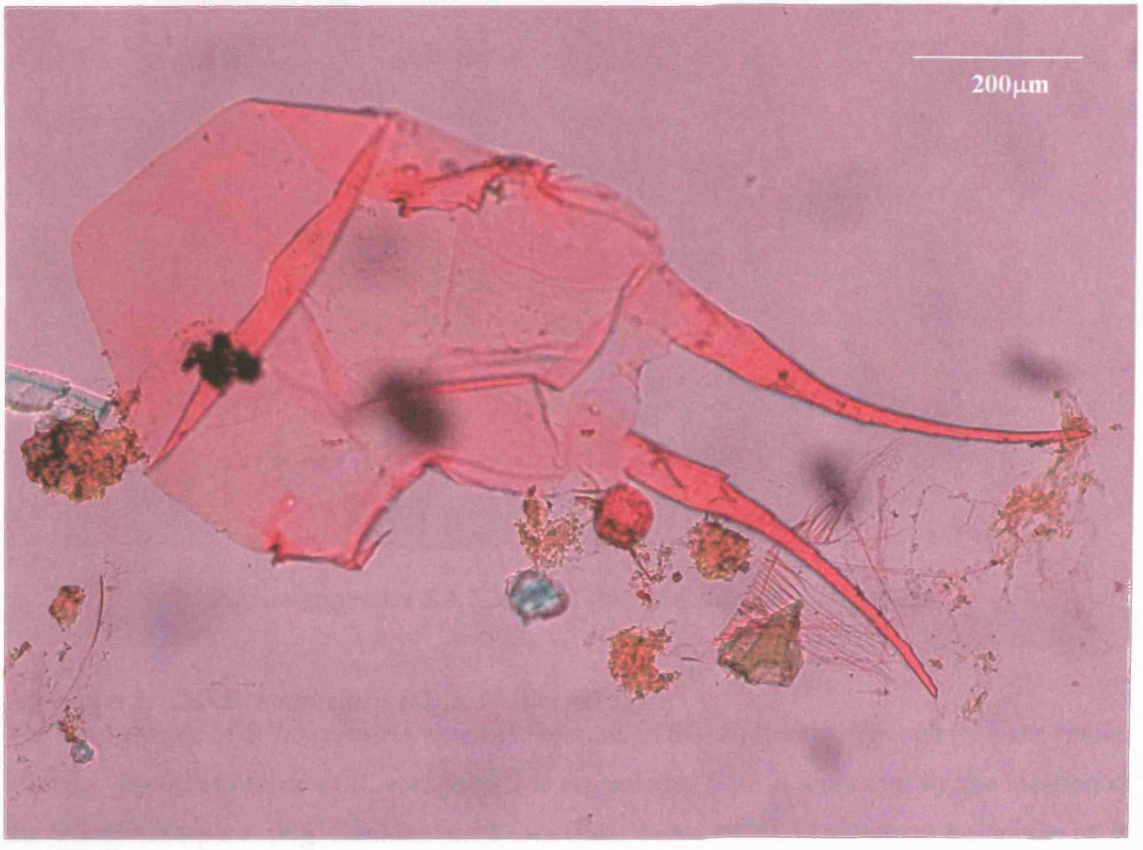


Figure-apppendix 3.1.2.1: Head-shield of *Bosmina coregoni*

Appendix 3.1.2.2 *(Eu)Bosmina longispina* (Leydig, 1860)

The head-shields of *B. longispina* in the training set were generally attributed to those of *B. coregoni* described earlier. Kořínek (1971) indicates that headpores are situated as in *B. coregoni*, though the distinction between the two species appears to be the patterning of the reticulae around the headpores (Figure-appendix 3.1.2.2). The forehead pore (FHP) was quite narrow, laterally compressed, horseshoe-shaped pore. The shells of *B. longispina* had an enlarged, straight, pointy mucro, often up to 50-100% of the size of the shell itself. Kotov (1996) reported that the mucro and the first antennae of *B. longispina* are relatively long. Hofmann (1998b) reported that the size of mucro of *B. longispina* exceeds 100μm while *B. coregoni* has a very short mucro (approximately 20μm). Shells of *B. longispina* that are small and have an elongate mucro are easily identifiable, but small shells with intermediate mucros are more obscure (e.g. Frey, 1986). In general, the remains of *B. longispina* were smaller than *B. longirostris* and *B. coregoni*. However, this is insufficient to split these species because it is unknown whether the remains are from lower instars, and as a result, remains can exhibit a wide degree of variation in the size of the remains (Frey, 1976).

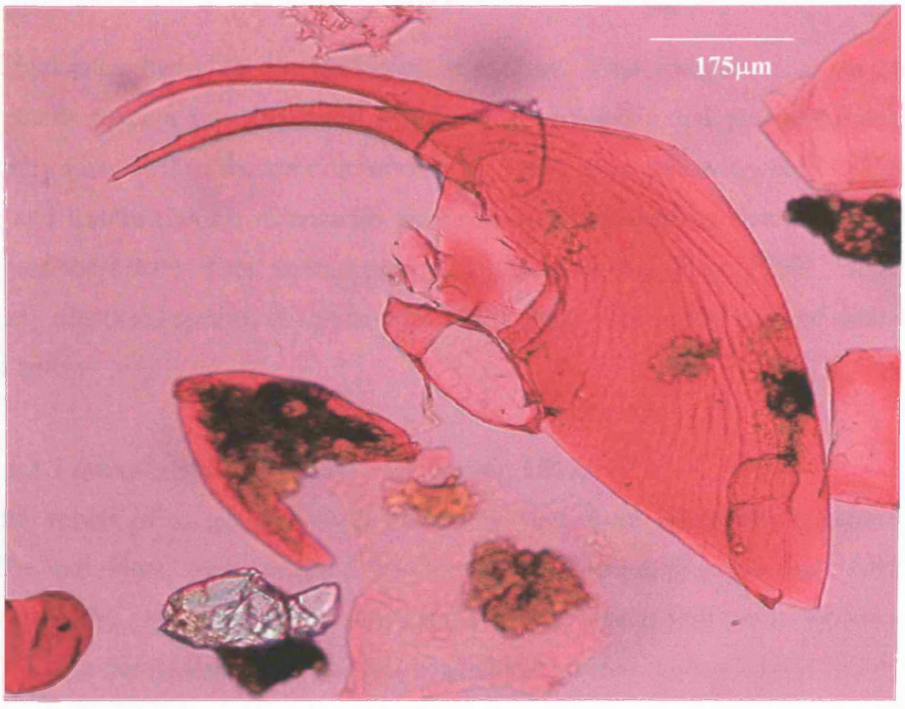


Figure-appendix 3.1.2.2: Head shield of *Bosmina longispina*

Appendix 3.1.2.3 *B. longirostris* (O. F. Müller, 1785)

The head-shields of *B. longirostris* were not recorded in the study sites. Though they are similar in many respects to those of *B. coregoni*. It is separatedm from *B. coregoni* by the location of the lateral head pores (e.g. Goulden and Frey, 1963; Frey, 1976). The lateral headpores of *B. longirostris* are located along the margin of the antennal articulation, not located some distance anterior to the mandibular articulation as they are in *B. coregoni* (Frey, 1976). On the other

hand, the pore of *B. longirostris* is oblong or rectangular in shape and is not surrounded by a thickening of the chitin. The shells *of B. longirostris* had very small mucro and were generally smaller than those of *B. coregoni* (e.g. Frey, 1958).

In spite of considerable attempts to identify *Bosmina* in the past, some confusions still exist on their viability, particularly between *B. coregoni* and *B. longispina*. Recently, Sarmaja-Korjonen (2001) provides a different key to identify *Eubosmina longispina* from that of Kořínek (1971) and Frey (1976). On the basis of material from Scandinavia and by Dr. U. Lieder, 1991 (see references on this), Fryer (1993) argued that *B. coregoni* has been incorrectly used and that species of the *B. coregoni* group should be known as *B. longispina*. Recently, Hellesten and Sundberg (2000) casts a doubt from that given by Frey (1993), using Random Amplified Polymorphic DNA to test genetic divergence between two populations of *Bosmina* species in Lake Östersjön, Sweden. Their results support the specific status of *B. coregoni* and *B. longispina* previously based on the morphological characteristics.

Appendix 3.1.3 Chydoridae

The family Chydoridae had great morphological variations. Four components of exoskeleton, head shield, shells (except in some small *Alona*), post-abdomens and post-abdominal claws were confidently identified to the species level in the study sites following Frey (1958; 1976) and Korhola and Rautio (2001). Chydorids were also distinguished by size and shape of the head-shields and the nature of the surface present on the head (e.g. Frey, 1959). Some of the most commonly identified species of Chydoridae in the study sites on the basis of their exuviae are discussed below.

Appendix 3.1.3.1 *Camptocercus rectirostris* (Schödler, 1862)

The body and valves of *C. rectirostris* in the study sites were bilaterally compressed and elongated. The individuals were comparatively large in their length (e.g. Smirnov, 1998). The shell of *C. rectirostris* had rather prominent parallel striae, which turn ventrally towards the anterior end. Unlike the American species, the head-shields were rounded behind and the shells had a corresponding embayment dorsally (e.g. Frey, 1960). Because of being keeled, the head-shield is always seen from the side in a microscope preparation (Frey, 1958). Frey (1959) described that there are three connected pores on the crest of the head near the posterior margin. Two minor pores are in lateral position near the base of the keel and are roughly opposite the middle one of the three major pores (Frey, 1959). The posterior end is truncated to fit under the corresponding angle of the shell (Frey, 1958). There are three median pores located near the posterior margin (Frey, 1958). The post-abdomen is elongated and tapered distally. Frey (1958) described that the most distinct distinguishing feature is on the dorsal surface with 13 to 17 serrate teeth increasing in size distally, with a series of fine hairs or setae on either side of the

anal furrow. The claw is long, slender, and evenly tapered. At the base is a stout spine with a series of evenly spaced hairs along the outer surface. The dorsal surface of the claw is concave and characterised by about 25 teeth increasing in size distally (e.g. Frey, 1958).

Appendix 3.1.3.2 *Acroperus harpae* (Baird, 1835)

A. harpae was distinguished by its shell, head-shield, post-abdomen and post-abdominal claws (Figure-appendix 3.1.3.2a and Figure-appendix 3.1.3.2b). The diagonal marking of the shells is a distinguishing character (e.g. Frey, 1958). The striae are parallel throughout. At the ventral posterior are typically 3-5 small teeth, with fine spinules in between, attached sub-marginally on the median surface (e.g. Frey, 1958). A row of submarginal spinules of varying length extends dorsally from the teeth along the posterior margin and the striae of the shell ended in this row of spinules (e.g. Frey, 1958). Usually the head shield was lying on its side (Figure-appendix 3.1.3.2a). The general shape was more similar to *C. rectirostris*, but the posterior end was less markedly truncated and there were no longitudinal striae. The three median pores were located in a region of thickened chitin at the posterior end (e.g. Frey, 1958). The post abdomen of *A. harpae* did not have prominent teeth along the dorsal surface. Instead there were groups of 4 to 6 very short spinules located marginally, the distal-most spinule of each group being the largest (Frey, 1958). The claw was characterised by a basal spine ciliated along the proximal two-third of its length, and by a row of setae distal to the spine increasing in length gradually and ending in a prominent spine distal to the middle of the claw (Frey, 1958).



Figure-appendix 3.1.3.2a: Head-shield of *Acroperus harpae*

Appendix 3.1.3.3 *Acroperus elongatus* (Sars, 1862)

The shells of *A. elongatus* had parallel, coarse, diagonal striae, with most closely spaced longitudinal striae found between them (Figure-appendix 3.1.3.3). The head shields had blunted rostrums and were covered in closely spaced longitudinal striae that curved around the headpore arrangement at the posterior margin. Frey (1959) described three major pores

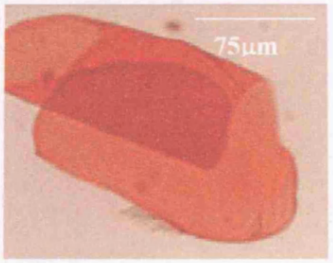


Figure-appendix 3.1.3.2b: Shell of *A. harpae*

Close on the midline and connected by a distinct channel. Minor pores were located almost at the edge of the head-shield. The post-abdomen of *A. elongatus* was slightly longer than *A. harpae*, and more teeth extended around the distal margin of the post-abdomen.

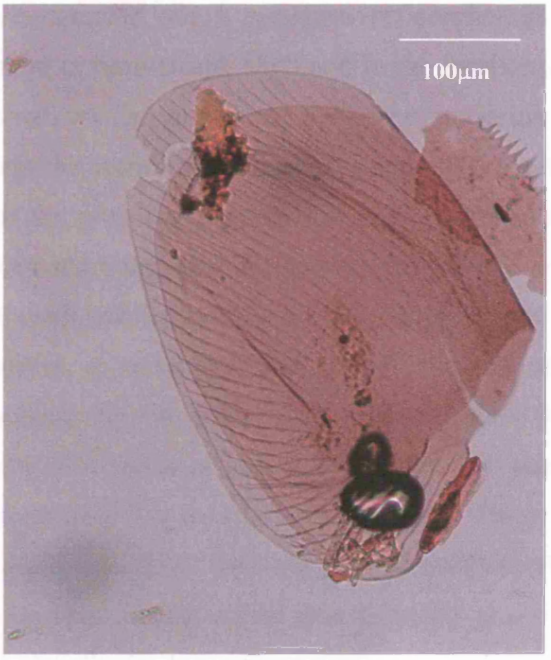


Figure-appendix 3.1.3.3: Shell of *Acroperus elongatus*

Appendix 3.1.3.4 *Graptoleberis testudinaria* (Fischer, 1848)

The shell and head-shields of *G. testudinaria* were very distinctive (Figure-appendix 3.1.3.4). The shell was characteristically reticulated with 2 (occasionally only 1 or 3) prominent upturned teeth at the posterior-ventral angle. The head-shield was reticulated and the rostrum was rounded and broadly expanded (e.g. Frey, 1959). There were three median pores near the caudal edge, the two end pores generally larger than the central one (e.g. Frey, 1959). The surrounding chitin of the head-shield was somewhat thickened and was bordered by minute punctae that resemble accessory pores (e.g. Frey, 1958; 1959).

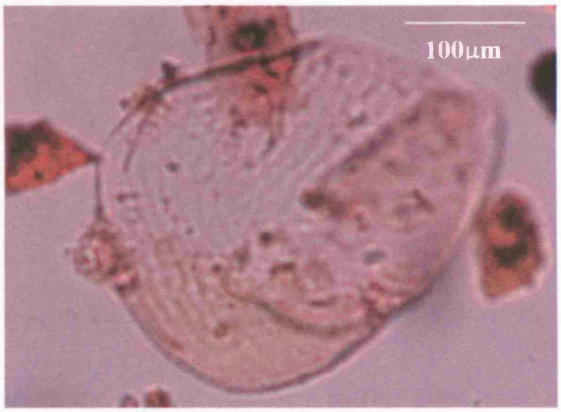


Figure-appendix 3.1.3.4: Head-shiled of *Graptoleberis testudinaria*

Appendix 3.1.3.5 Small *Alona* (*Alona rectangula* Sars 1861 and *Alona guttata* Sars 1862)

Two small chydorids, *A. rectangula* and *A. guttata* were morphologically much similar. The similarity was usually found in head-shield, shell and in the location of pores in head-shields. Both species had three small median pores near the posterior margin of the head-shields, the distance from the margin to the nearest pore being no greater than the distance from this pore to the middle pore. Besides the pore arrangement and the general size, the head-shields were characterised by being short and broad, scarcely longer than wide. The posterior portion, which attaches to the shell, was much smaller than the rostrum, which in turn is blunt or truncate (e.g. Frey, 1958; 1959). However, *A. rectangula* and *A. guttata* were distinguished by their post-abdomnen and post-abdominal claws more easily. *A. guttata* differed from *A. rectangula* by the absence of squamae on the post-abdomen (e.g. Frey, 1960). The post-abdomen of *A. guttata* had 6 to 9 teeth, mostly commonly 7 or 8 along the dorsal side. The proximal teeth had hairs at their base. However, *A. rectangula* has 7-9 groups of 1-2 teeth along the dorsal edge, the distal tooth in each group being the largest. The post-abdomen was relatively short, slightly expanded, and evenly rounded distally (e.g. Frey, 1958).

Appendix 3.1.3.6 *Alona intermedia* (Sars, 1862)

The head-shield of *A. intermedia* was found very well preserved in the sediment and easy to identify in the study sites (Figure-appendix 3.1.3.6). The head shields were distinct with two large round median headpores located on the midline approximately one inter-pore distance from the posterior margin of the head shield (e.g. Frey, 1959). The lateral headpores were located approximately one inter-pore distance from the median pores, about level with the posterior edge of the lower-most median pore (e.g. Frey, 1959).

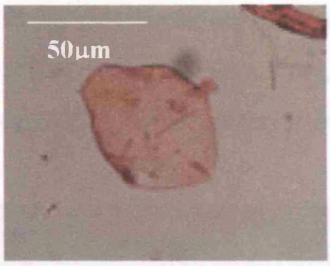


Figure-appendix 3.1.3.6: Head-shield of *Alona intermedia*

Appendix 3.1.3.7 Large *Alona* (*Alona affinis*, Leydig, 1886 and *A. quadrangularis* O. F. Müller, 1785)

Morphologically *A. affinis* and *A. quadrangularis* are very similar. They were distinguished by the pore arrangement on the head-shields. The caudal claws and postabdomens were also quite distinct. The shells were, however, less easy to distinguish. *A. affinis* usually had fine, closely spaced longitudinal striae, whereas, *A. quadrangularis* had only coarsely spaced longitudinal striae (e.g. Frey, 1958).

Appendix 3.1.3.8 *Monospilus dispar* (Sars, 1862)

M. dispar was readily recognized by the shape of the anterior edge of the shell, and by the ventral border with its characteristic denticles and setae (e.g. Frey, 1960). Usually the shell was rounded in the posterior and covered in faint reticulae. The head-shield of *M. dispar* is completely different from that in any other chydorids (e.g. Frey, 1959). It is broadly square in shape with an attenuated rostrum and a rounded tip (e.g. Frey, 1960). It has a single, irregular pore hole located near to the posterior margin (e.g. Frey, 1960).

Appendix 3.1.3.9 *Eurycercus lamellatus* (O. F. Müller, 1785)

Because of the large size of the skeletal remains and their characteristic morphology, *E. lamellatus* was one of the species most easily identified in the study sites. The shell was frequently fragmented. The posterior margin was very high, extending even above the posterior–dorsal angle (e.g. Frey, 1958). The head-shield was thin and often fragmented (e.g. Frey, 1958). The lateral pores in the head-shield were rather small but distinct, and were located at the equator of the pore (e.g. Frey, 1958; 1959). The surrounding chitinous thickening was quite regular, being narrower along the posterior edge. The dorsal edge of the post-abodmen looked like a saw (e.g. Frey, 1958)

Appendix 3.1.3.10 *Alonella nana* (Baird, 1850)

A. nana was readily recognized both from its head-shields and shell (Figure-appendix 3.1.3.10). Particularly the longitudinal striae on the shell were prominent (e.g. Frey, 1958; 1959). The shell had only one blunt tooth occurring just at the posterior ventral angle, except in one specimen having 2 teeth on the one valve only. Feathered hairs occurred along the ventral edge

to the base of the tooth, and these were sometimes well preserved in the sediments. Just dorsal to the tooth was a row of about 10 to 12 fine striae (e.g. Frey, 1958). In the head-shields, there were 2 median pores, widely separated, with the posterior one quite close to the margin (e.g. Frey, 1958; 1959).

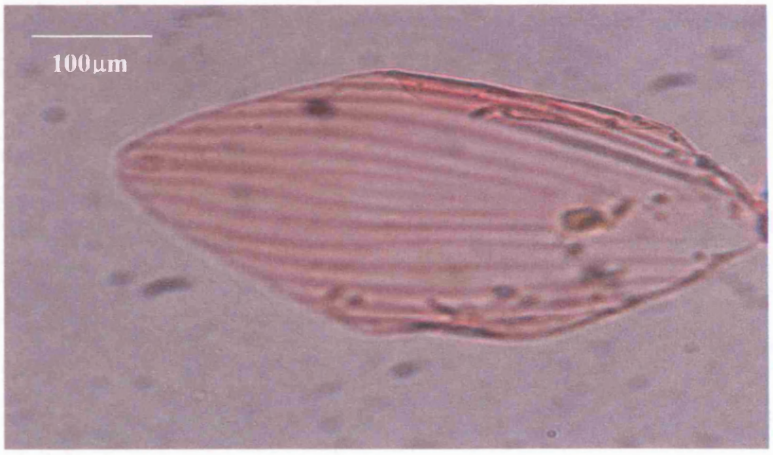


Figure-appendix 3.3.3.10: Head-shield of *Alonella nana*

Appendix 3.1.3.11 *Alonella excisa* (Fischer, 1854)

A. excisa was distinguished by fine striae within the reticulae of the shell (e.g. Frey, 1960). However, it was very difficult to distinguish small striae. In this situation, the species was identified by the teeth at the posterior ventral angle, which were strictly terminal (e.g. Frey, 1960).

