

1 Mobile marine predators: an understudied source of nutrients
2 to coral reefs in an unfished atoll
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4 Jessica J. Williams^{1*}, Yannis P. Papastamatiou², Jennifer E. Caselle³, Darcy
5 Bradley⁴ and David M.P. Jacoby^{5*}
6

7 ¹Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, Berkshire SL5 7PY, UK

8 ²Department of Biological Sciences, Florida International University, North Miami, FL 33181, USA

9 ³Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA 93106, USA

10 ⁴Bren School of Environmental Science and Management, University of California Santa Barbara, Santa Barbara, CA 93106,
11 USA

12 ⁵Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK
13

14 Corresponding authors:

15 [*jessica.williams.16@ucl.ac.uk](mailto:jessica.williams.16@ucl.ac.uk)

16 [*david.jacoby@ioz.ac.uk](mailto:david.jacoby@ioz.ac.uk)
17

18 **Abstract**

19 Animal movements can facilitate important ecological processes and wide-ranging
20 marine predators such as sharks, potentially contribute significantly towards nutrient
21 transfer between habitats. We applied network theory to four years of acoustic
22 telemetry data for grey reef sharks (*Carcharhinus amblyrhynchos*) at Palmyra, an
23 unfished atoll, to assess their potential role in nutrient dynamics throughout this
24 remote ecosystem. We evaluated the dynamics of habitat connectivity and used
25 network metrics to quantify shark-mediated nutrient distribution. Predator
26 movements were consistent within-year, but differed between years and by sex.
27 Females utilised higher numbers of routes throughout the system, distributing
28 nutrients over a larger proportion of the atoll. Extrapolations of tagged sharks to the
29 population-level suggests that prey consumption and subsequent egestion leads to
30 the heterogeneous deposition of 94.5 kg d^{-1} of nitrogen around the atoll, with
31 approximately 86% of this likely derived from pelagic resources. These results
32 suggest sharks may contribute substantially to nutrient transfer from offshore waters
33 to nearshore reefs, subsidies that are important for coral reef health.

34 **Key Words**

35 Acoustic telemetry; grey reef sharks, *Carcharhinus amblyrhynchos*; network theory;
36 nitrogen cycle; Palmyra Atoll;

37 **Introduction**

38 The movement patterns of animals can be highly complex, being influenced by both
39 their social and physical environments. Consequently, understanding and accurately
40 measuring population dynamics can be challenging [1–3]. Understanding movement
41 patterns however, is vital for identifying habitats critical for population connectivity or
42 migration [4], for predicting how stochastic or future environmental conditions will
43 affect populations [5], and for evaluating the effectiveness of protected areas [6]. It
44 cannot simply be assumed that the habitat in which a population is most commonly
45 observed, is that which provides a critical function (a source of food or location for
46 reproduction, for example; [7]). Therefore, to develop effective conservation
47 approaches, it is essential to understand how a species' behaviour and movement
48 varies across and between habitats [8,9].

49 In both terrestrial and marine environments, movements of predators can
50 directly and indirectly influence ecological processes such as nutrient cycling and
51 trophic interactions [10,11]. Indirectly, predators can affect nutrient cycling through
52 interactions with prey species; for example, the foraging activities of grazing
53 amphipods and isopods were shifted in response to the presence of predatory blue
54 crabs (*Callinectes sapidus*), contributing to increases in labile organic matter within
55 sea grass ecosystems [12]. More directly, animals can act as nutrient and organic
56 matter vectors, by egesting material within the same habitats to which the food was
57 consumed, or across habitat boundaries (translocation; [10,13,14]). In Alaska,
58 freshwater and/or marine-derived nutrients, released by brown bears, facilitate
59 growth in white spruce up to 1 km from riparian zones [15]. By foraging at depth and
60 then excreting faeces within the euphotic zone, marine mammals, such as
61 humpback and fin whales, have been found to replenish nitrogen concentrations at

62 the ocean's surface, thereby enhancing primary productivity (termed the upwards
63 "whale pump"; [16]). Wide-ranging predators, such as some whales and sharks, also
64 have the potential to contribute significantly to the horizontal transport of nutrients
65 between habitats within marine ecosystems [9,17].