Appendix 3.1.3.12 *Chydorus sphaericus* (O. F. Müller, 1785)

C. sphaericus was variable with respect to body shape and shell sculpturing. It had reticulae, but these were poorly developed in the dorsal and anterior portions of the shell. The dorsal margin of the shell was very short relative to the length of the shell. As in other chydorids, *C. sphaericus* has a shell fold turned in ventrally bearing feathery setae along the edge (e.g. Frey, 1958). The posterior ventral angle of the shell was quite well developed and without teeth (e.g. Frey, 1958). Frey (1960) reported that the tip of the rostrum of *C. sphaericus* is slightly emarginated and the males usually have a broadly rounded rostrum. Frey (1958) noted that the rostrum is shorter than the width of the head-shield at the fornices. The head-shields were characterised by prominent small tubercles along the edges of the reticulae. Within the reticulae, there were fine, wavy and non-anastomosing striae present (e.g. Frey, 1960).

Appendix 3.1.3.14 *Chydorus piger* (Sars, 1862)

The shells of *C. piger* were oval in shape and carried a distinctive, triangular shell flap in the anterior area. Sometimes radial striae were present on the shells, as were the strong ventral setae, which preserved well in sediments and were readily observable. The head-shild had a short, rounded rostrum anterior to well-developed fornices (e.g. Frey, 1959). The width of the

head-shild expanded after these fornices and the posterior end was broadly rounded. There were two major pores located on the midline approximately central between the fornices and the posterior edge. Two minor pores located between two major pores. Frey (1959) reported that there are no surface markings. Sarmaja-Korjonen (1999) reported that the head-shield of ephippial females of lakes of Northern Finish Lapland had not so pointed posteriors.

Appendix 4

Appendix 4.1: Abbreviations used for contemporary cladoceran zooplankton samples.

Sample Abbreviations	Sample Full-name (Month of sampling-year of sampling-type of habitat sampled	Temporal variables
May'01M	May 2001 Macrophyte	
May'01S	May 2001 Sand	
May'01B	May 2001 Boulder	Spring'01
May'01P	May 2001 Planktonic	
Aug'01M	August 2001 Macrophyte	
Aug'01S	August 2001 Sand	
Aug'01B	August 2001 Boulder	Summer'01
Aug'01P	August 2001 Planktonic	
Sep'01M	September 2001 Macrophyte	
Sep'01S	September 2001 Sand	
Sep'01B	September 2001 Boulder	Autumn'01
Sep'01P	September 2001 Planktonic	
Jan'02M	January 2002 Macrophyte	
Jan'02S	January 2002 Sand	
Jan'02B	January 2002 Boulder	Winter'02
Jan'02P	January 2002 Planktonic	
Apr'2M	April 2002 Macrophyte	
Apr'02S	April 2002 Sand	
Apr'02B	April 2002 Boulder	Spring'02
May'02P	May 2002 Planktonic	
Aug'02M	August 2002 Macrophyte	
Aug'02S	August 2002 Sand	
Aug'02B	August 2002 Boulder	Summer'02
Aug'02P	August 2002 Planktonic	

Appendix 5

Appendix 5.1: Abbreviation of samples used in numerical analyses and graphical representations for surface sediment samples along various transects constructed in Loch Coire Fionnaraich.

TRANSCT/SAMPLES	FULL MEANING
T1M2m	Transect 1-Macrophyte-2m depth
T1M5m	Transect 1-Macrophyte-5m depth
T1M8m	Transect 1-Macrophyte-8m depth
T1M11m	Transect1-Macrophyte-11m depth
T2S2m	Transect 2-Sand-2m depth
T2S5m	Transect 2-Sand-5m depth
T2S8m	Transect 2-Sand-8m depth
T2S11m	Transect 2-Sand-11m depth
T3B2m	Transect3-Boulder-2m depth
T3B5m	Transect3-Boulder-5m depth
T3B8m	Transect3-Boulder-8m depth
T3B11m	Transect3-Boulder-2m depth
T4M2m	Transect 4-Macrophyte-2m depth
T4M5m	Transect 4-Macrophyte-5m depth
T4M8m	Transect 4-Macrophyte-8m depth
T4M11m	Transect4-Macrophyte-11m depth
T5M2m	Transect 5-Macrophyte-2m depth
T5M5m	Transect 5-Macrophyte-5m depth
T5M8m	Transect 5-Macrophyte-8m depth
T5M11m	Transect5-Macrophyte-11m depth
T6B2m	Transect6-Boulder-2m depth
T6B5m	Transect6-Boulder-5m depth
T6B8m	Transect6-Boulder-8m depth
T6B11m	Transect6-Boulder-2m depth
T7B2m	Transect7-Boulder-2m depth
T7B5m	Transect7-Boulder-5m depth
T7B8m	Transect7-Boulder-8m depth
T7B11m	Transect7-Boulder-2m depth
T8S2m	Transect 8-Sand-2m depth
T8S5m	Transect 8-Sand-5m depth
T8S8m	Transect 8-Sand-8m depth
T8S11m	Transect 8-Sand-11m depth
CORE-TOP/CORE SAMPLE	Surface sediment from the lake centre

Appendix 5.2: Abbreviation of cladoceran zooplankton species used in the ordination for the taphonomic study in Loch Coire Fionnaraich, Scotland.

Species code	Scientific name
Dap spp	*Daphnia spp*
Bos lon	*Bosmina longispina*
Bos cor	*Bosmina coregoni*
Bos lngr	*Bosmina longirostris*
Gra tes	*Graptoleberis testudinaria*
Eur lam	*Eurycercus lamellatus*
Cam rec	*Camptocercus rectirostris*
Acr har	*Acroperus harpae*
Acr elo	*Acroperus elongatus*
Alo rec	*Alona rectangula*
Alo gut	*Alona guttata*
Alo gutu	*Alona guttata tuberculata*
Alo cos	*Alona costata*
Alo rus	*Alona rustica*
Alo int	*Alona intermedia*
Alo aff	*Alona affinis*
Alo qua	*Alona quadrangularis*
Alo nan	*Alonella nana*
Alo ros	*Alonella (Disparalona) rostrata*
Alo exi	*Alonella exigua*
Alo exc	*Alonella excisa*
Mon dis	*Monospilus dispar*
Chy sph	*Chydorus sphaericus*
Chy pig	*Chydorus piger*
Chy glo	*Chydorus globosus*
Ple adu	*Pleuroxus aduncus*
Ple tri	*Pleuroxus trigonellus*
Sid cry	*Sida crystallina*
Rhy fal	*Rhynchotalona falcata*

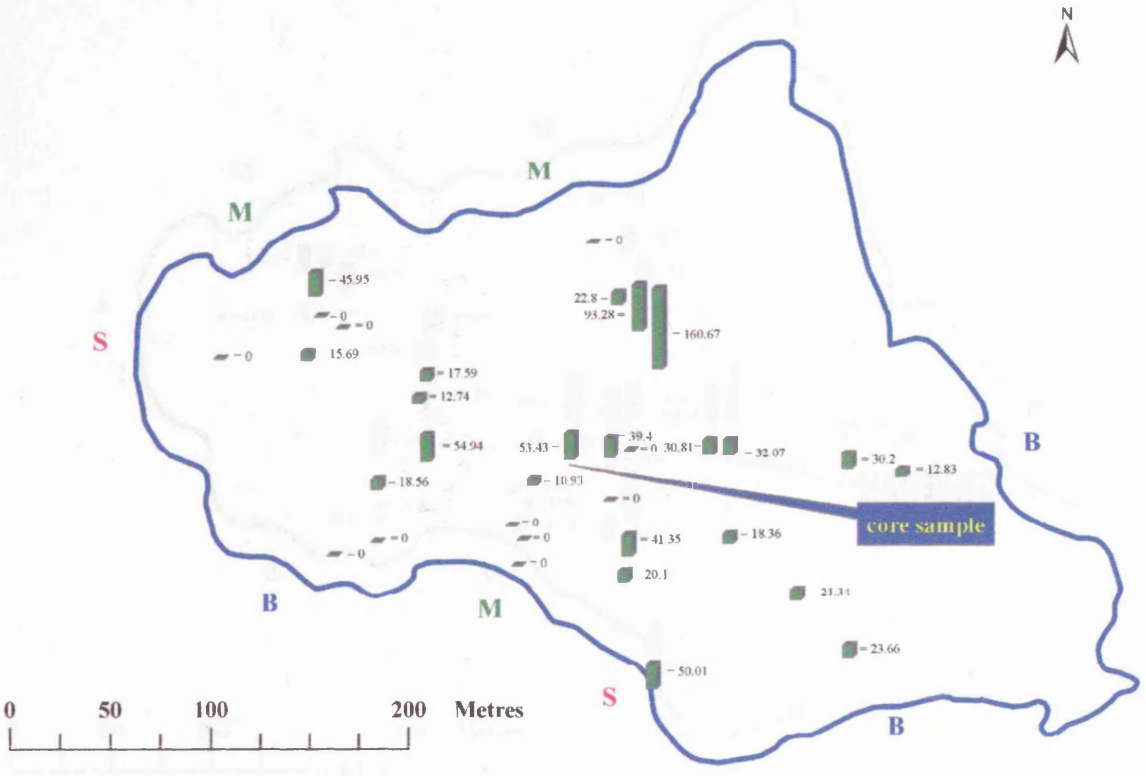
Appendix 5.3: Sediment samples taken with GPS co-ordinates and lake depths along 8 transects associated to shoreline habitat and a core-top in Loch Coire Fionnaraich, Scotland for taphonomic study. Depths of some sediment location are slightly different from the intended depth due to the wind-induced movement of the boat.

Transects(T) /Core	Shoreline habitat type	Intended depth (m)	Real depth (m)	National Grid Reference
T1	Macrophyte (M)	2	2	NG94368/49897
	M	5	5	NG94371/49894
	M	8	8	NG94382/49888
	M	11	11	NG94517/49800
T2	Sand (S)	2	2	NG94320/49873
	S	5	5	NG94364/49872
	S	8	8	NG94424/49862
	S	11	9.5	NG94420/49850
T3	Boulder (B)	2	2	NG94377/49772
	B	5	4.7	NG94399/49779
	B	8	7.2	NG94399/49806
	B	11	11	NG94424/49820
T4	Macrophyte (M)	2	2	NG94470/49767
	M	5	4.8	NG94473/49780
	M	8	7.7	NG94467/49787
	M	11	11	NG94478/49808
T5	Macrophyte (M)	2	1.9	NG94509/49932
	M	5	5.6	NG94525/49901
	M	8	8.3	NG94533/49887
	M	11	11	NG94542/49868
T6	Boulder (B)	2	2	NG94664/49812
	B	5	5.6	NG94637/49816
	B	8	8.2	NG94571/49823
	B	11	11.5	NG94567/49823
T7	Boulder (B)	2	2	NG94637/49720
	B	5	5	NG94611/49749
	B	8	8	NG94577/49778
	B	11	12	NG94521/49826
T8	Sand (S)	2	1.9	NG94538/49704
	S	5	5	NG94526/49772
	S	8	7.7	NG94524/49763
	S	11	10	NG94517/49822
Central Core	Core Sample	14	14	NG94497/49819

Appendix 5.4: An example of tabulated data in Excel showing the spatial interpolations of absolute counts (no. gdw^{-1}) of fossil Cladocera species (e.g. *Alona affinis*) along various depth points and the core-top (core sample) of Loch Coire Fionnaraich using inverse distance weighting (IDW) methods in Arc-GIS.

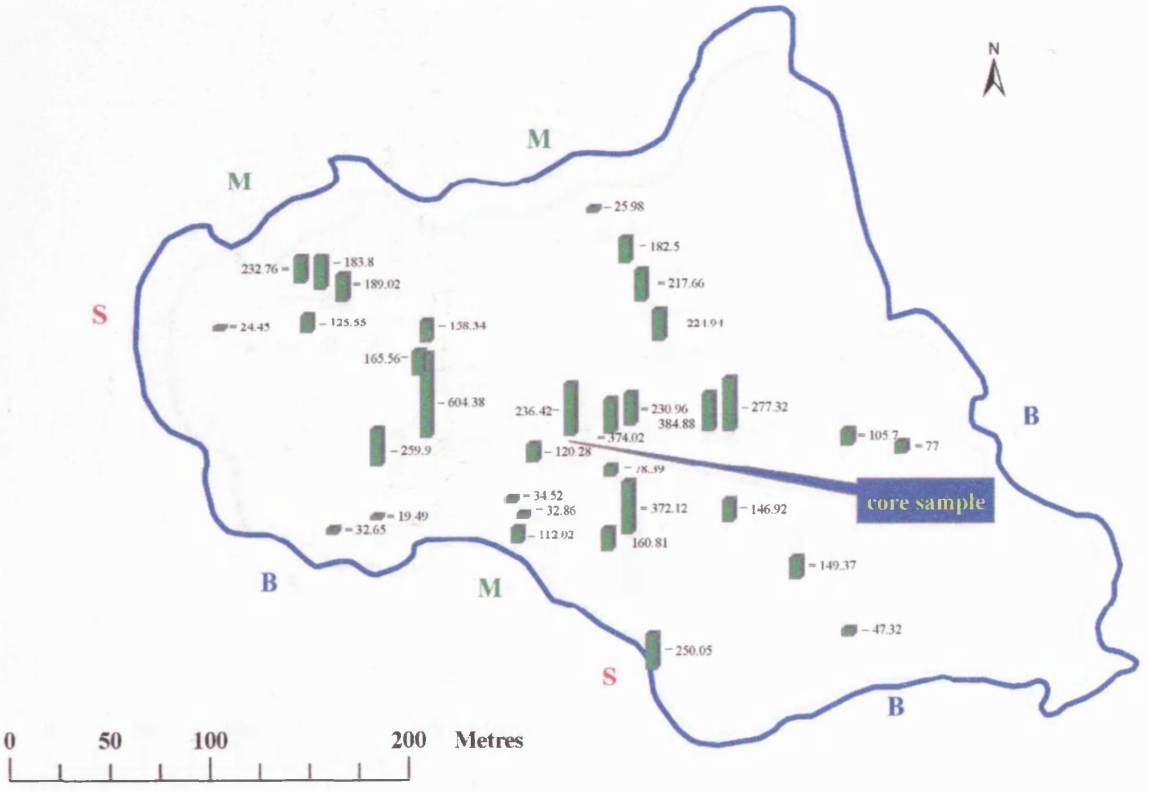
Cladocera species	Transects	Depth	Easting	Northing	Absolute Count
Alona affinis	**1**	2	194368	849897	45.95
Alona affinis	1	5	194371	849894	58.19
Alona affinis	1	8	194382	849888	18.90
Alona affinis	1	11	194517	849800	9.80
Alona affinis	**2**	2	194320	849873	13.97
Alona affinis	2	5	194364	849872	31.39
Alona affinis	2	8	194424	849862	0.00
Alona affinis	2	9.5	194420	849850	25.47
Alona affinis	**3**	2	194377	849772	8.16
Alona affinis	3	4.7	194399	849779	6.50
Alona affinis	3	7.2	194399	849806	111.39
Alona affinis	3	11	194424	849820	27.47
Alona affinis	**4**	2	194470	849767	0.00
Alona affinis	4	4.8	194473	849780	5.48
Alona affinis	4	7.7	194467	849787	3.14
Alona affinis	4	11	194478	849808	32.80
Alona affinis	**5**	1.9	194509	849932	25.98
Alona affinis	5	5.6	194525	849901	68.44
Alona affinis	5	8.3	194533	849887	62.19
Alona affinis	5	11	194542	849868	32.13
Alona affinis	**6**	2	194664	849812	51.33
Alona affinis	6	5.6	194637	849816	105.70
Alona affinis	6	8.2	194571	849823	64.15
Alona affinis	6	11.5	194567	849823	61.63
Alona affinis	**7**	2	194637	849720	23.66
Alona affinis	7	5	194611	849749	128.03
Alona affinis	7	8	194577	849778	36.73
Alona affinis	7	12	194521	849826	0.00
Alona affinis	**8**	1.9	194538	849704	0.00
Alona affinis	8	5	194526	849772	201.01
Alona affinis	8	7.7	194524	849763	41.35
Alona affinis	8	10	194517	849822	19.70
Alona affinis	**core sample**	14	194497	849821	160.29

Appendix 5.5: Distribution of *Daphnia* sp. in Loch Coire Fionnaraich, Scotland.



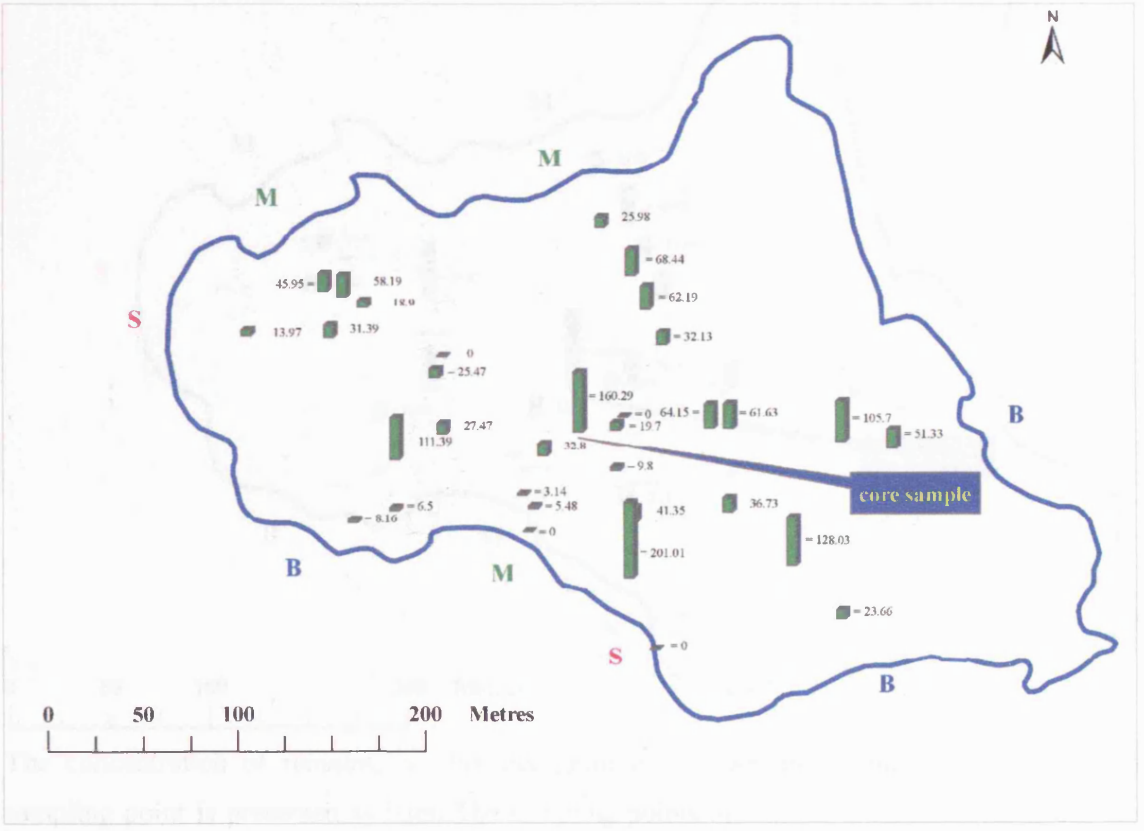
The concentration of remains, number per gram of dry weight sediment (gdw^{-1}), in each sampling point is presented as bars. The sampling points are the GPS coordinates, which are described details in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect started, are identified by M = Macrophyte, S = Sand and B= Boulder respectively. The deposition of the remains of *Daphnia* shows low representation in lake sediments. The bathymetry map (Figure 5.11) of the loch shows that the *Daphnia* remains are focused in a relatively deep offshore area of the loch ~10 m deep. Poor representation of *Daphnia* remains in LCFR could be due to a limited preservation of the remains in the surface sediments (Frey, 1986). However, in general the *Daphnia* populations in LCFR were not as frequent as expected (Chapter 4) resulting in poor contribution of remains to the sedimentary assemblages. Poor representation of *Daphnia* remains in lacustrine sediments could also be due to an increased fish predation in the loch. However, experiences on neighbouring loch, Loch Coire nan Arr indicate that LCFR is likely to have a limited role of fish in controlling the *Daphina* populations. The remains of *Daphnia* were not identified to species level however most remains were similar to *D. longispina*. Concentration of *Daphnia* in western shoreline habitats is almost nil indicating that the deposition of the remains in macrophyte dominated habitats is fairly limited. Fryer (1993) argued that *D. longispina* is a truly planktonic species, but also occurs in the littoral zone. In LCFR, the remains of *Daphnia* is widely distributed in offshore zone, particularly at transects originated from the eastern side of the loch. These transects are originated from rocky and sandy substrates, *Daphnia* is likely to prefer such habitats in oligotrophic mountain lakes, where limited vegetation beds are available.

Appendix 5.6: Distribution of *Acroperus elongatus* in Loch Coire Fionnaraich, Scotland.



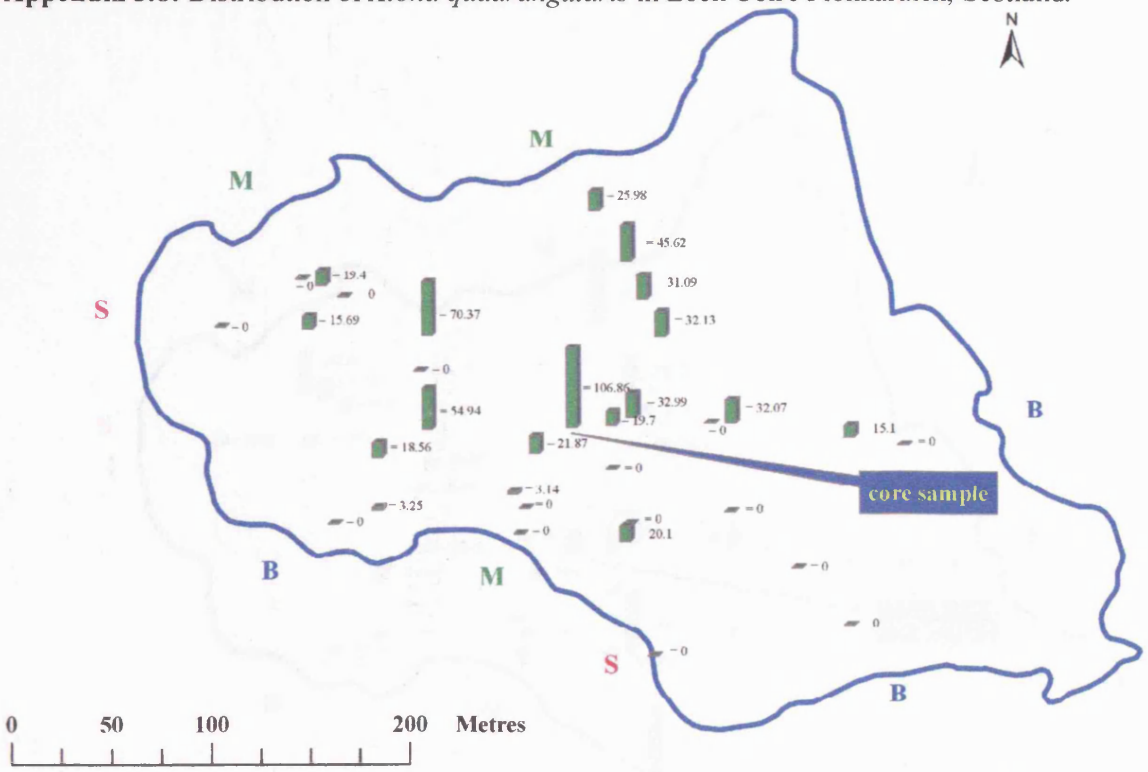
The concentration of remains, number per gram of dry weight sediment (gdw^{-1}), in each sampling point is presented as bars. The sampling points are the GPS coordinates, which are described details in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran, are identified by M = Macrophyte, S = Sand and B= Boulder respectively. The diverse distribution patterns of the remains of *A. elongatus* suggest that the presence of this taxon in the sediment may be influenced by multiple factors, in which the wind-induced water current is likely to have played a significant role. The LCFR is frequently influenced by both westerly and easterly winds with a seasonal basis. Activities of winds from both directions could push the water currents to be circulated around the lake centre. As a result, the remains are concentrated mainly at the offshore zone. The source habitats appear to have played a minimal role on the deposition of the remains of *A. elongatus* at shallower depths. In contrast, original habitats play higher role to many other Chydorid taxa. The contemporary survey of Cladocera in Chapter 4 suggests that this taxon dominates the chydorid populations in LCFR. However, the remains of this taxon in the surface sediment of LCFR were poorly recorded. Evidence suggests that the preservation of the remains of *A. elongatus* is as high as many other chydorid taxa (Frey, 1988). Why the remains of this taxon in LCFR are least concentrated in the surface sediment even though its presence is high in contemporary populations, is a very interesting question to address. This provides a possibility of biases in environmental reconstructions. The patterns of deposition of remains in LCFR also show the high concentration of remains in the second deepest basin (see Figure 5.3) suggesting that the remains of this taxon are deposited significantly regardless of the highest depth of the loch.

Appendix 5.7: Distribution of *Alona affinis* in Loch Coire Fionnaraich, Scotland.



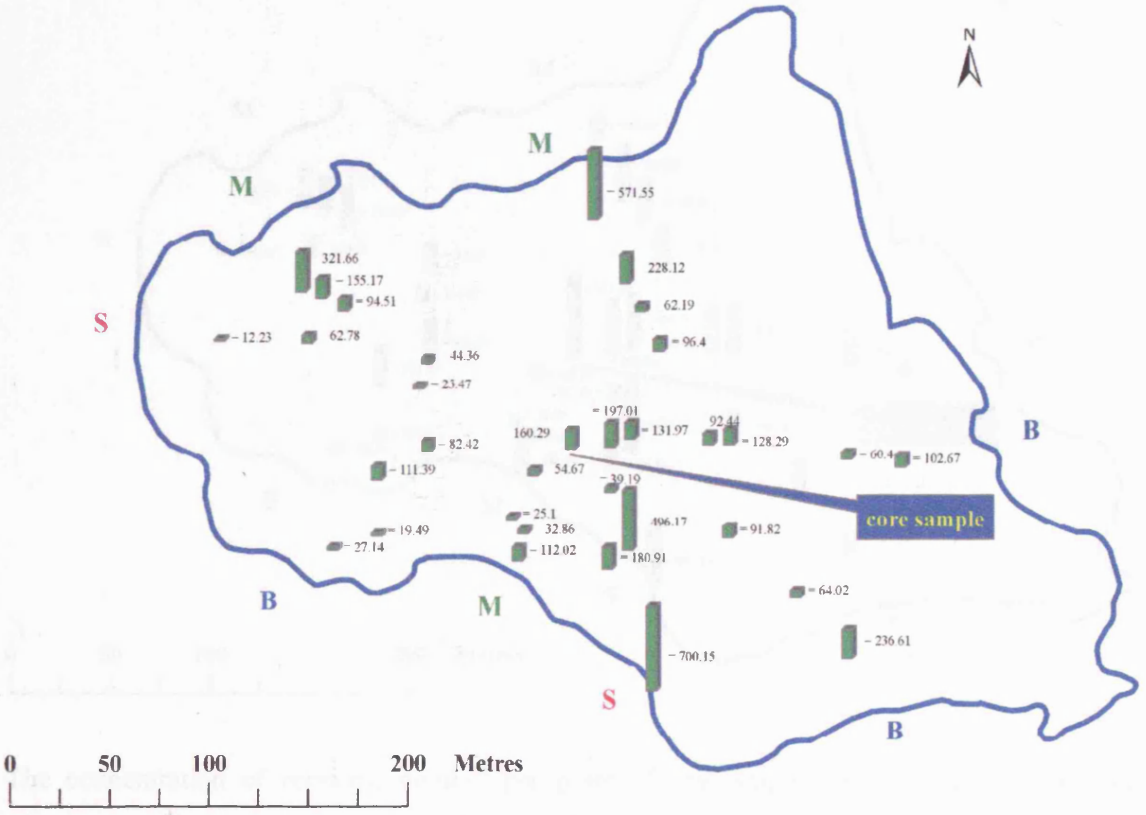
The concentration of remains, number per gram of dry weight sediment (gdw^{-1}), in each sampling point is presented as bars. The sampling points are the GPS coordinates, which are described details in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran, are identified by M = Macrophyte, S = Sand and B= Boulder respectively. Concentrations of *A. affinis* in the sediments are very low. *A. affinis* is a bottom dweller animal. This is frequently recorded in a variety of substrata including the hard and soft sediments. However, this taxon does not have a high preference to the vegetation beds (Fryer, 1993). It appears that the remains of this taxon in LCFR is transported towards the lake centre through transects associated with the source habitats (e.g. rocky and sandy) at the eastern part of the loch. The deposition of this taxon is high at the lake centre where the sediment focusing appears to have been playing the significant role. The size of the remains of *A. affinis* is much higher (>2mm) with the high specific gravity resulting in a higher deposition rate at the deepest areas of the loch.

Appendix 5.8: Distribution of *Alona quadrangularis* in Loch Coire Fionnaraich, Scotland.



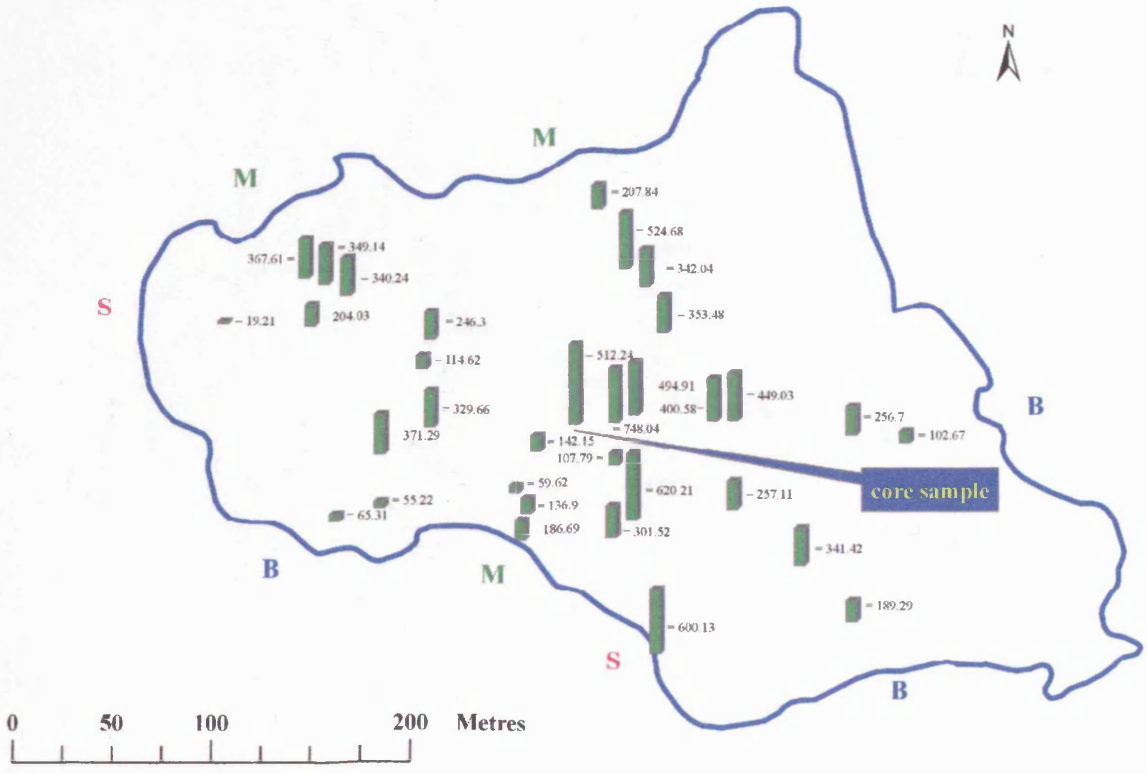
The concentration of remains, number per gram of dry weight sediment (gdw^{-1}), in each sampling point is presented as bars. The sampling points are the GPS coordinates, which are described details in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran, is identified by M = Macrophyte, S = Sand and B= Boulder respectively. Concentrations of *A. quadrangularis* are also rather low. However, the concentration is highest in the core-top sample (90-105gdw^{-1}). Except the macrophyte-associated transect in the northwest corner of the loch, the deposition of the remains of *A. quadrangularis* in many other transects with shallower depths is nil indicating that the remains of this taxon have faster rate of transportation and deposition towards the lake centre. Like *A. affinis* this taxon also prefers wider range of substrata, is also uncommon in vegetation beds (Fryer, 1993). Its dominance in macrophyte-associated transect in LCFR is unknown. While sampling surface sediments, the transect (T5) at the northwest corner of the loch was found to have mixed muddy and gritty substrates, which appear to have utilized by this taxon. Like *A. affinis* the effect of sediment focusing should also have been high on the deposition of this taxon in the lake centre.

Appendix 5.9: Distribution of *Alona guttata* in Loch Coire Fionnaraich, Scotland.



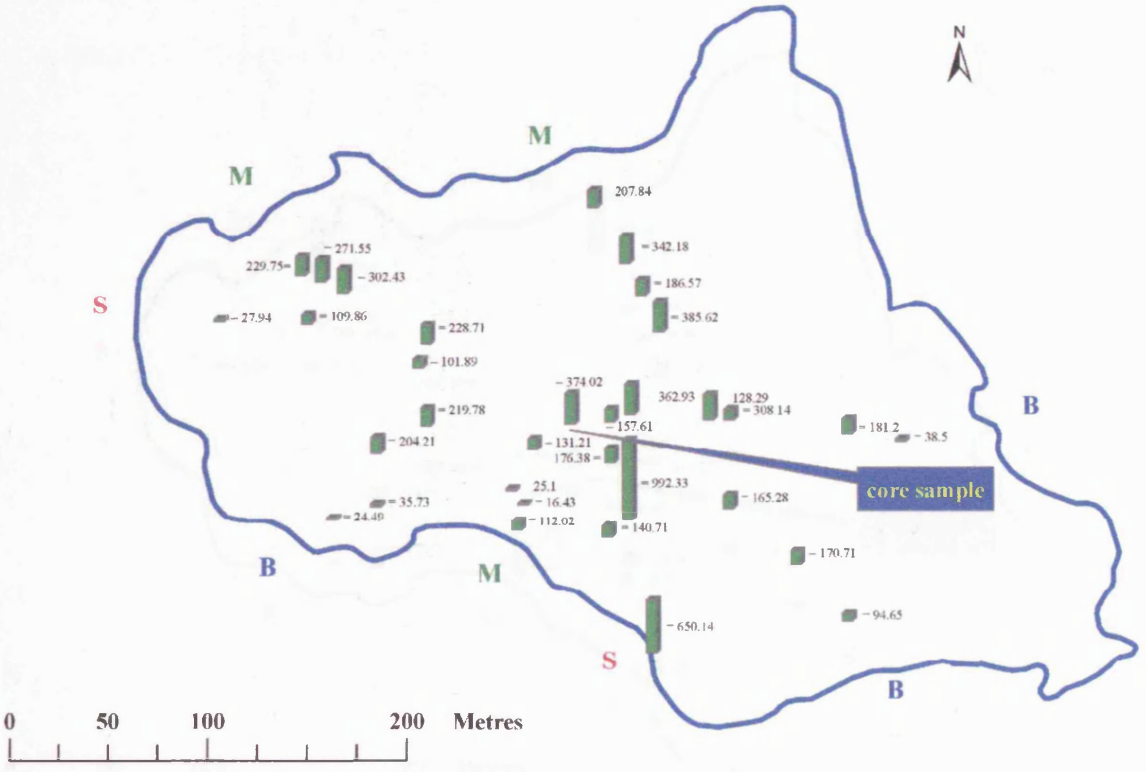
The concentration of remains, number per gram of dry weight sediment (gdw^{-1}), in each sampling point is presented as bars. The sampling points are the GPS coordinates, which are described details in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran, are identified by M = Macrophyte, S = Sand and B= Boulder respectively. Distribution of remains shows the highest concentration of *A. guttata* close to the southeast shoreline with relatively low concentrations in the core-top sample. *A. guttata* is a very small in size (<1mm). Because of its size, the food requirement for this taxon is also very low. This taxon prefers bottom detritus and the nature of the substratum do not seem to be very important for this taxon (Fryer, 1993). Rather regular patterns of the concentration of the remains of this taxon in LCFR indicate that this taxon utilizes a variety of substrates. The remains are also deposited at the source habitat and gradually transported towards the lake-centre by water currents. Due to the smaller size, the rate of deposition of the remains of this taxon in surface sediment may also be relatively low.

Appendix 5.10: Distribution of *Alona rustica* in Loch Coire Fionnaraich, Scotland.



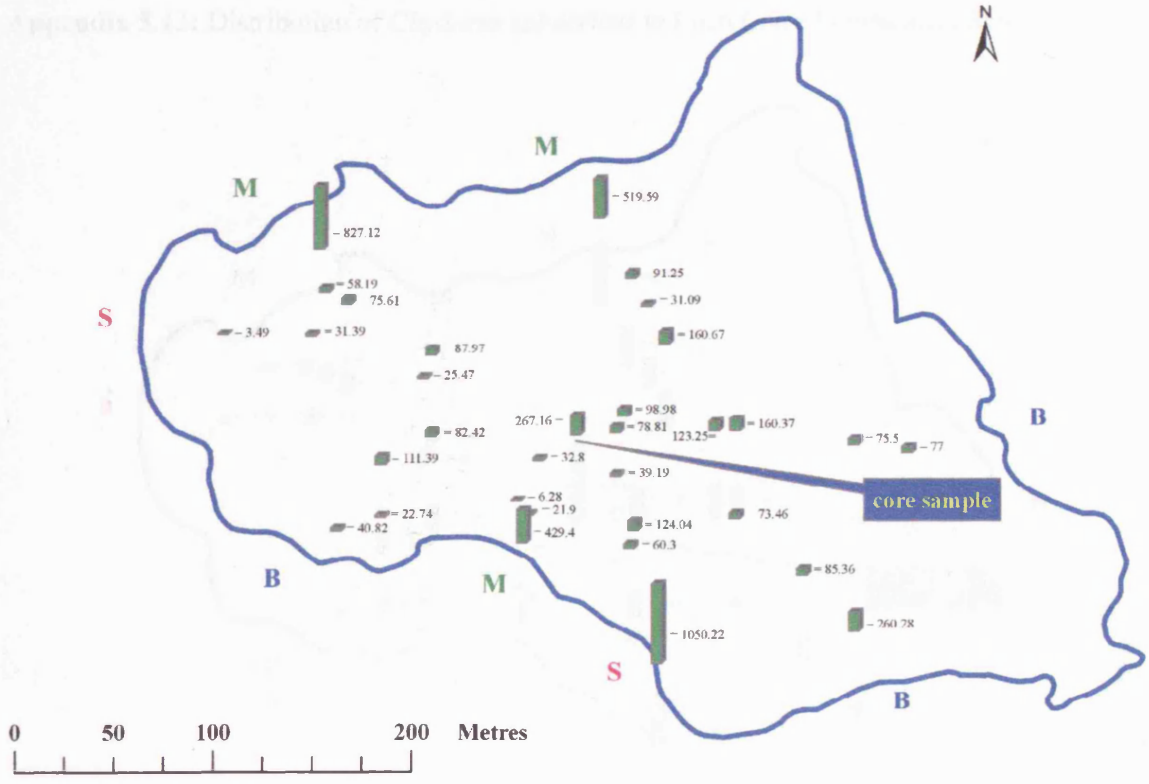
The concentration of remains, number per gram of dry weight sediment (gdw^{-1}), in each sampling point is presented as bars. The sampling points are the GPS coordinates, which are described details in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran are identified by M = Macrophyte, S = Sand and B= Boulder respectively. The distribution of the remains of *A. rustica* is patchy being highly concentrated (626-748 gdw^{-1}) around the core sample (core-top) with some high concentrations also occurring close to the southern shoreline. Unlike the remains of many other chydorid taxa, the remains of *A. rustica* are uniformly distributed in LCFR. The uniform distribution of the concentration of the remains of *A. rustica* is due to the preference of this taxon to a variety of substrata such as moss-covered stones and the vegetation beds (Fryer, 1993). All layers of shoreline substrata appear to have contributed to the deposition of the remains of this taxon in shallower depths and the remains at deeper depths were transported by wind-induced currents.

Appendix 5.11: Distribution of *Alona intermedia* in Loch Coire Fionnaraich, Scotland.



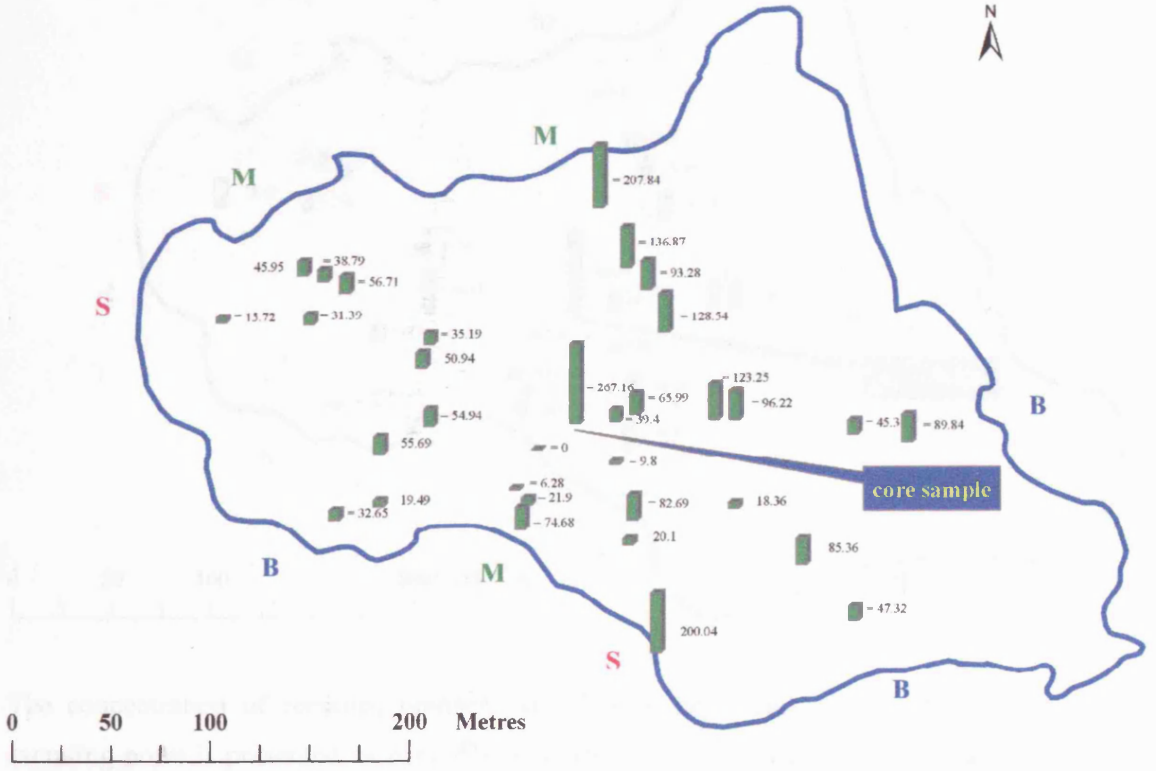
The concentration of remains, number per gram of dry weight sediment (gdw^{-1}), in each sampling point is presented as bars. The sampling points are the GPS coordinates, which are described details in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran are identified by M = Macrophyte, S = Sand and B= Boulder respectively. The distribution of the remains of *A. intermedia* is relatively uniform though the highest concentration (1000 gdw^{-1}) is in the sample T8-8m. The sandy habitat in the southeast corner has contributed higher concentration of the remains of this taxon to be deposited in shallower depths. The movement of the remains of *A. intermedia* in LCFR may also be influenced by the westerly wind-induced currents, though the deposition of the remains of this taxon in 8m depth suggests that caution should be taken while reconstructing the past environmental change.