66 Measuring nutrient transfer between areas and assessing the stability of such
67 flow however, is non-trivial. There is substantial evidence that the disruption of
68 animal movements can negatively impact productivity through the loss of certain
69 species, posing considerable threat to an ecosystem's long-term resilience
70 [11,18,19]. For example, in the Aleutian archipelago, seabirds act as vectors,
71 transporting nutrients from the ocean to land [20]. However, since the introduction of
72 arctic foxes (*Alopex lagopus*), which have preyed upon seabirds and thus reduced
73 this important nutrient supply, plant communities have been transformed and
74 productivity has decreased [20]. Understanding how predators link habitats and
75 transport nutrients through their environment, is therefore crucial for ecosystem
76 management.

77 Palmyra Atoll is a remote, relatively undisturbed coral reef ecosystem, and is
78 part of a U.S. National Wildlife Refuge within the central Pacific Ocean [21,22]. Due
79 to its protected status, Palmyra has a healthy predator population, with grey reef
80 sharks (*Carcharhinus amblyrhynchos*) being the most abundant predator on the
81 forereefs [23,24]. The grey reef shark population at Palmyra is likely at carrying
82 capacity [24] and may play a significant role in the transportation and flow of
83 nutrients onto the reef and throughout the atoll. Grey reef sharks are often detected
84 on, and suggested to favour, outer-reef slopes and drop-off habitats, but on occasion
85 are detected within lagoons [25,26,27]. Previous research has also highlighted
86 sexual segregation in some grey reef shark populations, which suggests that males

87 and females may connect habitats differently and thus transfer nutrients in differing
88 quantities [25]. Stable isotope analyses at Palmyra have demonstrated that grey reef
89 sharks acquire resources from different habitats, including from pelagic and
90 nearshore environments [7]. However, the use of these habitats for foraging is
91 uneven, with around 86% of grey reef shark biomass being derived from pelagic
92 resources [7]. Mobile species that transport nutrients between habitats have the
93 potential to impact new primary productivity and contribute to the modification of the
94 physical environment [28]. How mobile marine predators such as sharks facilitate
95 this nutrient transport, how much they contribute and how this is subsequently
96 distributed across shallow, productive reef habitats remains unexplored [25,29].
97 Thus, by transporting materials onto reef habitats that were produced elsewhere,
98 grey reef sharks may generate important linkages between ecosystems and possibly
99 play an ecologically important role in nutrient connectivity. Grey reef sharks show
100 quite strong residency to core areas of the reef, and low rates of movement between
101 reef habitats [27]. However, they are likely transporting pelagic nutrients to forereef
102 and potentially backreef habitats.

103 Using acoustic telemetry and network analyses we measure the connectivity
104 generated by the intra- and inter-habitat movements of predatory grey reef sharks.
105 We then quantify estimates of potential nitrogen transport onto the reef by these
106 sharks at Palmyra Atoll to understand how nitrogen is likely distributed along
107 different routes of the movement network. We use recent population estimates [24]
108 to extrapolate to the population level in order to assess how significant this nutrient
109 subsidy is likely to be to reef productivity. Due to previous evidence of sexual
110 segregation in this species in Palmyra Atoll (Y. Papastamatiou and D. Bradley,

111 personal observation), we hypothesise that male and female sharks will have a
112 different influence on nutrient dynamics.

113 **Method**

114 ***Study Site and Species***

115 Palmyra Atoll (5°53'N, 162°05'W) is situated in the northern Line Islands in the
116 central Pacific Ocean (Fig. 1). In 2001, the atoll became a U.S. National Wildlife
117 Refuge, prohibiting take of marine organisms. Since 2001, the only inhabitants have
118 been small (less than 20) groups of researchers and refuge staff [21]. Within the
119 wildlife refuge there is a spatial array of 65 VR2W acoustic receivers (Vemco,
120 Halifax, Nova Scotia, Canada; Fig. 1). Receivers detect animal-borne, acoustic
121 transmitters at an approximate range of 250-300 m; each time transmitters are
122 detected, the identification number, date and time are recorded by the receiver.
123 Receiver habitat was broadly classified by its geographic zone (lagoon, backreef or
124 forereef).