Appendix 5.12: Distribution of *Graptoleberis testudinaria* in Loch Coire Fionnaraich, Scotland.



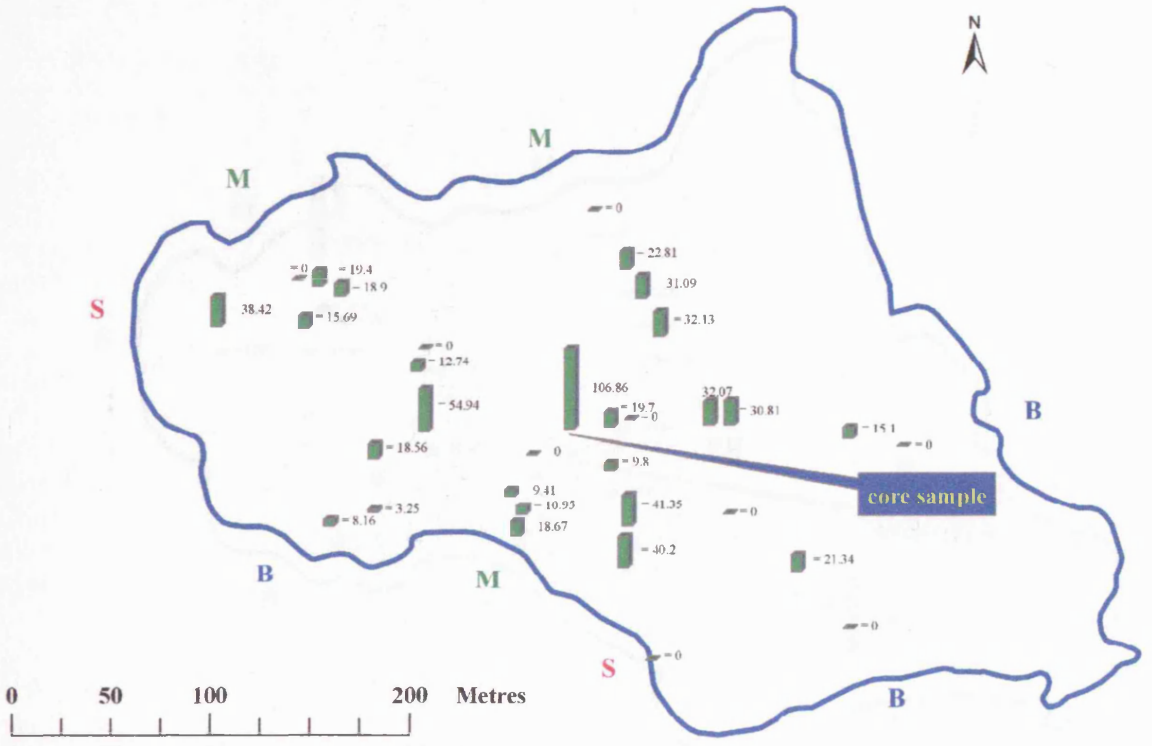
The concentration of remains, number per gram of dry weight sediment (gdw^{-1}), in each sampling point is presented as bars. The sampling points are the GPS coordinates, which are described details in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran are identified by M = Macrophyte, S = Sand and B= Boulder respectively. The highest concentration of the remains of *G. testudinaria* was close to the shoreline of the loch, where proximity to littoral habitats appears to be the most influential factor. The concentration of the remains in the core-top was however fairly low. *G. testudinaria* is a specialized species of chydorid Cladocera. Frey (1993) reported that this taxon can glide slowly over the surface of the emergent plants and browse on tiny particles available in the leaves. Thus the increased concentration of the remains of *A. intermedia* in macrophyte dominated shoreline habitat is not a surprise. However, an increased deposition of the remains of this taxon in sandy substrate in LCFR indicates that this may either have been transported by wind-induced currents or the patchy growth of small macrophytes on the sandy substrate during summer could have provided a significant habitat for this taxon. However, the latter cause may be the very much likely explanation for this taxon. The deposition of the remains of this taxon has also been reported very less frequently in bare substrata (Fryer, 1993). On the basis of remains of *G. testudinaria* is deposited in LCFR, it is very likely that a bias may occur while reconstructing the past environmental change of the lake where the deposition of the remains is often concentrated at the shore with dominant macrophytes.

Appendix 5.13: Distribution of *Chydorus sphaericus* in Loch Coire Fionnaraich, Scotland.



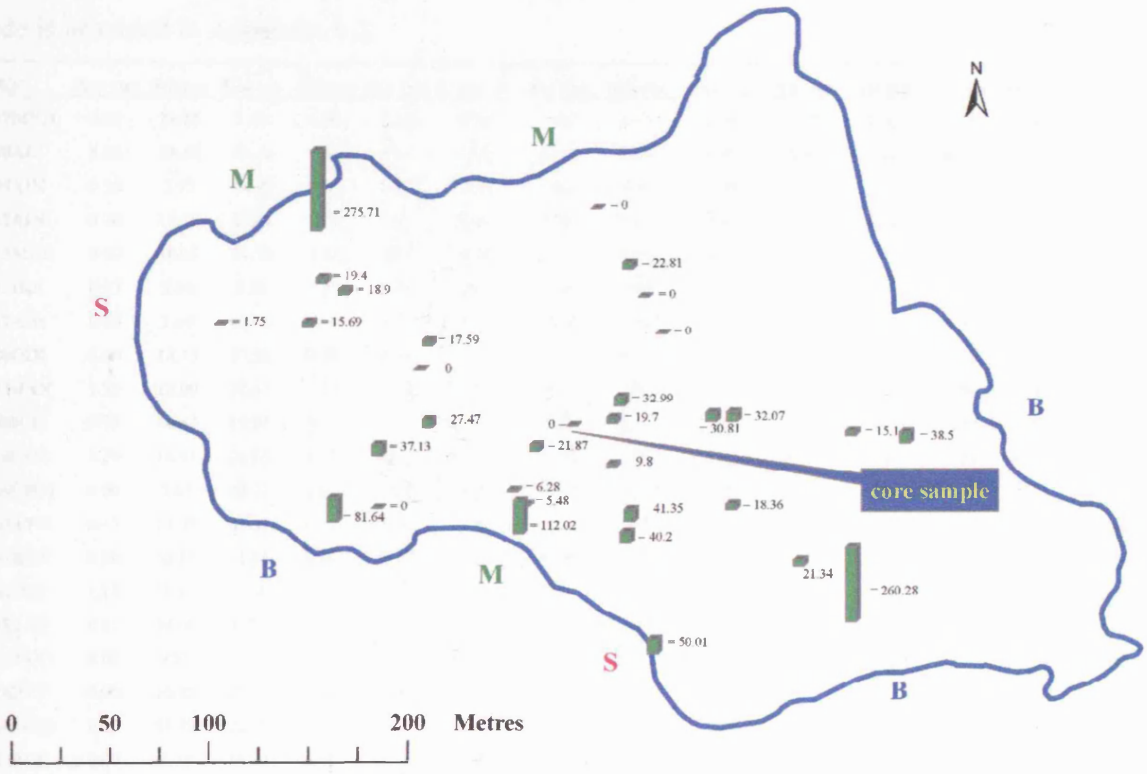
The concentration of remains, number per gram of dry weight sediment (gdw^{-1}), in each sampling point is presented as bars. The sampling points are the GPS coordinates, which are described details in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran are identified by M = Macrophyte, S = Sand and B= Boulder respectively. *C. sphaericus* occurred only in low concentrations in the loch. The highest concentration was in the core-top sample. *C. sphaericus* is very common to a variety of lakes in Europe, but the occurrence of this taxon in LCFR is not common. The transportation of the remains of this taxon appears to be influenced by easterly winds since the majority of remains are deposited towards the eastern side of the loch.

Appendix 5.14: Distribution of *Rhynchotalona falcata* in Loch Coire Fionnaraich, Scotland.



The concentration of remains, number per gram of dry weight sediment (gdw^{-1}), in each sampling point is presented as bars. The sampling points are the GPS coordinates, which are described details in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran are identified by M = Macrophyte, S = Sand and B= Boulder respectively. Remains of *R. falcata* are present only in low concentrations, the highest being in the core-top sample (89-105 gdw^{-1}). The distribution patterns show the influence of both habitat type, particularly sand, and lake morphometry. It is very interesting to note that the remains of *R. falcata* are not associated with the preferred habitat type (e.g. sand) of this taxon. The concentration of the remains of *R. falcata* is however high in the lake centre indicating that the remains associated with sand substrata would move towards the lake centre faster and reduce the biases in environmental reconstruction.

Appendix 5.15: Distribution of *Camptocercus rectirostris* in Loch Coire Fionnaraich, Scotland.



The concentration of remains, number per gram of dry weight sediment (gdw^{-1}), in each sampling point is presented as bars. The sampling points are the GPS coordinates, which are described details in Appendix 5.3 and Figure 5.1 respectively. The shoreline habitat types, from which each transect ran are identified by M = Macrophyte, S = Sand and B= Boulder respectively. *C. rectirostris* concentraions are very low. They were distributed mainly in two separate littoral locations, southeast and northwest corners of the loch close to boulders and macrophytyes. *C. rectirostris* is also associated with the habitats of sand, gravel, grit, rocks, clay or soft mud. Korhola (1999) recorded this taxon abundantly in bottom-epiphytic environment. The poor representation of this taxon in LCFR indicates that it may cause the biases in past environmental reconstruction. Because of poor occurrence of the remains, the concentration of this taxon is very low at the lake centre.

Appendix 6

Appendix 6.1: Cladocera assemblages (%) in selected training set sites. The table for species code is provided in Appendix 6.2.

LAKE	Dap spp	Bos lon	Bos cor	Gra tes	Eur lam	Cam rec	Acr har	Acr elo	Oxy ten	Alo rec	Alo gut	Alo cos	Alo rus	Alo int
L007MED	0.00	29.15	5.38	0.90	3.14	0.00	7.62	6.73	0.00	1.35	0.90	0.45	2.69	3.59
L008AIS	5.83	18.45	35.44	0.00	1.94	0.00	10.19	3.40	0.00	0.97	1.46	0.49	4.85	0.49
L009AIN	0.28	3.95	14.69	2.26	1.69	0.00	9.04	8.76	0.00	2.54	2.26	0.56	7.34	1.98
L011AIN	0.00	12.29	26.96	0.34	0.34	0.00	4.78	3.07	0.00	3.07	1.37	1.02	1.02	2.73
L013MED	0.00	0.44	11.56	1.33	0.00	0.44	12.44	5.33	0.00	0.89	5.78	0.00	5.33	2.22
L015IRE	0.87	3.04	1.30	0.87	4.78	0.00	7.39	3.48	0.00	4.78	3.91	1.74	18.70	3.48
L017AIR	0.00	1.69	47.46	0.00	1.27	0.00	19.49	4.66	0.00	2.12	2.12	0.00	2.97	0.00
L020OIR	0.00	14.15	37.56	0.98	0.49	0.00	6.34	3.90	0.00	0.98	2.44	0.49	5.37	1.46
L021HAN	1.30	12.99	32.47	1.30	4.33	0.00	8.23	9.96	0.00	2.16	3.03	0.00	3.46	0.43
L022ICH	0.93	14.42	19.07	0.47	0.47	0.93	9.77	4.19	0.00	2.79	2.79	0.93	5.58	1.40
L023DHE	1.39	14.81	26.85	4.17	0.93	1.39	11.11	1.39	0.00	1.85	1.85	0.00	0.93	3.70
L026ORM	0.00	3.65	45.21	1.83	0.91	0.00	13.24	8.22	0.00	3.20	0.91	0.00	2.74	0.00
L033ATN	0.15	13.35	68.55	0.74	1.34	2.08	3.56	0.15	0.00	1.19	0.45	0.00	0.89	0.00
L035RVT	0.00	33.18	11.66	0.00	0.90	0.45	1.35	0.45	0.00	1.79	0.90	0.00	1.79	0.90
L036SVT	1.19	15.81	5.14	0.79	12.25	6.72	20.16	0.00	0.00	9.09	1.58	0.40	3.16	1.19
L041KTJ	0.67	14.06	8.71	0.00	2.01	0.00	0.89	0.67	0.22	1.34	2.46	0.22	11.38	1.56
L044TVT	0.00	9.85	14.29	0.00	0.49	0.00	7.88	0.49	0.00	0.00	0.00	0.00	0.49	0.00
L046EVT	0.00	10.20	22.86	0.00	2.04	0.00	1.22	1.22	0.00	3.67	1.22	0.00	4.08	0.41
L048MED	0.39	33.33	22.35	3.53	1.18	2.35	3.53	1.18	0.00	5.10	1.18	0.00	2.35	2.75
L050SVT	0.00	7.44	16.90	2.21	3.22	12.27	8.65	1.61	0.00	1.21	1.21	0.00	2.21	0.20
L051MED	0.67	21.74	25.08	0.33	1.00	0.00	1.34	2.01	0.00	0.67	1.00	0.00	6.02	1.00
L054147	1.66	45.70	15.56	1.66	0.99	0.00	2.98	0.66	0.00	1.32	2.65	0.00	4.30	0.00
L055SVT	2.32	21.19	42.72	0.00	0.17	0.17	0.66	1.32	0.00	2.48	1.99	0.17	1.66	0.50
L056GVT	0.00	80.99	7.60	0.00	0.76	0.00	1.14	0.00	0.00	0.00	0.38	0.38	1.52	0.00
L057SVT	0.00	34.55	41.36	0.00	1.36	0.45	4.09	0.00	0.00	0.91	1.82	0.00	1.82	1.36
L058EVT	0.83	38.02	51.52	0.00	0.28	0.28	0.55	0.28	0.00	0.55	0.00	0.00	1.38	0.00
L060DTJ	6.94	0.00	0.46	0.93	0.93	0.00	9.72	1.39	0.93	2.31	8.33	1.85	13.89	1.39
L063SVT	0.00	66.09	14.78	0.00	1.30	0.87	2.61	0.87	0.00	0.43	1.30	0.00	1.30	0.00
L065AVT	2.48	47.99	8.05	0.93	0.31	0.93	3.10	0.00	0.00	0.31	1.24	0.31	4.95	0.00
L066MED	1.39	37.63	10.45	0.35	1.05	0.35	3.48	2.44	0.00	0.35	0.00	0.00	1.05	2.09
L069ØNN	1.30	66.23	13.95	0.19	0.37	0.28	0.37	0.37	0.00	0.93	1.02	0.28	1.58	0.47
L078ØNN	0.70	44.70	37.57	0.52	0.52	0.17	1.39	0.87	0.00	0.00	0.70	0.00	1.91	0.35
L081MED	0.00	87.34	6.46	0.00	0.52	0.00	0.52	0.78	0.00	0.00	0.52	0.00	1.29	0.00
L082MED	0.00	22.29	63.16	0.31	0.00	0.31	1.24	0.31	0.00	0.00	2.48	0.00	0.00	0.00
L084RNI	0.38	25.38	30.00	0.00	3.08	0.00	5.38	5.77	0.00	0.00	0.00	0.00	0.77	0.38
L088ØNN	0.46	3.67	12.39	3.67	1.38	0.46	10.09	3.21	0.00	1.83	4.59	1.83	10.55	0.00
L091ATN	0.84	28.27	27.85	9.28	0.84	0.00	5.06	0.42	0.00	0.42	0.84	0.00	0.00	0.00
L092ØNN	0.00	11.01	39.18	0.19	0.19	0.19	2.05	0.19	0.37	2.80	1.68	0.75	3.92	1.31
L093RNI	1.89	17.92	49.53	0.47	0.94	0.47	3.30	0.94	0.00	3.77	2.36	0.00	1.89	0.00
L095ØNN	8.10	43.83	21.55	0.18	0.37	0.18	1.66	0.37	0.00	2.21	2.21	0.00	4.60	0.55
L096ØNN	0.27	13.14	63.54	0.00	1.61	0.00	0.27	0.80	0.00	0.80	1.88	0.00	2.41	0.54
L097ØNN	0.40	69.48	7.63	0.00	2.01	0.00	3.61	0.80	0.00	0.80	0.00	0.40	1.61	0.80
L098ØNN	0.65	35.48	16.13	0.00	6.45	0.00	1.61	0.65	0.00	1.61	0.32	0.00	0.97	0.65
L103ØNN	1.10	14.59	62.65	0.11	0.11	0.00	0.88	0.44	0.00	0.99	0.99	0.00	0.99	0.99
L107MED	2.90	39.07	37.33	1.55	0.58	0.00	2.13	0.19	0.00	0.00	1.16	0.58	1.93	0.39
L109MED	2.67	24.67	3.67	0.50	0.83	0.00	2.33	0.83	0.00	0.50	3.17	0.00	11.00	1.33
L113ØNN	45.37	5.09	15.28	0.46	0.46	0.00	2.31	0.00	0.00	2.31	2.31	0.00	1.39	1.85
L114ØNN	4.10	28.02	38.04	0.46	0.23	0.00	2.28	0.46	0.00	0.68	3.19	0.23	4.10	0.46
L123TØL	7.80	0.00	59.60	1.20	0.80	0.20	1.80	0.00	0.00	1.00	1.80	0.00	2.80	1.00
L125ØNN	14.39	8.77	15.79	0.70	0.70	0.70	4.21	0.35	0.00	2.11	4.91	0.00	2.46	1.05

L131TØL	25.83	3.33	4.58	2.92	0.83	1.67	3.75	0.42	0.00	2.50	4.17	0.00	2.08	1.67
L134NET	7.83	19.22	27.76	1.42	0.71	0.00	2.85	1.78	0.36	0.00	4.63	0.36	1.07	0.00
L135MED	0.00	2.09	1.26	1.26	0.42	0.00	5.44	0.00	0.00	2.09	2.51	0.00	3.77	1.26
L138TØL	13.09	18.55	10.91	5.82	0.73	0.00	7.64	0.36	0.00	1.45	3.64	0.00	4.36	1.45
L144MED	0.00	0.00	6.64	0.00	0.00	0.00	16.61	7.38	0.00	0.00	0.00	0.00	0.00	0.00
L148ATN	0.00	0.00	68.78	0.49	0.00	1.95	1.46	1.46	0.00	2.44	0.98	0.00	0.00	0.00
L163NET	2.20	0.00	84.98	0.00	4.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
L166ERN	1.00	49.33	8.67	0.00	7.33	0.33	4.33	0.67	1.67	0.00	0.33	0.33	1.67	2.00
L169NET	0.00	18.84	28.02	0.00	0.97	0.00	23.19	2.90	0.00	0.00	0.48	0.00	2.42	0.00
L184MED	0.00	3.41	0.76	0.00	0.00	0.76	29.55	0.76	0.38	0.38	1.14	0.76	0.76	0.38
L186MED	0.00	17.05	26.27	0.00	3.69	0.00	12.44	6.45	0.00	0.46	0.46	2.76	0.46	1.38
L188MED	0.00	2.37	22.27	0.00	8.53	0.00	19.91	0.00	0.00	5.69	0.00	0.00	0.00	4.27
L190MED	0.00	10.58	5.77	0.00	5.29	0.48	13.46	1.44	0.00	0.00	0.48	0.48	0.00	1.44
L193MED	0.00	1.35	20.20	0.00	5.72	0.00	22.90	4.71	0.00	0.67	0.00	0.00	0.00	0.34
L198ØRN	0.53	38.83	11.97	0.27	0.00	1.06	2.13	0.80	0.00	2.39	1.86	0.27	2.39	0.53
L204ØEN	1.01	47.74	13.57	1.01	0.00	0.00	6.03	0.50	0.00	0.50	1.01	1.01	3.02	2.01
L221IDH	4.06	26.56	12.81	0.63	1.56	0.00	5.31	6.56	0.31	3.75	0.94	0.00	4.69	1.25
L223ICH	0.21	28.57	47.76	1.06	1.28	0.00	1.91	1.49	0.00	0.64	0.64	0.00	2.98	1.49

LAKE	Alo aff	Alo qua	Alo nan	Alo ros	Alo exi	Alo exc	Mon dis	Chy sph	Chy pig	Chy glo	Pleu adu	Ple tri	Sid cry	Rhy fal
L007MED	8.52	1.35	6.73	0.00	0.00	5.38	0.00	4.04	12.11	0.00	0.00	0.00	0.00	0.00
L008AIS	3.40	0.00	8.25	0.00	0.00	0.00	0.00	0.49	3.40	1.45	0.00	0.00	0.00	0.00
L009AIN	2.54	0.56	22.03	0.28	0.00	3.39	0.85	4.52	9.89	0.00	0.00	0.00	0.56	0.00
L011AIN	3.75	0.00	29.01	0.00	0.00	5.12	0.00	2.73	1.71	0.00	0.00	0.00	0.34	0.34
L013MED	9.78	0.44	31.56	0.00	0.00	4.89	0.44	3.11	3.11	0.00	0.00	0.00	0.44	0.44
L015IRE	5.22	1.30	19.57	0.00	0.00	2.17	0.87	6.96	9.13	0.43	0.00	0.00	0.00	0.00
L017AIR	5.51	0.00	5.51	0.00	0.00	0.85	0.00	0.42	5.93	0.00	0.00	0.00	0.00	0.00
L020OIR	3.41	0.00	6.83	0.00	0.00	5.37	0.00	3.90	5.85	0.00	0.00	0.00	0.49	0.00
L021HAN	4.76	0.43	4.76	0.00	0.00	0.87	2.60	1.30	5.19	0.00	0.00	0.00	0.00	0.00
L022ICH	3.72	3.26	8.37	1.39	0.00	4.65	0.00	6.98	7.44	0.00	0.00	0.00	0.00	0.00
L023DHE	12.04	0.93	6.02	0.00	0.00	4.17	0.00	2.31	4.17	0.00	0.00	0.00	0.00	0.00
L026ORM	8.22	0.91	0.46	0.00	0.00	3.65	0.00	6.39	0.00	0.00	0.00	0.00	0.46	0.00
L033ATN	2.52	0.45	3.12	0.00	0.00	0.59	0.00	0.59	0.00	0.00	0.00	0.00	0.30	0.00
L035RVT	19.73	2.24	6.28	0.00	0.00	0.90	0.00	8.52	8.97	0.00	0.00	0.00	0.00	0.00
L036SVT	8.30	4.35	6.32	0.00	0.00	0.00	0.00	1.58	1.58	0.00	0.00	0.00	0.40	0.00
L041KTJ	7.81	1.12	37.50	0.00	0.00	1.34	0.00	6.92	0.22	0.00	0.00	0.22	0.67	0.00
L044TVT	0.00	0.00	42.86	0.00	0.00	4.93	1.48	16.26	0.99	0.00	0.00	0.00	0.00	0.00
L046EVT	31.84	0.82	4.49	0.00	0.00	0.41	0.00	2.45	12.65	0.00	0.00	0.00	0.00	0.00
L048MED	5.88	0.00	5.88	0.00	0.00	0.78	0.00	5.88	1.96	0.00	0.00	0.00	0.39	0.00
L050SVT	6.84	0.40	8.85	0.00	0.20	11.07	0.40	8.65	5.03	0.00	0.00	0.00	0.80	0.00
L051MED	22.41	0.33	2.01	0.00	0.00	0.33	0.67	7.02	5.02	0.00	0.00	1.00	0.33	0.00
L054147	6.95	0.99	8.61	0.00	0.00	2.98	0.00	1.32	0.99	0.33	0.00	0.00	0.33	0.00
L055SVT	5.96	0.17	14.07	0.00	0.00	2.32	0.00	0.66	0.99	0.00	0.00	0.00	0.33	0.00
L056GVT	0.00	0.00	4.18	0.00	0.00	1.52	0.00	0.76	0.38	0.00	0.00	0.00	0.38	0.00
L057SVT	2.73	0.00	4.09	0.00	0.00	0.00	0.00	2.27	0.91	0.00	1.36	0.00	0.00	0.00
L058EVT	0.83	1.10	2.20	0.00	0.00	1.10	0.00	0.55	0.28	0.00	0.00	0.00	0.28	0.00
L060DTJ	5.09	0.00	30.56	0.00	0.00	7.87	1.39	3.24	1.85	0.00	0.46	0.00	0.00	0.00
L063SVT	1.30	0.00	3.48	0.43	0.00	0.00	0.43	1.74	1.30	0.00	0.00	0.87	0.87	0.00
L065AVT	2.48	0.00	12.38	0.00	0.31	2.79	0.00	7.74	2.17	0.00	0.62	0.00	0.62	0.00
L066MED	14.98	5.57	6.97	0.00	0.00	1.05	0.00	8.71	1.39	0.00	0.35	0.00	0.00	0.00
L069ØNN	2.33	0.00	6.98	0.00	0.00	0.93	0.00	1.40	0.09	0.09	0.19	0.00	0.47	0.00
L078ØNN	2.09	0.00	5.04	0.00	0.00	1.57	0.00	0.87	0.87	0.00	0.00	0.00	0.17	0.00
L081MED	0.52	0.26	0.52	0.26	0.00	0.26	0.00	0.52	0.00	0.00	0.00	0.00	0.26	0.00
L082MED	0.93	0.00	3.72	0.00	0.00	0.31	0.00	3.72	0.62	0.31	0.31	0.00	0.00	0.00
L084RNI	2.69	0.00	5.77	0.00	0.00	5.38	0.38	11.92	2.31	0.00	0.00	0.00	0.00	0.00
L088ØNN	1.83	0.00	19.72	0.46	0.00	5.96	0.46	8.72	6.88	0.00	0.00	0.00	0.46	1.37
L091ATN	11.81	1.27	5.91	0.00	0.00	1.27	0.00	5.06	0.00	0.00	0.00	0.00	0.84	0.00

L092ØNN	20.34	0.37	5.60	0.00	0.00	5.22	0.00	2.43	2.24	0.00	0.00	0.00	0.00	0.00
L093RNI	1.89	0.00	8.02	0.00	0.00	4.25	0.00	0.94	0.94	0.00	0.00	0.00	0.47	0.00
L095ØNN	1.84	0.55	5.89	0.00	0.00	1.66	0.00	2.03	1.47	0.00	0.00	0.00	0.18	0.00
L096ØNN	4.02	0.00	4.29	0.00	0.00	1.34	0.00	2.41	1.34	0.00	0.80	0.00	0.54	0.00
L097ØNN	2.41	0.40	3.21	0.00	0.00	2.41	0.00	3.61	0.00	0.00	0.00	0.40	0.00	0.00
L098ØNN	6.13	0.32	16.13	0.00	0.00	5.48	0.32	6.13	0.97	0.00	0.00	0.00	0.00	0.00
L103ØNN	4.97	0.11	5.97	0.00	0.00	2.21	0.00	1.10	1.66	0.00	0.00	0.00	0.11	0.00
L107MED	0.77	0.00	5.42	0.00	0.39	1.55	0.00	1.93	0.77	0.00	0.77	0.00	0.19	0.39
L109MED	7.33	0.17	32.00	0.00	0.00	2.50	0.00	3.83	1.33	0.00	0.00	0.00	1.00	0.17
L113ØNN	3.24	0.00	12.04	0.00	0.00	4.63	0.00	1.85	0.46	0.00	0.00	0.00	0.46	0.00
L114ØNN	2.05	0.00	9.11	0.00	0.00	3.42	0.00	1.59	0.46	0.00	0.23	0.00	0.46	0.00
L123TØL	1.80	0.20	16.00	0.00	0.00	2.20	0.00	1.00	0.20	0.20	0.00	0.00	0.20	0.00
L125ØNN	1.75	0.35	28.77	0.00	0.00	2.46	0.00	9.82	0.35	0.00	0.00	0.00	0.00	0.00
L131TØL	2.92	0.42	32.50	0.00	0.00	3.75	0.00	4.58	1.25	0.00	0.00	0.00	0.42	0.00
L134NET	1.07	0.00	20.28	0.00	1.07	4.98	0.00	3.20	0.71	0.00	0.00	0.00	0.71	0.00
L135MED	4.18	0.00	55.65	0.00	0.00	7.95	0.00	6.28	2.09	0.00	0.00	0.00	3.35	0.42
L138TØL	3.27	0.36	20.00	0.00	0.00	2.18	0.00	5.09	0.36	0.00	0.00	0.00	0.36	0.00
L144MED	50.92	1.11	14.02	0.00	0.00	2.95	0.00	0.37	0.00	0.00	0.00	0.00	0.00	0.00
L148ATN	0.98	0.00	0.98	0.00	0.00	7.80	0.00	10.24	1.95	0.00	0.00	0.00	0.49	0.00
L163NET	0.00	0.00	1.10	0.00	0.00	0.00	0.00	5.86	0.73	0.00	0.37	0.00	0.00	0.00
L166ERN	5.67	0.67	8.33	0.00	0.00	1.67	0.00	3.67	1.33	0.00	0.00	0.33	0.33	0.00
L169NET	0.00	0.00	2.42	0.00	0.00	1.45	0.00	19.32	0.00	0.00	0.00	0.00	0.00	0.00
L184MED	6.44	0.00	32.95	0.00	0.38	3.79	0.00	16.67	0.76	0.00	0.00	0.00	0.00	0.00
L186MED	0.46	0.00	25.81	0.00	0.00	0.46	0.00	0.92	0.46	0.46	0.00	0.00	0.00	0.00
L188MED	0.00	23.22	0.00	0.00	0.00	0.95	0.00	12.80	0.00	0.00	0.00	0.00	0.00	0.00
L190MED	1.44	0.00	51.44	0.00	0.00	1.44	0.00	3.85	0.96	0.48	0.48	0.00	0.00	0.00
L193MED	0.00	0.00	12.46	0.00	0.00	0.00	0.00	30.64	0.00	0.00	0.67	0.00	0.00	0.00
L198ØRN	2.66	0.53	22.34	0.00	0.00	7.71	0.00	3.19	0.27	0.00	0.00	0.00	0.00	0.00
L204ØEN	1.51	0.00	6.03	0.00	0.00	5.53	0.00	8.54	0.50	0.00	0.00	0.00	0.00	0.00
L221IDH	4.69	1.25	10.63	0.00	0.00	1.25	0.94	5.31	5.63	0.00	1.25	0.00	0.63	0.00
L223ICH	0.64	0.43	2.98	0.00	0.00	0.85	3.19	1.06	1.91	0.00	0.00	0.00	0.43	0.43

Appendix 6.2: Abbreviation of cladoceran species used in the training set.

Species code	Scientific name
Dap spp	*Daphnia spp*
Bos lon	*Bosmina longispina*
Bos cor	*Bosmina coregoni*
Bos lngr	*Bosmina longirostris*
Gra tes	*Graptoleberis testudinaria*
Eur lam	*Eurycercus lamellatus*
Cam rec	*Camptocercus rectirostris*
Acr har	*Acroperus harpae*
Acr elo	*Acroperus elongatus*
Oxy ten	*Oxyurella tenuicaudis*
Alo rec	*Alona rectangula*
Alo gut	*Alona guttata*
Alo cos	*Alona costata*
Alo rus	*Alona rustica*
Alo int	*Alona intermedia*
Alo aff	*Alona affinis*
Alo qua	*Alona quadrangularis*
Alo nan	*Alonella nana*
Alo ros	*Alonella rostrata*
Alo exi	*Alonella exigua*
Alo exc	*Alonella excisa*
Mon dis	*Monospilus dispar*
Chy sph	*Chydorus sphaericus*
Chy pig	*Chydorus piger*
Chy glo	*Chydorus globosus*
Ple adu	*Pleuroxus aduncus*
Ple tri	*Pleuroxus trigonells*
Sid cry	*Sida crystallina*
Rhy fal	*Rhynchotalona falcata*

Appendix 6.3: Estimated Weighted Averaging (WA) of mean January air temperature optima (Opt. ^{0}C) and tolerance (Tol ^{0}C) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway.

Species	Optima (^{0}C)	Tolerance ($\pm^0$C)	Model
Daphnia spp	-3.46	3.06	IV
Bosmina longispina	-3.41	3.36	I
Bosmina coregoni	-3.61	3.93	I
Graptoleberis testudinaria	-1.59	2.71	II increasing
Eurycercus lamellatus	-3.87	4.28	II decreasing
Camptocercus rectirostris	-2.40	3.26	II increasing
Acroperus harpae	-3.37	4.04	I
Acroperus elongatus	-2.72	3.81	I
Alona rectangula	-2.64	3.75	I
Alona guttata	-2.48	3.14	IV
Alona costata	-2.64	3.41	I
Alona rustica	-2.50	3.41	I
Alona intermedia	-3.18	4.02	I
Alona affinis	-2.87	3.32	I
Alona quadrangularis	-3.97	5.01	II decreasing
Alonella nana	-3.35	3.43	I
Alona excisa	-3.36	3.82	I
Monospilus dispar	-1.29	3.48	II increasing
Chydorus sphaericus	-4.10	4.24	II decreasing
Chydorus piger	-2.07	3.32	II increasing
Pleuroxus aduncus	-4.16	3.66	I
Sida crystallina	-2.61	3.32	I
Rhynchotalona falcata	-1.08	2.47	I

Appendix 6.4: Estimated Weighted Averaging (WA) of precipitation optima (Opt. mm) and tolerance (Tol mm) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway are presented in HOF models.

Species	Optima (mm)	Tolerance (±mm)	Model
Daphnia spp	1488.685	555.7157	IV
Bosmina longispina	1695.636	668.03	I
Bosmina coregoni	1611.52	653.5952	I
Graptoleberis testudinaria	1782.719	515.2933	IV
Eurycercus lamellatus	1529.663	691.4144	I
Camptocercus rectirostris	1760.346	540.2776	I
Acroperus harpae	1537.555	665.6288	I
Acroperus elongatus	1622.202	626.5826	I
Alona rectangula	1690.196	580.0996	I
Alona guttata	1716.991	581.6364	I
Alona costata	1602.476	685.1671	I
Alona rustica	1720.996	580.4041	I
Alona intermedia	1528.543	643.3044	I
Alona affinis	1653.946	604.3519	I
Alona quadrangularis	1560.448	684.4023	I
Alonella nana	1519.04	636.9587	I
Alona excisa	1560.52	636.0039	I
Monospilus dispar	1800.073	556.2567	I
Chydorus sphaericus	1463.982	651.9859	II decreasing
Chydorus piger	1764.572	585.1576	I
Pleuroxus aduncus	1496.958	762.9438	I
Sida crystallina	1722.694	569.2258	I
Rhynchotalona falcata	1721.36	513.3018	I

Appendix 6.5: Estimated Weighted Averaging (WA) of Ca optima (Opt. μeql^{-1}) and tolerance (Tol μeql^{-1}) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway.

Species	Optima (μeql^{-1})	Tolerance ($\pm\mu eql^{-1}$)	Model
Daphnia spp	89.671	52.8	II increasing
Bosmina longispina	69.7405	27.7535	I
Bosmina coregoni	69.3698	29.1742	II decreasing
Graptoleberis testudinaria	81.6091	45.9773	I
Eurycercus lamellatus	68.881	29.6317	I
Camptocercus rectirostris	71.6568	41.6373	I
Acroperus harpae	70.6324	32.0054	I
Acroperus elongatus	65.5309	26.6259	I
Alona rectangula	70.4297	36.8332	I
Alona guttata	74.1993	39.8519	I
Alona castata	69.4596	23.3416	IV
Alona rustica	70.7569	34.6045	I
Alona intermedia	75.1917	38.3873	I
Alona affinis	70.7263	33.1111	I
Alona quadrangularis	70.3375	33.5406	I
Alonella nana	76.5139	38.6124	I
Alona excisa	74.4551	35.5339	I
Monospilus dispar	51.6444	13.6796	II decreasing
Chydorus sphaericus	73.1967	32.7015	II increasing
Chydorus piger	64.7335	31.6555	I
Pleuroxus aduncus	63.6561	21.1749	I
Sida crystallina	77.2522	38.3526	I
Rhynchotalona falcata	69.9246	30.7104	I

Appendix 6.6: Estimated Weighted Averaging (WA) of conductivity optima (Opt. µS/cm) and tolerance (Tol. µS/cm) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway.

Species	Optima (μScm^{-1})	Tolerance ($\pm(\mu Scm^{-1})$)	Model
Daphnia spp	27.49	18.86	I
Bosmina longispina	22.63	11.96	V
Bosmina coregoni	23.18	12.07	I
Graptoleberis testudinaria	30.46	14.66	IV
Eurycercus lamellatus	24.62	14.88	I
Camptocercus rectirostris	26.50	17.66	I
Acroperus harpae	26.52	14.99	I
Acroperus elongatus	25.29	12.82	I
Alona rectangula	25.65	13.27	I
Alona guttata	26.06	14.66	I
Alona costata	25.90	13.69	I
Alona rustica	24.05	12.30	I
Alona intermedia	27.11	15.22	II increasing
Alona affinis	24.18	13.52	I
Alona quadrangularis	24.09	12.17	I
Alonella nana	27.14	16.89	I
Alona excisa	25.33	14.42	I
Monospilus dispar	23.67	10.02	I
Chydorus sphaericus	25.39	14.57	I
Chydorus piger	24.77	13.13	I
Pleuroxus aduncus	25.30	18.09	I
Sida crystallina	25.60	14.21	I
Rhynchotalona falcata	28.23	9.80	I

Appendix 6.7: Estimated Weighted Averaging (WA) of Mg optima (μeql^{-1}) and tolerance (Tol. μeql^{-1}) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway.

Species	Optima (μeql^{-1})	Tolerance ($\pm\mu eql^{-1}$)	Model
Daphnia spp	39.31	23.68	I
Bosmina longispina	34.94	21.42	I
Bosmina coregoni	36.27	20.38	I
Graptoleberis testudinaria	45.12	19.33	IV
Eurycercus lamellatus	40.66	29.28	I
Camptocercus rectirostris	41.12	28.44	I
Acroperus harpae	43.30	27.30	I
Acroperus elongatus	41.25	23.85	I
Alona rectangula	40.70	19.37	I
Alona guttata	40.04	21.78	I
Alona costata	41.39	26.55	I
Alona rustica	37.08	17.63	I
Alona intermedia	43.46	26.75	II
Alona affinis	37.49	21.32	I
Alona quadrangularis	39.20	20.14	I
Alonella nana	43.06	29.62	I
Alona excisa	39.69	22.63	I
Monospilus dispar	39.81	18.42	I
Chydorus sphaericus	40.73	24.97	I
Chydorus piger	39.87	22.16	I
Pleuroxus aduncus	44.98	41.55	I
Sida crystallina	38.56	19.73	IV
Rhynchotalona falcata	44.59	14.99	I

Appendix 6.8: Estimated Weighted Averaging (WA) of Na optima (μeql^{-1}) and tolerance (Tol. μeql^{-1}) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway.

Species	Optima (μeql^{-1})	Tolerance ($\pm\mu eql^{-1}$)	Model
Daphnia spp	115.31	90.54	I
Bosmina longispina	96.66	74.05	I
Bosmina coregoni	102.51	73.62	I
Graptoleberis testudinaria	143.54	74.88	IV
Eurycercus lamellatus	113.44	90.72	I
Camptocercus rectirostris	119.23	96.30	I
Acroperus harpae	124.83	87.70	I
Acroperus elongatus	123.92	82.47	I
Alona rectangula	118.99	73.12	I
Alona guttata	119.13	77.72	I
Alona costata	122.70	83.01	I
Alona rustica	109.21	68.48	I
Alona intermedia	125.48	87.17	II increasing
Alona affinis	108.32	78.80	I
Alona quadrangularis	106.55	71.96	I
Alonella nana	122.68	94.45	I
Alona excisa	112.55	81.12	I
Monospilus dispar	125.89	71.87	I
Chydorus sphaericus	112.71	83.95	I
Chydorus piger	118.83	77.40	I
Pleuroxus aduncus	115.37	119.95	I
Sida crystallina	114.01	76.10	I
Rhynchotalona falcata	133.63	45.20	I

Appendix 6.9: Estimated Weighted Averaging (WA) of Cl optima (μeql^{-1}) and tolerance (Tol. μeql^{-1}) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway.

Species	Optima (μeql^{-1})	Tolerance ($\pm\mu eql^{-1}$)	Model
Daphnia spp	119.88	126.97	I
Bosmina longispina	88.24	91.22	I
Bosmina coregoni	96.22	88.54	I
Graptoleberis testudinaria	143.65	101.49	IV
Eurycercus lamellatus	110.36	112.15	I
Camptocercus rectirostris	113.02	123.15	I
Acroperus harpae	122.93	108.68	I
Acroperus elongatus	122.09	100.06	I
Alona rectangula	115.85	93.35	I
Alona guttata	115.74	101.85	I
Alona costata	115.10	101.98	I
Alona rustica	102.89	87.19	I
Alona intermedia	125.91	111.49	II decreasing
Alona affinis	103.90	96.08	I
Alona quadrangularis	103.77	89.99	I
Alonella nana	122.71	120.68	I
Alona excisa	108.72	101.91	I
Monospilus dispar	120.61	83.36	I
Chydorus sphaericus	108.75	103.50	I
Chydorus piger	114.75	95.88	I
Pleuroxus aduncus	112.03	150.59	I
Sida crystallina	110.57	98.62	I
Rhynchotalona falcata	126.07	54.62	I

Appendix 6.10: Estimated Weighted Averaging (WA) of K optima (Opt. μeql^{-1}) and tolerance (Tol μeql^{-1}) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway.