125 Detections were recorded from 41 grey reef sharks, comprising approximately
126 0.49% of the grey reef shark population at Palmyra Atoll [24]. These sharks were
127 tagged with acoustic transmitters (Vemco V16 and V13 coded transmitters) that had
128 been surgically inserted into their body cavities (for details on the method of shark
129 capture and tagging see Papastamatiou et al. [21]). Shark tagging took place on 10
130 days between 2010 and 2013 at various locations around the atoll. For each
131 individual tagged, we recorded sex and size. Weekly sea surface temperature
132 readings from Palmyra Atoll were obtained from the Coral Reef Ecosystem Program,
133 National Oceanic and Atmospheric Administration (NOAA; ESM 1).

134 ***Network Analyses***

135 Applying network theory to acoustic telemetry data allows the movement of sharks to
136 be viewed as a system of connections, in which acoustic receivers are linked by
137 shark movements (for further details on network theory and how it is applied to
138 telemetry data, see Jacoby et al. [30]). This technique offers insight into how species
139 move between and, thus connect habitats [6].

140 To construct the movement networks, data were initially filtered to include only
141 detections relating to movements of individuals between receivers (i.e. departures
142 and arrivals). However, residency patterns of sharks at each receiver location were
143 calculated from the full data set (see below for details on residency). To limit
144 transmitters being detected by more than one receiver at the same time (due to
145 some overlap in detection range for a few receivers), the receivers with the greatest
146 overlap were removed from analyses, ensuring that, within the same habitat
147 classification, no two receivers were closer than 150 metres (detection distance
148 determined during range testing). Following data filtering, detections from 47
149 acoustic receivers between January 2011 and December 2014 (1461 days) were
150 included in the analyses. Network theory was employed to analyse these detections,
151 where movement networks measure the relationship between nodes (the acoustic
152 receivers), which are linked by edges (shark movements) [30]. A key temporal
153 measure associated with an edge is its duration: the time between an individual's
154 last detection at one receiver and its first detection at a different receiver (time taken
155 to make the movement; [3]). As we were interested in movements that potentially led
156 to the transfer of nutrients around Palmyra Atoll, we filtered the data to only include
157 movements within ≤ 110 hour time windows. This duration represents the length of
158 time, post-feeding, that lemon sharks (*Negaprion brevirostris*) have been observed to
159 continue producing faeces [31]. Lemon sharks are the only species, to our

160 knowledge, for which faecal production time has been measured, and this quantity
161 has been used in previous studies to filter edge duration when focusing on nutrient
162 transfer by marine predators (e.g. [9]). From January 2011 to December 2014,
163 tagged grey reef sharks were detected 848,100 times by the 47 acoustic receivers,
164 this included 99,752 movements between receivers of which 99,342 were ≤ 110
165 hours apart (Table 1). To explore temporal dynamics, the data were divided into four
166 'seasons' by examining sea surface temperature data to determine thermally similar
167 three-month periods. These were December – February, March – May, June –
168 August and September – November.

169 Connectivity within the network

170 To assess the connectivity within the reef ecosystem generated by grey reef shark
171 movements, monthly network edge densities were extracted for each sex for every
172 month of the study. Edge density is the proportion of edges (movements connecting
173 receivers) existing in the network, out of the total number of edges possible for that
174 network (if all receivers were linked by movements to every other receiver; [30]).
175 Movement networks with higher edge densities are more densely connected and
176 thus, individuals have a greater number of routes they can choose from to move
177 through the system [2]. Analyses of variance were run to explore whether network
178 edge densities (the dependent variable) differed between sexes, seasons and years
179 (the independent variables).

180 Estimating nitrogen transfer throughout the atoll

181 In order to estimate shark-mediated nutrient flow around Palmyra Atoll and highlight
182 areas important to nutrient connectivity, we calculated the potential quantity of
183 nitrogen (N) that these predators may distribute within Palmyra Atoll during the ≤ 110