Species	Optima (μeql^{-1})	Tolerance ($\pm\mu eql^{-1}$)	Models
Daphnia spp	10.36	5.49	II increasing
Bosmina longispina	8.15	3.84	I
Bosmina coregoni	8.21	4.23	I
Graptoleberis testudinaria	9.34	5.08	I
Eurycercus lamellatus	7.68	3.92	I
Camptocercus rectirostris	8.29	5.18	I
Acroperus harpae	7.80	4.36	I
Acroperus elongatus	7.03	3.89	I
Alona rectangula	8.38	4.46	I
Alona guttata	8.72	4.66	I
Alona costata	8.54	3.72	I
Alona rustica	8.13	4.23	I
Alona intermedia	8.10	4.53	I
Alona affinis	7.56	4.48	I
Alona quadrangularis	7.01	4.26	I
Alonella nana	8.68	4.74	I
Alona excisa	8.23	4.70	I
Monospilus dispar	6.47	2.12	I
Chydorus sphaericus	7.88	4.30	I
Chydorus piger	7.48	4.03	I
Pleuroxus aduncus	8.50	3.84	I
Sida crystallina	8.68	5.00	I
Rhynchotalona falcata	8.83	5.49	I

Appendix 6.11: Estimated Weighted Averaging (WA) of Abs-250 optima (Opt.) and tolerance (Tol) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway.

Species	Optima	Tolerance (±)	Models
Daphnia spp	0.17	0.18	I
Bosmina longispina	0.18	0.21	I
Bosmina coregoni	0.14	0.16	II decreasing
Graptoleberis testudinaria	0.17	0.20	I
Eurycercus lamellatus	0.12	0.09	I
Camptocercus rectirostris	0.15	0.11	I
Acroperus harpae	0.13	0.18	I
Acroperus elongatus	0.13	0.15	I
Alona rectangula	0.15	0.16	I
Alona guttata	0.17	0.17	I
Alona costata	0.18	0.28	I
Alona rustica	0.17	0.18	I
Alona intermedia	0.16	0.21	I
Alona affinis	0.14	0.15	I
Alona quadrangularis	0.11	0.08	II decreasing
Alonella nana	0.15	0.16	I
Alona excisa	0.16	0.21	I
Monospilus dispar	0.13	0.09	V
Chydorus sphaericus	0.14	0.20	I
Chydorus piger	0.14	0.14	I
Pleuroxus aduncus	0.15	0.15	I
Sida crystallina	0.16	0.11	I
Rhynchotalona falcata	0.14	0.09	I

Appendix 6.12: Estimated Weighted Averaging (WA) of Al-NL optima (Opt. μgl^{-1}) and tolerance (Tol (μgl^{-1}) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway.

Species	Optima (μgl^{-1})	Tolerance ($\pm(\mu gl^{-1})$	Models
Daphnia spp	28.90	35.74	I
Bosmina longispina	34.13	42.67	I
Bosmina coregoni	24.92	33.34	II decreasing
Graptoleberis testudinaria	31.87	39.36	I
Eurycercus lamellatus	18.65	19.20	II decreasing
Camptocercus rectirostris	31.35	32.94	I
Acroperus harpae	23.05	35.07	I
Acroperus elongatus	21.87	30.84	I
Alona rectangula	26.69	35.27	I
Alona guttata	29.65	35.13	I
Alona costata	31.69	53.42	I
Alona rustica	29.93	36.93	I
Alona intermedia	27.09	41.41	I
Alona affinis	23.58	31.56	I
Alona quadrangularis	18.92	25.78	I
Alonella nana	25.60	34.99	I
Alona excisa	29.35	42.59	I
Monospilus dispar	21.70	17.00	V
Chydorus sphaericus	25.20	39.07	I
Chydorus piger	23.96	29.16	I
Pleuroxus aduncus	20.91	25.50	I
Sida crystallina	27.78	22.63	I
Rhynchotalona falcata	24.88	13.88	I

Appendix 6.13: Estimated Weighted Averaging (WA) of Al-L optima (Opt. μgl^{-1}) and tolerance (Tol μgl^{-1}) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway.

Species	Optima ((μgl^{-1})	Tolerance ($\pm(\mu gl^{-1})$	Models
Daphnia spp	6.89	11.18	I
Bosmina longispina	7.75	12.16	I
Bosmina coregoni	5.75	10.00	I
Graptoleberis testudinaria	6.88	12.02	I
Eurycercus lamellatus	4.33	6.98	I
Camptocercus rectirostris	5.78	8.36	I
Acroperus harpae	6.25	10.64	II increasing
Acroperus elongatus	5.44	9.90	I
Alona rectangula	6.69	10.61	I
Alona guttata	7.51	11.34	I
Alona costata	7.11	13.30	I
Alona rustica	7.17	11.34	I
Alona intermedia	6.02	10.78	I
Alona affinis	7.34	11.28	I
Alona quadrangularis	5.90	10.12	I
Alonella nana	7.29	11.23	I
Alona excisa	7.82	12.68	I
Monospilus dispar	3.27	4.43	I
Chydorus sphaericus	6.02	10.76	I
Chydorus piger	5.15	9.03	I
Pleuroxus aduncus	5.51	8.15	I
Sida crystallina	7.19	9.67	I
Rhynchotalona falcata	6.81	8.75	I

Appendix 6.14: Estimated Weighted Averaging (WA) of alkalinity optima (Opt.μeql^{-1}) and tolerance (Tol μeql^{-1}) of the dominant cladoceran taxa in the 68 training set sites of Scotland and Norway.

Species	Optima (μeql^{-1})	Tolerance (±μeql^{-1})	Models
Daphnia spp	34.44	11.22	I
Bosmina longispina	33.19	9.57	I
Bosmina coregoni	32.51	10.12	I
Graptoleberis testudinaria	33.18	11.07	I
Eurycercus lamellatus	34.69	10.20	I
Camptocercus rectirostris	33.89	11.18	I
Acroperus harpae	33.37	9.99	I
Acroperus elongatus	33.11	9.95	I
Alona rectangula	32.76	10.50	I
Alona guttata	32.26	10.51	I
Alona costata	35.44	9.60	I
Alona rustica	33.01	10.31	I
Alona intermedia	35.43	10.93	I
Alona affinis	33.74	10.82	I
Alona quadrangularis	35.61	10.67	I
Alonella nana	33.58	10.23	I
Alona excisa	33.21	10.07	I
Monospilus dispar	30.35	8.96	I
Chydorus sphaericus	34.26	9.50	I
Chydorus piger	33.40	10.53	I
Pleuroxus aduncus	33.60	8.09	IV
Sida crystallina	32.32	10.12	I
Rhynchotalona falcata	26.78	8.30	I

Appendix 7

Appendix 7.1: Cladoceran zooplankton recovered in the sub-fossil assemblage of Loch Coire Fionnaraich, Scotland.

SN	Code	Cladoceran zooplankton species
1	*Dap spp*	*Daphnia* spp.
2	*Bos longs*	*Bosmina longispina*
3	*Bos cor*	*Bosmina coregoni*
4	*Gra tes*	*Graptoleberis testudinaria*
5	*Eur lam*	*Eurycercus lamellatus*
6	*Cam rec*	*Camptocercus rectirostris*
7	*Acr har*	*Acroperus harpae*
8	*Acr elo*	*Acroperus elongatus*
9	*Alo rec*	*Alona rectangula*
10	*Alo gut*	*Alona guttata*
11	*Alo rus*	*Alona rustica*
12	*Alo int*	*Alona intermedia*
13	*Alo aff*	*Alona affinis*
14	*Alo qua*	*Alona quadrangularis*
15	*Alo nan*	*Alonella nana*
16	*Alo exc*	*Alonella excisa*
17	*Mon dis*	*Monospilus dispar*
18	*Rhy fal*	*Rhynchotalona falcata*
19	*Chy sph*	*Chydorus sphaericus*
20	*Chy pig*	*Chydorus piger*
21	*Ple adu*	*Pleuroxus aduncus*
22	*Sid cry*	*Sida crystallina*
23	*Acc eme*	*Anchistropus emarginatus*
24	*Oxy ten*	*Oxyurella tenuicaudis*
25	*Kur lat*	*Kurzia latissima*
26	*Alo ros*	*Alonella rostrata*

Appendix 7.2: Monthly mean Central England Temperature (^{0}C) series. 1659-1973 and 2001 (www.met-office.gov.uk).

YEAR	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	AVG
1659	3	4	6	7	11	13	16	16	13	10	5	2	8.83
1660	0	4	6	9	11	14	15	16	13	10	6	5	9.08
1661	5	5	6	8	11	14	15	15	13	11	8	6	9.75
1662	5	6	6	8	11	15	15	15	13	11	6	3	9.5
1663	1	1	5	7	10	14	15	15	13	10	7	5	8.58
1664	4	5	5	8	11	15	16	16	13	9	6	4	9.33
1665	1	1	5	7	10	14	16	15	13	9	6	2	8.25
1666	4	5	6	8	11	15	18	17	14	11	6	3	9.83
1667	0	4	2	7	10	15	17	16	13	9	6	3	8.5
1668	5	5	5	8	10	14	16	16	14	10	6	5	9.5
1669	1	4	5	7	11	15	17	16	14	10	6	2	9
1670	3	1	5	8	11	14	16	16	14	10	6	3	8.92
1671	4	3.5	5	7.5	11.5	13.5	16	15.5	13.5	8.5	6	4	9.04
1672	1.5	1.5	5	7	12	16	15	14	11	11.5	6.5	4.5	8.79
1673	5	1.5	5.5	7	11	14.5	16	15.5	11.5	7.5	5	0.5	8.33
1674	5	2	1	7.5	11	13.5	14	13.5	10.5	9	6.5	3.5	8.08
1675	3	2	3	7	10.5	11.5	15	14.5	10.5	8	4.5	4.5	7.83
1676	5.5	5	5	7.5	10.5	18	16	16.5	12	7	3.5	-0.5	8.83
1677	3	3.5	7	7.5	10	13	18	15	13	8.5	4.5	2	8.75
1678	1.5	2	4	6.5	11	14.5	17	15	15	8.5	6	0.5	8.42
1679	1	1.5	4.5	7	12	15.5	16	17	13	11	3.5	2.5	8.71
1680	3.5	3.5	6	6.5	10.5	13	16	15	14.5	10.5	6.5	1	8.88
1681	0.5	1.5	4	8	10.5	14	15	16	14	11.5	6.5	3	8.71
1682	6	2	4.5	6.5	11.5	14	15	14.5	13	9.5	5.5	6	9
1683	3.5	2	5.5	9.5	11.5	16	16	13.5	13	6.5	4.5	0.5	8.46
1684	-3	1	3	6.5	13	15	16	15.5	12	11	3	4	7.92
1685	0.5	3.5	5	8.5	12.5	14.5	14	14.5	11.5	11.5	7	6.5	9.13
1686	6.5	6	7	8.5	12.5	15.5	17	14.5	13	9	6.5	6	10.13
1687	3.5	4.5	4.5	6.5	11	13	16	15	11	11	6	6	8.96
1688	3.5	1.5	3.5	5.5	10.5	13	16	15	12	7	4	3	7.83
1689	0.5	4.5	5	8	11	12	16	15.5	13	8	5	4.5	8.54
1690	4	4.5	4.5	8	9.5	13.5	16	15	13	8.5	6.5	4.5	8.92
1691	1	1	5	6.5	10	14.5	16	15.5	11	9	5	3.5	8.13
1692	2	0	4	7.5	9	13.5	15	15	11.5	6.5	5	3.5	7.71
1693	3	5	3	6.5	9	14.5	15	15	12	9.5	6	3	8.46
1694	0	5	3.5	7.5	9	13	15	13	10.5	7.5	5.5	2.5	7.67
1695	-1	0.5	3.5	5.5	9	13	14	13	11.5	9	5.5	4	7.25
1696	5.5	4.5	3.5	5.5	10.5	13	16	15.5	11.5	9	5.5	2.5	8.5
1697	1	0.5	5.5	7	11.5	13	16	14.5	12	9	4	2.5	8
1698	0	0.5	3.5	7.5	8.5	12	15	15	13	9	4	3.5	7.63
1699	3.4	3.4	3.9	6.4	10	14.4	17	15	13.3	9.4	5.6	3.6	8.8
1700	3.9	2.5	3.6	6.4	12	13.6	15	15	12.8	8.9	5	4.2	8.57
1701	2.8	2.5	2.8	4.7	10.9	14.2	18	16.1	14.7	7.5	6.4	3.6	8.71
1702	5	6.7	5.8	5.8	10.6	13.3	15	16.1	14.4	10	4.4	4.4	9.29
1703	2.2	3.9	5.6	8.3	11.9	13.9	16	16.1	10.6	7.8	7.2	5.1	9.06
1704	2	3.3	5.3	8.3	11.5	14.4	17	16.9	11.9	8.3	6.4	3.6	9.05
1705	2.8	3.9	4.4	7.8	11.2	12.2	16	17.5	11.9	8.9	3.9	4.4	8.71
1706	2.8	4.2	6.4	8.9	12.2	15.6	16	16.7	12.5	11.2	6.1	4.7	9.78
1707	3.5	3	5	8.5	11	16	17	16	14	8.5	6.5	3.5	9.38
1708	6	4	6.5	9.5	10.5	14	15	17	15	8.5	7	3	9.67

1709	-1.5	2	3	9	12	14.5	16	15.5	13.5	10	7.5	3.5	8.71
1710	2.5	3.5	6	6.5	11.5	14.5	15	15.5	13.5	9.5	8	7.5	9.46
1711	5	2	5.5	9.5	11	15.5	16	15	13	9.5	7	4	9.38
1712	3	4.5	5	7.5	11	15	16	15	13	9.5	6	4	9.13
1713	3	5.5	4.5	5.5	10.5	13.5	14	15	14	9.5	4.5	4	8.63
1714	4	5.5	5	7.5	10	14.5	18	15	13	10.5	6	4	9.42
1715	4	5	6.5	9.5	11	14	16	15	14	10.5	6.5	1.5	9.42
1716	-2	3	4.5	9	10.5	14	16	15.5	12.5	9.5	5.5	3	8.38
1717	4.5	2.5	4.5	7.5	11	14	15	15.5	13.5	9.5	5.5	5	9
1718	1.5	3	5.5	7.5	11	14.5	17	17	14.5	9.5	5.5	4.5	9.25
1719	3	4	5	7	11.5	15	18	17	14	9.5	6	3.5	9.46
1720	4.5	4	4	7.5	11	13	16	15	13.5	9	6	5.5	9.08
1721	4	2	3.5	8.5	9.5	14	16	16	14	9	6	4.5	8.88
1722	4	5	6	7.5	10.5	14	15	15	13.5	10	7.8	3.9	9.35
1723	1.1	4.4	7.5	8.9	11.7	15	15	15.6	13.3	11.1	7.5	5.8	9.77
1724	5.6	4.2	4.7	7.2	11.4	15.3	15	16.2	14.4	8.6	5.3	3.3	9.27
1725	4.4	3.3	5	8.1	10.8	12.2	14	13.3	12.8	9.4	6.9	3.9	8.66
1726	1.1	4.2	4.2	8.4	13.4	16.4	16	15.6	14.7	10.2	6.1	1.8	9.34
1727	4.2	5	5.1	9.2	13.6	14.9	17	16.9	14.4	10.8	4.7	3.6	9.94
1728	3.9	2.4	7.1	8.3	12.5	16.4	17	16	12.8	9.1	7.2	1.6	9.52
1729	1.2	2.3	2.8	7.1	10.3	15.1	17	15.7	16.6	10.1	8.1	5	9.26
1730	4.1	4.7	6.2	8.7	12.4	14	15	16.3	15.3	10.9	9.2	3.4	10.04
1731	1.9	2.2	6	6.8	12.1	15.6	16	16.7	15.3	12.3	7.8	5.2	9.85
1732	2.4	6.4	6.1	8.9	11.4	14.6	16	16.6	14.5	10.9	6.3	2.2	9.69
1733	6.9	6	5.9	0	11.2	15.2	18	16.1	12.8	9.1	6.5	7.6	10.47
1734	4.3	6.4	8.1	9.3	11.1	14.1	16	16.2	13.3	8.4	6.2	4	9.8
1735	4.4	4	5.8	8.9	10.9	13.3	15	16.2	14.2	10.3	6.3	5.4	9.54
1736	6.4	3.1	6.9	8.6	10.6	15.7	16	17.8	14.4	10.4	6.9	6.4	10.3
1737	6.2	4.2	6.1	8.8	12.5	15.9	17	13.8	14.2	8.9	6.1	4.9	9.92
1738	4.6	4.6	5.5	9.9	11.4	14.2	16	16	12.5	10.2	6.3	6.1	9.81
1739	4	6.8	5.8	6.7	11.6	15.2	16	14.7	13.1	9.6	3.7	3.2	9.2
1740	-2.8	1.6	3.9	6.4	8.6	12.8	15	14.7	14	5.3	3.3	2.2	6.84
1741	1.7	4.4	4.2	7.1	9.3	15.2	16	16.7	14.7	11	7.8	3.9	9.3
1742	1.9	3.6	4.1	6.6	10.6	15	16	15.8	12.2	9.2	4.4	1.1	8.36
1743	3.6	5.4	5.3	5.4	13.3	15.6	15	16.9	14.2	8.9	9.3	4.9	9.81
1744	1.4	2.9	4.8	6.7	10.8	14.4	16	15.4	12.8	9.4	6.9	3.5	8.78
1745	3.8	2.3	4.4	7.5	11.4	12.2	16	15	14.2	10.3	5.8	2.7	8.81
1746	2.5	1.4	3.1	6.9	12.8	14.3	16	15.9	14.2	7.8	3.3	5.3	8.61
1747	3.3	5.8	2.5	8.1	12.2	14.7	17	18.3	14.4	9.4	6.9	5.3	9.82
1748	2.5	1.8	1.8	6.3	10.4	14.8	15	15.8	14.2	9.2	7.1	6	8.77
1749	5.3	3.6	5.3	6.8	12.3	11.9	17	15.6	13.8	10.1	6.7	4.7	9.44
1750	4	6.7	8.2	7.7	10.7	14.2	17	15	15.2	9.2	4	4.2	9.69
1751	4	1.5	6.2	7.1	9.3	14.9	15	14.6	12.6	8.3	4.3	3	8.42
1752	3.2	3.1	5.6	6.8	10.3	14.8	16	15.7	13.9	10.6	6.5	4.2	9.19
1753	2.2	3.6	6	7.5	12.1	14.6	15	15.7	13.1	10	4.6	4.4	9.08
1754	3.3	2.8	3.4	6.7	12.2	13.6	15	15.7	13.9	10.4	5.7	3.6	8.83
1755	2.2	1.2	3.9	0	9.4	15.7	15	14.6	13.5	8.4	4.7	3.9	8.54
1756	4.4	4.6	6	6.7	9.1	13.8	16	14.7	13.6	9.4	3.9	2.9	8.77
1757	0.3	4	4.9	8.1	10.7	14	18	15.2	13.3	8.2	7.1	3.2	8.95
1758	2.6	3.8	5.2	7.2	13.8	14.6	14	16.4	11.9	8.1	5.7	3.9	8.95
1759	5.9	5.8	6.1	8.6	12.1	15	18	16.3	13.5	10.9	5.1	2.5	10
1760	1.9	3.8	6.6	9.4	11.7	15.2	17	15.8	15.7	9.2	5.7	6.1	9.83
1761	5.4	5.8	6.8	9.4	11.9	14.3	16	16.4	14.2	9.4	6.2	4.4	10
1762	4.7	4	3.7	0	12.9	16.9	18	15.3	13.6	7.9	4.6	3.6	9.58
1763	-0.8	4.9	5.4	8.9	10.2	14.6	15	15.3	13.1	8.3	5.8	6.2	8.93
1764	3.7	3.8	3.9	7.2	12.2	13.9	16	15.2	12.5	8.9	4.4	2.8	8.72
1765	4.8	0.4	5	7.5	11.4	13.8	16	15.3	13.3	9.2	3.9	1.7	8.5

1766	0.7	1.7	4.2	8.1	9.7	13.7	16	16.6	13.3	9.3	7.2	3.3	8.63
1767	0.1	5.4	4.7	7.3	10	12.8	14	16.1	14.1	9.2	6.9	3.3	8.69
1768	0.8	4.8	4.7	8.1	12.2	13.9	16	16	11.7	9.2	5.6	4.6	8.93
1769	2.5	2.7	5	7.8	11.3	13.1	16	15	12.8	8.2	5.7	4.8	8.77
1770	3.7	4.6	2.5	5.4	10	13.1	15	15.8	13.9	8.9	5.3	3.6	8.51
1771	1	3.2	3.1	5.5	12.2	14.3	16	14.3	12.2	9.2	6.3	5.6	8.55
1772	1.2	1.9	4.4	6.4	10.1	16.1	17	16.1	13	11.7	7.2	4.8	9.15
1773	4	2.6	6.5	8.3	10.3	14.7	16	17.2	12.4	9.9	5.3	3.8	9.24
1774	0.6	4.3	6.4	8.6	10.9	14.7	16	16.1	12.5	10.3	4.8	3.5	9.07
1775	4.6	6.1	6	9.8	12.6	16.6	17	15.8	14.3	9.3	4.8	4.5	10.09
1776	-1.6	3.8	6.4	9.4	10.8	14.1	16	15.2	12.9	10.2	6.2	4.4	9.01
1777	1.9	2.3	6.8	7.2	11.7	13.6	15	15.9	14.6	10.2	6.9	2.6	9.08
1778	1.9	3.2	4.6	8.2	10.6	15.4	17	16.8	12.2	7.4	6.7	6.1	9.2
1779	2.9	7.9	7.9	9.4	11.9	14.4	18	17.6	15.2	10.9	5.7	3.1	10.4
1780	-0.9	2.1	7.9	6.3	12.8	14.2	17	17.6	15.6	9.1	4.4	3.2	9.09
1781	2.1	4.8	6.6	9.2	12.1	16.2	17	17.3	14.2	10.6	6.5	5.4	10.2
1782	5.2	1.9	4.1	5.2	9	14.9	16	14.2	13.3	7.6	2.3	2.8	8.01
1783	3.4	3.3	3.3	0.1	10.4	14.8	19	15.8	12.8	9.8	6.2	2.7	9.28
1784	-0.6	1.4	2.7	5.7	13.5	13.7	15	14	14.8	7.8	5.5	0.3	7.83
1785	3.4	0.4	1.2	8.4	12.3	16.1	16	13.9	13.6	8.7	5.6	2.8	8.54
1786	2.7	3.4	2.1	8.1	11.2	16.1	15	15.1	11.7	7.5	3.3	2.8	8.25
1787	3.6	5.9	6.8	7.4	11.5	13.9	16	15.6	12.8	9.8	4.5	3.8	9.28
1788	3.9	3.8	3.6	9.4	13.8	15.4	16	15.8	13.4	9.8	6.1	-0.3	9.21
1789	1.5	5	2.1	7.4	12.5	14	15	16.6	13.1	8.6	4.6	6.1	8.91
1790	4.3	6.6	6.4	6.1	11.9	14.6	15	15.6	12.2	10.3	6.1	4.3	9.44
1791	4.3	4.7	6.5	9.6	10.6	14.7	15	15.9	13.8	8.9	5.9	1.1	9.27
1792	2.3	4.5	5.9	0	10.2	13.2	15	16.9	11.8	8.8	7.1	4.3	9.19
1793	2.8	4.6	4.2	6.2	10.9	13.5	18	15	11.7	11.3	6	5.3	9.09
1794	1.8	7.2	7	0.2	11.3	15.7	18	15.5	12.5	9.6	6.1	3.7	9.89
1795	-3.1	0.8	3.9	7.7	10.9	13.2	15	16.6	16	11.7	4.5	6.6	8.67
1796	7.3	4.7	4.2	0.2	10.3	13.9	15	15.9	14.6	8.1	4.6	-0.3	9.02
1797	3.5	4.6	4.3	7.4	11.3	13.6	17	15.8	12.5	8.2	4.7	4.8	9
1798	3.6	4	5.1	0.4	12.9	16.9	16	16.4	13.6	9.9	4.7	1.5	9.61
1799	1.7	2.8	3.4	5.4	9.6	14.1	15	14.4	12.9	8.3	5.6	1.3	7.89
1800	2.8	2.2	4	9.3	12.3	13.9	18	16.8	13.9	9.2	5.4	3.3	9.23
1801	4.6	4.8	6.7	8.3	12.1	14.8	16	17.1	14.2	10.2	4.8	1.5	9.6
1802	1.6	3.7	5.6	8.9	10.6	13.7	14	17.2	13.8	10.1	5.1	3.6	8.95
1803	1.8	3.4	6.3	9.1	10.5	13.7	18	16.1	11.4	9.3	5	4.4	9.05
1804	5.8	2.9	4.7	6.9	13.3	16.1	16	15.6	14.2	10.7	6.6	2.1	9.57
1805	2.1	4.1	6.2	8.3	10.2	13.2	16	16.4	14.6	8.2	4.8	3.6	8.97
1806	4.2	4.3	5.1	6.8	12.1	14.9	15	16.2	13.4	10.6	7.8	6.8	9.8
1807	2.8	3.7	2.9	7.7	11.8	14.2	17	16.9	10.5	11.4	2.9	1.9	8.65
1808	2.6	2.8	3.2	5.8	13.7	14.8	18	16.7	12.7	7.2	6	2.2	8.84
1809	2	5.7	6	5.2	13.1	13.7	15	14.8	12.7	10.2	4.6	4.1	8.93
1810	2.2	3.5	4.9	8.2	9.2	14.6	15	14.6	13.9	9.8	5.4	3.6	8.76
1811	1.2	4.6	7.1	8.9	12.8	14.1	16	14.4	13.7	12.3	7.7	3.1	9.67
1812	2.6	5.3	3.5	5.5	10.9	13	14	14.3	13.2	9.3	4.9	1.7	8.2
1813	1.9	5.8	6.8	7.6	11.6	13.6	15	14.5	12.5	8.1	4.3	2.8	8.71
1814	-2.9	1.4	2.9	9.6	9.2	12.2	16	14.7	12.8	8.1	4.7	4.3	7.75
1815	0.3	6.5	7.3	8.1	12.6	14.3	15	15.3	13.4	10.3	3.4	2.3	9.06
1816	2.7	2.1	3.9	6.6	9.9	12.8	13	13.9	11.8	10.3	3.9	3.1	7.87
1817	4.5	6.4	5.5	7.6	8.7	15.1	14	13.6	13.2	6.4	9.1	2.5	8.89
1818	4.4	2.7	4.5	6.9	11.3	16.4	18	15.3	13.3	12	9.5	3.6	9.84
1819	4.4	4.3	6.8	8.6	11.5	13.4	16	17.4	13.4	9.1	4.1	1.4	9.23
1820	-0.3	3.2	4.7	8.9	11.4	13.6	16	14.7	12.3	8.1	5.6	4.7	8.55
1821	3.6	2.1	5.7	9.5	9.4	12.3	15	16.4	14.9	10.4	8.6	6.4	9.51
1822	4.7	6.3	7.8	8.3	12.7	17.1	16	15.2	12.4	10.7	8.2	1.6	10.05

1823	-0.1	3.1	5	6.7	12.2	12.3	14	14.4	12.5	8.4	7.1	4.8	8.38
1824	4.3	4.7	4.6	7.4	10.7	13.4	16	15.1	13.7	9.5	7.2	5.1	9.31
1825	3.8	3.9	5	9.1	11.6	14.1	17	16.3	15.1	10.8	5.2	4.6	9.72
1826	0.4	6.4	6.3	8.8	11.2	17.3	18	17.6	13.6	11.1	4.4	5.8	10.07
1827	1.7	0.7	5.9	8.9	11.9	14.2	17	14.8	13.7	11.4	6.9	6.9	9.46
1828	5.1	5.2	6.6	8.3	12.4	15.4	16	15.3	14.3	10.2	7.4	7.4	10.3
1829	0.3	4.3	4.3	6.7	12.5	14.9	15	14.3	11.3	8.3	4.5	1.4	8.16
1830	-0.2	2.2	7.7	8.9	12	12.7	16	13.7	11.9	10.4	6.9	1.8	8.68
1831	1.6	4.8	7.2	9.2	11.5	15.4	17	16.9	13.7	12.7	5.6	5.8	10.09
1832	3.1	3.4	5.8	8.6	10.9	15.2	16	15.4	13.6	10.7	5.9	5.2	9.47
1833	1.2	5.6	3.9	7.7	15.1	14.6	16	14.3	12.1	10.1	6.6	6.9	9.49
1834	7.1	5.6	7.1	7.7	13	15.4	17	16.2	13.8	10.6	6.7	5.6	10.47
1835	2.9	5.7	5.8	8.6	11.3	15	16	16.9	13.4	8.9	6.6	3.1	9.55
1836	3.7	3.5	5.8	7.2	11.1	15.3	15	14.6	11.7	8.6	5.3	4.1	8.86
1837	2.7	4.7	2.3	4.7	9.9	15.5	17	15.7	12.5	10.5	5.2	5.3	8.82
1838	-1.5	0.4	4.9	6.1	10.5	14.4	16	15.1	12.7	9.8	4.6	4	8.05
1839	2.8	4.1	4.2	6.4	10.2	14.3	15	14.6	12.4	9.3	7.3	3.7	8.68
1840	4.1	3.6	3.8	9.7	11.4	14.1	14	15.9	11.1	7.5	5.8	1.3	8.51
1841	1.1	2.4	7.5	7.8	12.7	12.9	14	14.6	13.4	8.7	5.2	4.4	8.71
1842	0.6	4.2	6.4	7.8	11.4	15.6	15	17.1	13.2	7.2	5.5	7.2	9.22
1843	4	1.9	5.6	8.5	10.4	12.8	15	15.3	14.4	7.9	5.7	7.4	9.06
1844	3.8	1.6	4.7	9.8	10.8	14.7	15	13.5	13.3	9.2	5.9	0.4	8.59
1845	3.2	0.9	2	8.6	9.5	14.9	14	13.5	11.4	9.5	6.7	4.6	8.26
1846	6.3	6.4	6.1	7.8	12.3	18.2	17	16.6	14.7	9.5	6.9	0.5	10.15
1847	2.2	2.4	5.6	6.6	12.3	13.9	18	15.2	11.5	10.7	7.9	4.8	9.22
1848	1.3	6.1	5.9	8.2	13.9	14.5	16	13.6	12.8	9.7	5.8	5.6	9.42
1849	3.9	5.7	6.1	6.4	12.1	13.9	15	15.6	13.3	9.2	6.6	3.4	9.3
1850	0.7	6.4	4.7	9	10.1	15.4	16	14.5	12.3	7.9	7.4	4.6	9.1
1851	5.6	4.7	5.8	7.4	10.4	14.3	15	15.5	12.7	10.8	3.1	4.8	9.14
1852	4.9	4.7	5.2	8.2	10.6	13.2	19	15.8	12.9	7.8	7.9	7.7	9.8
1853	5.1	0.6	3.4	7.6	10.9	14.3	15	14.7	12.3	10.1	5.2	1.3	8.37
1854	3.6	4.3	6.7	9.2	10.3	13.2	15	15.2	14.4	9.4	4.9	5.1	9.31
1855	2.4	1.7	3.3	7.1	8.8	13.3	17	15.7	13.2	9.7	5.3	2.4	8.02
1856	3.7	5.3	4.4	8.1	9.4	13.5	15	16.9	12.5	10.7	4.8	4.4	9.08
1857	2.6	4.3	5.3	7.5	11.3	15.8	16	17.4	14.5	11.3	7.2	7.3	10.07
1858	3.4	1.8	4.9	7.7	10.8	16.8	15	15.8	14.7	9.6	4.3	4.8	9.12
1859	4.9	5.7	7.3	7.5	11.7	14.8	18	16.2	12.9	9.6	4.8	1.6	9.61
1860	3.5	1.7	4.7	5.9	11.5	12.3	15	13.6	11.2	9.8	4.5	1.5	7.89
1861	1.7	4.9	6.3	7.5	10.4	14.8	15	15.9	13.1	11.8	4.2	3.9	9.13
1862	3.9	5.1	5.5	8.8	12.3	12.7	14	14.6	13	10.3	3.2	6.5	9.17
1863	4.9	5.8	6.5	8.8	10.6	13.6	15	15.5	11.6	9.9	7.3	6.3	9.67
1864	2.4	2.3	4.7	8.8	12.4	13.6	16	14.2	13.3	9.8	5.5	3.7	8.85
1865	2.1	2.3	2.9	0.6	12.6	15.6	17	15.1	16.3	9.7	6.7	5.8	9.69
1866	5.8	4.4	4.8	8.6	10	15.5	16	14.7	12.8	10.7	6.9	6.1	9.65
1867	1.2	6.9	3.1	9.3	11.4	14.1	15	16.3	13.6	9.3	4.8	3.4	9.02
1868	3.9	6.3	6.8	8.7	13.5	15.5	18	16.8	14.3	8.4	4.9	7.2	10.38
1869	5.6	7.5	3.8	0.1	9.6	13.2	17	15.5	14.4	9.7	5.8	2.9	9.62
1870	3.3	2.8	4.7	9.2	11.7	15.2	18	15.7	12.9	9.5	4.7	0.6	8.98
1871	0.5	6.1	7.3	8.7	11.3	12.8	15	17.2	12.7	9.8	3.4	3.6	9.05
1872	5	6.9	6.8	8.2	9.7	14.1	17	15.3	13.2	8.4	7	5.3	9.75
1873	5.2	1.8	5.4	7.7	9.9	14.2	16	15.4	11.8	8.6	6.3	5.3	8.98
1874	5.5	3.9	6.7	9.8	10	13.9	17	15.1	13.6	10.4	5.6	-0.2	9.3
1875	6.4	2.3	5.1	8.6	12.3	14.2	15	16.1	14.9	8.9	5.4	4.2	9.43
1876	3.2	4.8	4.5	7.9	9.6	14.3	17	16.5	12.7	11.3	6.1	6	9.51
1877	5.5	6.2	4.9	7	9.1	15.2	15	15.2	11.2	9.3	7.1	4.7	9.17
1878	4.6	5.6	5.4	8.9	11.8	15.1	17	16.2	13.3	10.2	3.5	-0.3	9.24
1879	-0.7	3.1	4.7	5.7	8.9	12.9	14	14.5	12.6	8.9	4.1	0.7	7.42

1880	0.9	5.8	6.2	7.9	10.4	13.8	16	16.4	14.6	7.1	5.4	5.1	9.09
1881	-1.5	3.2	5.3	7.3	11.8	13.7	16	13.9	12.7	7.3	8.9	3.9	8.56
1882	5.2	6.1	7.4	8.4	11.5	13.1	15	14.9	12.1	9.9	5.7	3.9	9.45
1883	4.7	5.9	1.9	8.1	10.6	13.9	15	15.3	13.3	9.7	5.8	4.6	9.02
1884	6.5	5.3	6.5	7.2	11.3	14.1	16	17.2	14.5	9.4	5.3	4.4	9.83
1885	2.9	5.8	4.5	7.7	8.9	13.9	16	13.6	12.2	7.5	5.9	3.7	8.57
1886	2.1	1.5	4.2	7.6	10.3	13.6	16	15.8	13.6	11.3	6.6	1.9	8.7
1887	2.4	3.8	3.3	6.2	9.4	15.3	17	15.7	11.8	7.1	4.4	2.6	8.27
1888	3.2	1.8	3.1	6.2	10.7	13.2	14	14.1	12.2	7.9	7.7	4.9	8.22
1889	3.4	2.9	4.7	7.1	12.9	15.3	15	14.7	12.8	8.6	6.9	3.3	8.99
1890	5.7	3.1	6.2	7.1	11.7	13.5	15	14.1	14.6	9.4	5.7	-0.8	8.73
1891	1.3	3.9	3.8	6.2	9.5	14.7	15	14.1	14.2	9.4	5.6	4.1	8.49
1892	2.3	3.6	2.7	7.3	11.6	13.4	14	15.2	12.4	7.1	6.4	1.8	8.17
1893	2.2	4.7	7.2	0.3	13.1	15.6	16	17.4	12.9	9.9	5.2	4.8	9.97
1894	3.4	5.1	6.7	9.7	9.2	13.5	16	14.2	11.6	9.3	7.9	5.1	9.3
1895	0.2	1.8	5.1	8.2	12.4	14.8	15	15.8	15.4	7.1	7.5	3.9	8.65
1896	4.8	4.6	6.7	9.1	11.9	16.2	16	14.3	13.1	6.9	4.3	3.9	9.33
1897	1.6	5.8	6.5	7.1	10	15.1	17	16.2	12.1	9.9	7.6	4.7	9.42
1898	6.6	4.8	4.3	8.5	10.2	13.6	15	16.5	15.2	11.3	7.2	7.3	10.07
1899	4.9	5.1	5.1	7.8	9.9	15.7	17	17.8	13.2	8.8	8.5	2.2	9.69
1900	4.4	2.6	3.7	8.3	10.3	14.7	18	15.1	13.6	9.8	7.3	7.2	9.56
1901	3.5	2.3	4.1	8.6	11.5	13.9	18	15.6	13.9	9.7	4.8	3.4	9.11
1902	4.7	1.5	6.7	7.5	8.9	13.9	15	14.3	12.8	9.6	6.8	4.6	8.83
1903	4.2	7.1	7.1	6.4	11.1	13	15	14.3	13.1	10.5	6.4	3.3	9.32
1904	4.1	3.4	4.3	8.7	10.9	13.3	17	15.1	12.5	9.7	5.2	3.7	9
1905	3.6	5.2	6.8	7.3	10.8	14.7	17	14.7	12.4	7.1	4.9	4.9	9.13
1906	5.3	3.1	5.1	7.3	10.5	14.3	16	16.7	13.9	10.9	7.3	3	9.43
1907	3.6	2.8	6.3	7.6	10.5	12.4	14	14.3	13.6	9.8	6.5	4.6	8.84
1908	2.5	5.3	4.3	6	12.4	14.3	16	14.6	12.9	11.8	7.4	3.9	9.27
1909	3.5	2.9	3.7	8.7	11	11.8	15	15.4	11.9	10.4	4.8	3.9	8.55
1910	3.5	5.1	6.1	7.3	11.2	14.7	14	15.2	12.5	10.6	3.2	6.4	9.17
1911	3.8	4.8	5.2	7.5	12.9	14.5	18	18.2	13.9	9.3	6.1	6.2	10.05
1912	3.6	5.4	7.2	8.8	12.1	13.9	16	12.9	11.1	8.2	6.3	6.7	9.36
1913	4.5	4.8	6.2	8.1	11.4	14.3	15	15.2	14.1	10.9	8.4	5.1	9.8
1914	3.7	6.8	6.1	9.8	10.8	14.5	16	16.1	13.3	10.3	6.8	4.6	9.88
1915	4.1	4.3	5.2	7.9	10.8	14.4	15	15.3	13.4	9.1	2.8	5.3	8.93
1916	7.5	3.8	3.3	8.2	11.6	11.8	15	16.4	13	10.6	6.8	1.9	9.18
1917	1.6	0.9	3.2	5.4	12.8	15.2	16	15.3	14	7.5	7.8	2.3	8.51
1918	3.8	6.5	5.7	6.7	13	13.3	15	16.1	11.9	9.3	5.5	6.9	9.51
1919	2.9	1.9	3.6	7.1	13.5	14.3	14	15.7	12.7	7.4	3.3	5.5	8.48
1920	5.2	6	7.2	8.2	11.8	14.4	14	13.6	13	10.4	6.8	4.2	9.57
1921	7.3	4.8	7.4	8	11.5	14.7	19	15.4	14.1	12.8	4.6	6.5	10.47
1922	3.7	4.4	4.6	5.5	12.7	13.8	14	13.6	12.2	8.2	5.9	5.8	8.67
1923	5.6	5.6	6.5	7.6	9.2	12.5	18	15.2	12.5	9.7	3.3	3.8	9.08
1924	4.7	3.3	4.1	6.9	11.6	13.9	15	14.1	13.3	10.1	7.1	6.8	9.27
1925	5.3	5.2	4.9	7.5	11.6	15	17	15.4	11.5	10.4	3.6	2.8	9.17
1926	4.6	6.8	6.3	9.3	10.2	13.6	17	16.2	14.4	8.1	5.9	4.2	9.72
1927	4.6	3.9	7.3	7.9	11.2	12.6	16	15.7	12.5	10.5	6.2	2.1	9.2
1928	5.2	5.8	6.3	8.5	10.9	12.9	16	15.3	12.8	10.1	7.6	3.4	9.57
1929	1.3	0.4	6.2	6.8	11.3	13.3	16	15.4	15.3	9.6	6.7	5.8	9.01
1930	5.6	2.5	5.3	8.3	10.7	15.3	15	15.7	13.6	10.5	6.2	4.3	9.43
1931	3.2	3.9	4.2	7.7	11.4	14.4	15	14.4	11.5	8.8	7.8	5.3	8.99
1932	6.3	2.9	4.7	6.9	10.5	14.1	16	17.1	12.9	8.8	6.6	5.7	9.38
1933	2.2	4.3	7.3	8.8	12.2	15.6	18	17.6	14.9	10.1	5.6	1.6	9.83
1934	4.1	3.8	4.8	8	11.3	14.9	18	15.4	14.6	10.6	6.1	8.1	9.99
1935	4.5	5.8	6.6	8.2	9.9	15.1	17	16.6	13.6	9.5	6.9	2.8	9.72
1936	3.7	2.6	7.1	6.3	11.5	14.7	15	16.1	14.4	9.4	5.5	5.3	9.32

1937	5.2	5.6	3.6	9.2	12.2	14.1	16	16.9	13.4	10.4	5.1	3	9.57
1938	5.7	5.1	9.1	7.6	10.7	14.4	15	16.3	13.8	10.5	9.4	4.4	10.18
1939	4.2	5.6	5.8	8.8	11.4	14.2	16	16.4	14.2	8.2	8.7	3.2	9.68
1940	-1.4	2.6	6	8.7	12.5	16.4	15	15.6	12.8	9.6	6.9	3.8	9.05
1941	0.5	3.5	5.1	6.4	9.4	15.1	17	14.7	14.5	10.4	6.6	5.6	9.09
1942	0.9	0.1	5.2	9.2	11.1	14.4	16	16.6	13.6	10.4	4.9	6.7	9.05
1943	4.9	6.1	6.5	0.5	11.8	14.4	16	16.1	13.3	10.6	6.3	3.5	10.03
1944	5.8	3.6	5.2	0.2	11.4	13.5	17	17	12.5	9.3	6.2	3.6	9.57
1945	0.4	7.1	7.9	0.1	12.2	14.6	17	15.9	14.4	11.9	7.2	4.9	10.27
1946	2.7	5.9	5.1	9.9	10.7	13.1	16	14.7	14	9.8	8.1	3.1	9.45
1947	2.2	1.9	3.6	8.6	13.5	15.5	17	18.6	14.9	10.6	7.2	5.1	9.57
1948	5.4	4.7	8.3	9	11.4	13.5	16	15.1	13.8	10.1	7.3	5.7	10.01
1949	5.5	5.7	5.1	0	11.2	15.3	17	16.8	16.3	11.7	6.6	5.8	10.62
1950	4.2	5.3	7.4	7.6	11.3	16.2	16	15.6	12.9	9.6	5.7	1.2	9.41
1951	3.9	3.7	4.1	6.8	10.1	14	16	14.8	14.1	9.4	8.5	5.5	9.27
1952	2.7	3.4	6.6	9.6	13.4	14.4	17	15.8	10.7	8.8	4.2	2.8	9.1
1953	3.3	4.3	5.6	7.3	12.6	14.4	16	16.2	13.8	9.7	8.5	6.9	9.84
1954	2.9	2.6	5.8	7.6	11.2	13.4	14	14.6	12.7	11.9	6.9	6.8	9.22
1955	2.6	1.2	3.2	9.3	9.7	13.8	18	18.1	14.2	9.2	7	5.4	9.28
1956	3.6	0.2	6.2	6.9	11.7	13.1	16	13.5	14.3	9.4	6	5.7	8.83
1957	5.5	5.3	9.2	8.9	10.3	15.2	16	15.4	12.5	10.8	6.4	4.5	10.02
1958	3.4	4.7	3.7	7.4	11.1	14.1	16	15.8	15.1	10.8	6.4	4.7	9.42
1959	1.6	4.4	7.3	9.4	12.8	15.2	17	17.2	14.9	12.6	7.1	6	10.48
1960	3.8	4.1	6.4	8.9	12.8	16.1	15	15	13.1	10.3	7.3	3.9	9.73
1961	3.9	6.9	8.2	0	11	14.4	15	15.4	15.2	10.9	6	2.2	9.94
1962	4.3	4.4	2.8	7.7	10.3	13.7	15	14.5	12.6	10.4	5.5	1.8	8.59
1963	-2.1	0.7	6	8.7	10.6	14.9	15	14.3	12.9	11.1	8.2	2.6	8.47
1964	3.4	4.5	4.3	8.7	13.3	13.8	16	15.5	14.1	8.9	7.4	3.6	9.47
1965	3.3	3.1	5.2	8	11.7	14.7	14	14.9	12.3	11	4.5	4.7	8.95
1966	2.9	5.7	6.5	7.2	11	15.4	15	14.7	13.8	10.1	5.6	5.5	9.45
1967	4.5	5.4	7	7.7	10.4	14	17	15.7	13.5	10.8	5.4	4.2	9.61
1968	4.4	1.9	6.3	8.1	9.8	14.8	15	15.4	13.9	12.5	6.5	3	9.3
1969	5.5	1	3.3	7.4	11.2	13.9	17	16.4	13.9	13	5.4	3.3	9.26
1970	3.7	2.9	3.7	6.7	13	16.4	15	16	14.4	10.7	7.8	4.3	9.57
1971	4.5	4.5	4.9	7.9	11.6	12.4	17	15.6	14	11.3	6	6.6	9.68
1972	3.9	4.3	6.5	8.2	10.5	11.8	16	15.1	11.7	10.6	6.3	5.8	9.19
1973	4.5	4.3	6.2	7	11.4	14.8	16	16.5	14.3	9	6	4.9	9.54
1974	5.9	5.4	5.8	8.2	11	13.9	15	15.2	12.1	7.8	6.8	8.1	9.62
1975	6.8	4.4	4.8	8.3	9.9	14.7	17	18.7	13.5	9.9	6.3	5.3	10
1976	5.9	4.5	4.8	8.1	12.1	17	19	17.6	13.4	10.6	6.3	2	10.08
1977	2.8	5.2	6.9	7.2	10.6	12.2	16	15.2	13.3	11.8	6.6	6.1	9.48
1978	3.4	2.8	6.7	6.5	11.7	13.7	15	15	14.2	11.9	8.5	3.9	9.42
1979	-0.4	1.2	4.7	7.8	10	13.9	16	14.9	13.5	11.3	6.8	5.8	8.81
1980	2.3	5.7	4.7	8.8	11.2	13.8	15	15.9	14.7	9	6.6	5.6	9.42
1981	4.9	3	7.9	7.8	11.2	13.2	16	16.2	14.5	8.6	7.8	0.3	9.24
1982	2.6	4.8	6.1	8.6	11.6	15.5	17	15.7	14.2	10.1	8	4.4	9.84
1983	6.7	1.7	6.4	6.8	10.3	14.4	20	17.3	13.7	10.5	7.5	5.6	10.03
1984	3.8	3.3	4.7	8.1	9.9	14.5	17	17.6	13.7	11.1	8	5.2	9.73
1985	0.8	2.1	4.7	8.3	10.9	12.7	16	14.6	14.6	11	4.1	6.3	8.86
1986	3.5	1.1	4.9	5.8	11.1	14.8	16	13.7	11.3	11	7.8	6.2	8.74
1987	0.8	3.6	4.1	0.3	10.1	12.8	16	15.6	13.6	9.7	6.5	5.6	9.05
1988	5.3	4.9	6.4	8.2	11.9	14.4	15	15.2	13.2	10.4	5.2	7.5	9.77
1989	6.1	5.9	7.5	6.6	13	14.6	18	16.6	14.7	11.7	6.2	4.9	10.5
1990	6.5	7.3	8.3	8	12.6	13.6	17	18	13.2	11.9	6.9	4.3	10.63
1991	3.3	1.5	7.9	7.9	10.8	12.1	17	17.1	14.7	10.2	6.8	4.7	9.52
1992	3.7	5.4	7.5	8.7	13.6	15.7	16	15.3	13.4	7.8	7.4	3.6	9.86
1993	5.9	4.6	6.7	9.5	11.4	15	15	14.6	12.4	8.5	4.6	5.5	9.49

1994	5.3	3.2	7.7	8.1	10.7	14.5	18	16	12.7	10.2	10.1	6.4	10.24
1995	4.8	6.5	5.6	9.1	11.6	14.3	19	19.2	13.7	12.9	7.7	2.3	10.52
1996	4.3	2.5	4.5	8.5	9.1	14.4	17	16.5	13.6	11.7	5.9	2.9	9.2
1997	2.5	6.7	8.4	9	11.5	14.1	17	18.9	14.2	10.2	8.4	5.8	10.53
1998	5.2	7.3	7.9	7.7	13.1	14.2	16	15.9	14.9	10.6	6.2	5.5	10.34
1999	5.5	5.3	7.4	9.4	12.9	13.9	18	16.1	15.6	10.7	7.9	5	10.63
2000	4.9	6.3	7.6	7.8	12.1	15.1	16	16.6	14.7	10.3	7	5.8	10.3
2001	3.2	4.4	5.2	7.7	12.6	14.3	17	16.8	13.4	13.3	7.5	3.6	9.93

Appendix 7.3: Data on North Atlantic Oscillation Index (NAOI) based on Climate Research Unit, the University of East Anglia (www.cri.uea.ac.uk).

Year	December	January	February	March	December	Average	Annual Average
1821		-99.99	-99.99	-99.99	-99.99		-99.99
1822	-99.99	-99.99	-99.99	2.99	-0.73	-74.245	-99.99
1823	-0.73	-3.39	-99.99	-99.99	-0.2	-51.025	-99.99
1824	-0.2	-0.16	0.25	-1.44	-0.01	-0.3875	-99.99
1825	-0.01	-0.23	0.21	0.33	-1.31	0.075	0.16
1826	-1.31	-3.05	4.87	-0.97	-0.59	-0.115	0.27
1827	-0.59	-0.45	-3.72	1.83	2.7	-0.7325	-0.45
1828	2.7	1.27	0.37	-0.18	3.04	1.04	-0.88
1829	3.04	-2.48	0.32	-2.54	-0.43	-0.415	-0.09
1830	-0.43	-2.33	1.2	3.58	-3.13	0.505	0.88
1831	-3.13	-2.91	1.4	1.48	0.36	-0.79	-0.62
1832	0.36	-0.04	0.83	2.12	3.32	0.8175	0.15
1833	3.32	-0.36	2.52	-2.89	4.17	0.6475	0.15
1834	4.17	3.07	2.66	1.37	0.11	2.8175	-0.01
1835	0.11	0.37	3.37	1.54	-1.46	1.3475	0.42
1836	-1.46	1.47	0.06	2.28	-1.41	0.5875	0.93
1837	-1.41	-1.16	4.67	-3.08	1.37	-0.245	-0.09
1838	1.37	-2.16	-1.81	1.23	2.55	-0.3425	-0.09
1839	2.55	1.24	4.2	0.79	-0.63	2.195	0.35
1840	-0.63	2.97	-0.4	-3.05	-2.43	-0.2775	-0.25
1841	-2.43	-0.71	-1.37	2.41	0.21	-0.525	0.18
1842	0.21	2.45	4.26	3.43	0.51	2.5875	-0.68
1843	0.51	2.99	-3.51	-1.28	3.13	-0.3225	0.55
1844	3.13	0.2	0.11	1.09	-1.9	1.1325	-0.22
1845	-1.9	1.17	0.06	-0.54	0.83	-0.3025	0.34
1846	0.83	2.26	0.63	1.75	-2.55	1.3675	0.26
1847	-2.55	0.03	0.1	-1.59	1.76	-1.0025	0.62
1848	1.76	-0.79	1.77	0.76	2.55	0.875	0.07
1849	2.55	2.42	2.77	-0.56	-1.24	1.795	-0.08
1850	-1.24	-0.16	4.13	-2.22	2.36	0.1275	0.2
1851	2.36	3.29	1.03	1.5	1.74	2.045	0.24
1852	1.74	1.46	0.41	-2.5	1.03	0.2775	-0.3
1853	1.03	1.31	-4.04	-0.32	-4.28	-0.505	-0.79
1854	-4.28	1.28	1.72	2.67	2.42	0.3475	0.76
1855	2.42	-1.84	-3.8	-0.05	-1.66	-0.8175	-0.78
1856	-1.66	-1.25	-0.1	-2.27	-0.23	-1.32	-0.18
1857	-0.23	-0.69	2.02	1.09	3.51	0.5475	0.97
1858	3.51	2.26	-0.54	-1.24	3.01	0.9975	-0.04
1859	3.01	2.74	2.37	1.5	-1.31	2.405	0.44
1860	-1.31	1.54	0.32	1.08	-2.14	0.4075	-0.66
1861	-2.14	-0.56	0.8	2.06	-1.5	0.04	-0.29
1862	-1.5	1.15	-1.26	-2.25	2.92	-0.965	-0.18
1863	2.92	1.12	3.1	1.88	2.17	2.255	0.98
1864	2.17	2.03	-0.27	-1.78	-0.77	0.5375	-0.44
1865	-0.77	0.15	-0.42	-1.03	2.57	-0.5175	0.33
1866	2.57	2.06	0.7	-2.1	2.14	0.8075	0.31
1867	2.14	-2.17	3.63	-3.03	-0.55	0.1425	-0.07
1868	-0.55	1.46	3.95	2.94	2.01	1.95	1.58
1869	2.01	3.25	3.9	-1.91	-0.69	1.8125	0.54
1870	-0.69	0.32	-1.98	-2.07	-3.52	-1.105	-0.42
1871	-3.52	0.67	1.71	1.15	-0.18	0.0025	-0.12
1872	-0.18	1.15	0.45	-1.2	-1.09	0.055	-0.8
1873	-1.09	2.3	0.18	-0.39	2.01	0.25	0.12

1874	2.01	1.56	2.07	1.47	-2.12	1.7775	0.47
1875	-2.12	2.06	-1.47	-0.61	0.08	-0.535	-0.11
1876	0.08	1.1	0.75	-0.29	-1.13	0.41	-0.22
1877	-1.13	2.39	1.96	-0.45	2.16	0.6925	0.05
1878	2.16	1.18	2.2	-0.01	-3.31	1.3825	-0.92
1879	-3.31	-0.71	0.85	-0.08	0.58	-0.8125	-0.36
1880	0.58	0.42	1.92	0.06	0.52	0.745	-0.01
1881	0.52	-3.6	-1.62	-0.51	2.77	-1.3025	0.09
1882	2.77	3.07	3.2	3.61	-1.69	3.1625	1.09
1883	-1.69	1.67	4.25	-3.04	0.91	0.2975	0.64
1884	0.91	3.32	1.48	0.19	1.94	1.475	0.58
1885	1.94	-0.8	0.09	-1.06	-0.03	0.0425	0.19
1886	-0.03	-1.41	-0.39	0.56	0.12	-0.3175	-0.32
1887	0.12	1.9	2.03	-0.85	-1.62	0.8	-0.64
1888	-1.62	0.21	-2.25	-1.5	1.25	-1.29	0.01
1889	1.25	0.65	-0.2	0.11	2.3	0.4525	0.64
1890	2.3	4.32	-1.37	0.5	-2.75	1.4375	0.6
1891	-2.75	0.27	2.81	-1.17	2.86	-0.21	0.03
1892	2.86	-0.77	-2.21	-1.53	-1.05	-0.4125	-0.64
1893	-1.05	-1.61	2.54	-0.04	1.86	-0.04	-0.1
1894	1.86	1.4	3.95	1.12	0.94	2.0825	0.87
1895	0.94	-2.61	-4.14	-0.27	0.02	-1.52	-0.24
1896	0.02	-0.23	2.33	1.39	1.86	0.8775	0.35
1897	1.86	-2.36	3.32	2.31	1.35	1.2825	0.85
1898	1.35	1.97	1.9	-2.33	3.14	0.7225	0.53
1899	3.14	0.68	-0.17	-1.5	-0.87	0.5375	0.04
1900	-0.87	1.38	-2.36	-3.12	3.5	-1.2425	0.08
1901	3.5	0.98	-2.58	-0.91	-1.38	0.2475	-0.4
1902	-1.38	1.41	-1.4	0.5	1.27	-0.2175	-0.43
1903	1.27	1.28	4.86	4.05	-1.09	2.865	0.87
1904	-1.09	2.24	1.21	-0.7	0.88	0.415	0.62
1905	0.88	1.81	2.09	2.23	1.85	1.7525	0.1
1906	1.85	2.64	1.26	-0.25	0.03	1.375	0.28
1907	0.03	1.58	1.22	2.41	1.18	1.31	0.56
1908	1.18	0.64	1.98	0.74	1.47	1.135	0.63
1909	1.47	1.82	-0.54	-2.09	-0.48	0.165	-0.1
1910	-0.48	2.57	3.85	0.55	-0.1	1.6225	-0.05
1911	-0.1	0.82	2.05	-1.4	3.02	0.3425	0.48
1912	3.02	-0.91	-0.17	2.22	3	1.04	0.21
1913	3	1.83	1.19	2.73	1.23	2.1875	0.87
1914	1.23	0.58	2.45	1.72	2.23	1.495	0.8
1915	2.23	0.08	1.82	-1.91	-0.65	0.555	-0.87
1916	-0.65	3.82	2.03	-3.84	-1.8	0.34	-0.42
1917	-1.8	-3.08	-1.59	-0.21	-2.8	-1.67	-0.38
1918	-2.8	-0.48	3.87	0.37	2.32	0.24	0.51
1919	2.32	-0.01	-0.49	-0.25	2.86	0.3925	0.35
1920	2.86	2.84	1.39	3.08	-0.46	2.5425	0.62
1921	-0.46	3.2	0.07	2.68	2.18	1.3725	0.16
1922	2.18	0.64	2.97	-0.23	1.47	1.39	0.52
1923	1.47	1.84	2.77	-0.1	1.25	1.495	0.82
1924	1.25	0.86	-1.62	-1.88	3.86	-0.3475	-0.01
1925	3.86	4.23	1.95	-2	-0.72	2.01	0.29
1926	-0.72	1.7	1.84	0.56	-0.51	0.845	0.1
1927	-0.51	2.15	1.09	2.58	-3.14	1.3275	-0.26
1928	-3.14	3.04	3.52	-0.94	0.44	0.62	0.22
1929	0.44	-1.26	0.27	-0.48	3.8	-0.2575	0.17
1930	3.8	1.51	-0.6	-0.7	1.21	1.0025	0.13

1931	1.21	-0.09	1.29	-2.18	0.77	0.0575	-0.32
1932	0.77	3.47	-3.31	-1.57	1.22	-0.16	-0.06
1933	1.22	1.41	-1.81	1.26	-1.84	0.52	-0.42
1934	-1.84	3.27	0.49	0.3	1.32	0.555	0.42
1935	1.32	-0.5	2.7	0.39	-1.37	0.9775	0.25
1936	-1.37	-1.22	-2.44	-1.09	2.37	-1.53	-0.13
1937	2.37	2.15	1.73	-2.02	-1.09	1.0575	0.17
1938	-1.09	2.64	0.6	3.13	-0.39	1.32	0.92
1939	-0.39	-0.69	2.91	-0.03	-1.07	0.45	-0.46
1940	-1.07	-2.27	-0.93	-0.72	1.46	-1.2475	-0.5
1941	1.46	-3.5	-0.42	-1.29	1.44	-0.9375	-0.73
1942	1.44	0.75	-3.1	-0.92	1.47	-0.4575	-0.53
1943	1.47	1.17	2.78	0.03	-0.39	1.3625	0.97
1944	-0.39	3.63	-1.59	-0.82	0.26	0.2075	-0.1
1945	0.26	-2.12	4.67	2.51	-0.25	1.33	0.22
1946	-0.25	1.41	0.99	-0.39	1.22	0.44	0.47
1947	1.22	0.39	-4.6	-1.28	-0.72	-1.0675	-0.09
1948	-0.72	1.53	0.66	3.48	1.09	1.2375	0.8
1949	1.09	1.5	4.01	-0.96	0.11	1.41	0.48
1950	0.11	0.55	3.31	0.82	-1.88	1.1975	0.49
1951	-1.88	0.82	0.93	-2.01	2.54	-0.535	-0.07
1952	2.54	0.92	0.15	-1.14	-0.31	0.6175	-0.37
1953	-0.31	-0.02	0.54	1.25	0.15	0.365	0.4
1954	0.15	0.1	0.57	-0.29	1.44	0.1325	0.51
1955	1.44	-1.17	-2.21	-2.9	0.51	-1.21	-0.64
1956	0.51	-0.76	-2.96	0.01	2.57	-0.8	0.17
1957	2.57	2.53	1.08	0.42	-0.12	1.65	-0.02
1958	-0.12	0.37	-0.03	-1.28	-1.7	-0.265	0.12
1959	-1.7	-1.15	2.46	1.82	1.98	0.3575	0.49
1960	1.98	-0.7	-1	-0.87	0.46	-0.1475	-0.3
1961	0.46	1.46	4.06	2.08	-1.72	2.015	1.05
1962	-1.72	2.44	0.77	-3.78	-0.66	-0.5725	-0.13
1963	-0.66	-4.09	-1.9	2.79	-3.09	-0.965	-0.39
1964	-3.09	0.93	-0.13	-0.77	-1.24	-0.765	0.24
1965	-1.24	0.01	-3.03	0.23	1.24	-1.0075	-0.23
1966	1.24	-1.01	-0.38	1.05	1.68	0.225	-0.22
1967	1.68	0.04	1.7	3	-0.53	1.605	0.56
1968	-0.53	1.65	-1.53	0.34	-1.73	-0.0175	-0.62
1969	-1.73	-1.64	-3.16	-1.81	-0.26	-2.085	-0.44
1970	-0.26	-1.16	1.1	-1.78	-1.58	-0.525	0.18
1971	-1.58	-0.43	1.21	-1.76	0.76	-0.64	-0.55
1972	0.76	-0.52	-0.2	0.26	2.11	0.075	-0.04
1973	2.11	1.37	1.22	1.04	-1.65	1.435	-0.09
1974	-1.65	3.75	0.68	-0.81	3.06	0.4925	0.59
1975	3.06	2.43	0.4	-1.26	-1.57	1.1575	0.05
1976	-1.57	0.75	1.29	1.87	-3.63	0.585	-0.07
1977	-3.63	-2.36	0.28	1.33	-0.25	-1.095	-0.21
1978	-0.25	0.46	-1.99	3.1	-2.08	0.33	0.21
1979	-2.08	-3.22	-0.62	0.54	2.07	-1.345	0.19
1980	2.07	-1.8	0.7	-0.68	1.55	0.0725	-0.37
1981	1.55	1	1.04	0.01	-2.2	0.9	-0.09
1982	-2.2	-0.72	2.25	1.66	2.64	0.2475	0.67
1983	2.64	4.82	-1.25	1.79	0.83	2	0.34
1984	0.83	2.53	1.73	-2.12	1.52	0.7425	0.26
1985	1.52	-2.87	-0.24	0.07	-0.43	-0.38	-0.47
1986	-0.43	1.46	-4.02	2.86	3.42	-0.0325	0.56
1987	3.42	-2.12	-0.24	0.29	-0.81	0.3375	-0.51

1988	-0.81	0.53	-0.11	0.78	1.85	0.0975	-0.32
1989	1.85	3.53	3.61	2.45	-2.23	2.86	0.57
1990	-2.23	3.5	5.11	3.11	0.34	2.3725	1.23
1991	0.34	1.87	-0.02	-1.37	1.24	0.205	0.34
1992	1.24	0.64	3.18	1.66	0.21	1.68	1.11
1993	0.21	3.91	0.11	1.47	2.17	1.425	0.12
1994	2.17	1.28	0.07	3.68	2.86	1.8	0.51
1995	2.86	2.7	3.13	1.06	-3.33	2.4375	-0.61
1996	-3.33	-3.27	-0.12	-2.57	-4.7	-2.3225	-1.01
1997	-4.7	-1.95	5.26	2.09	-0.2	0.175	-0.18
1998	-0.2	-0.28	2.44	1.24	1.95	0.8	0.25
1999	1.95	0.9	1.8	-0.72	2.13	0.9825	0.04
2000	2.13	0.35	4.37	0.54	-99.99	1.8475	-99.99
	-99.99						