184 hour filtered movement network. Length-weight relationships from [32] were used to
185 estimate the weight of each tagged individual (for all but one female for which total
186 length was not recorded). Egestion rates of N for each individual within Palmyra Atoll
187 per day were then calculated by using the upper limit of 2% (for carcharhinid sharks)
188 of body weight ingested per day [33]. Absorption efficiency was set at 76% for
189 organic matter based on estimates from lemon sharks [31]. We estimated N transfer
190 using the method described in Nelson et al. [34], where the total egested kg N per
191 day is the product of the biomass ingested by an individual shark, the biomass
192 egested, the absorption efficiency, and the percent N found in grey reef shark tissue
193 at Palmyra Atoll (14.84 ± 0.065 % N mean \pm SE [7]). For every tagged individual, we
194 multiplied their estimated daily egested N (kg) by their residency time within the
195 array, to give a cumulative estimate over the entire study period. To extrapolate to
196 the population level, we took the average length of a male (138.7 cm) and female
197 (146 cm) grey reef shark from [35], and the species abundance and sex ratio
198 estimates from [24]. For all equations used, see ESM 2.

199 Finally, the estimates of daily egested N by tagged sharks were then mapped
200 spatially to explore which areas around Palmyra Atoll were likely to experience the
201 largest influx of shark-derived N. In order to incorporate the movement of the grey
202 reef sharks with the time they spent in different areas of the atoll, we calculated a
203 sex-dependent dynamic residency score for each receiver. This score incorporated,
204 a residency index (the proportion of days the receiver detected a male/female shark
205 over the study period), and the receiver's node strength (which combines the number
206 of connections a node had (i.e. weighted degree) and the relative frequency with
207 which those connections were used). Estimates of N distribution by the tagged male
208 and female sharks were then spatially mapped according to the relative dynamic

209 residency score of each receiver; see ESM 2 for further information. Statistical
210 analyses were completed in R (R Core Team 2016, [36]) and mapping in QGIS
211 2.14.0 (QGIS Development Team 2016, [37]).

212 **Results**

213 ***Connectivity Within the Network***

214 Across the study period, combining both sex's movements, just under half of all
215 edges possible in the network were present each year (edge density per year, mean
216 [SD] = 0.477 [0.014]; ESM 3). Females utilised a larger proportion of possible routes
217 within the atoll than males, indicated by the female's significantly higher monthly
218 edge density ($F_{1, 94} = 98.8, P < 0.01$; Fig. 2). Unlike females, the monthly edge density
219 of the male network differed significantly between years (females, $F_{1, 46} = 0.358, P =$
220 0.55 ; males, $F_{1, 46} = 17.3, P < 0.01$; Fig. 2), suggesting that, over the study period,
221 males were less consistent in the linkages generated across the atoll. Between
222 seasons, there was no significant difference in monthly edge density for either sex
223 (females, $F_{3, 44} = 0.920, P = 0.44$; males, $F_{3, 44} = 0.960, P = 0.42$).

224 ***Estimating Nitrogen Transfer Throughout the Atoll***

225 In total, over the four-year duration of the study, tagged male ($n = 13$) and
226 female ($n = 27$) grey reef sharks were estimated to have egested 42.11 ± 0.19 and
227 119.05 ± 0.52 kg, respectively, of N across the atoll and nearshore ecosystem.
228 Given that 86% of biomass consumed by grey reef sharks at Palmyra is thought to
229 be derived from pelagic resources [7], we predict that over the study period (1461
230 days) there was a maximum potential biomass subsidy of 138.60 ± 0.61 kg N
231 transported onto Palmyra Atoll reefs by the tagged individuals. Based on the
232 frequency with which the tagged sharks moved between, and spent time at specific

233 receiver locations, derived from our sex-specific movement networks, we then
234 predict where the nitrogen is likely deposited (Table 2; Fig. 3). We also visualise the
235 relative frequency of shark movements between each geographic zone (backreef,
236 forereef and lagoon), to further explore the relative fluxes of N between different
237 habitats (Fig. 3).

238 Using the mean length of male and female grey reef sharks sampled by [35],
239 an average male and female individual was estimated to egest as much as $0.008 \pm$
240 0.00004 and 0.011 ± 0.00005 kg d⁻¹ of pelagic nitrogen in Palmyra Atoll,
241 respectively. Taking recent population estimates and sex ratios (8344 individuals,
242 44% male, 56% female) from [24], we extrapolate to the population, estimating a
243 total biomass transfer of 94.52 ± 0.42 kg N d⁻¹, of which as much as 81.28 ± 0.36 kg
244 N d⁻¹ is a subsidy from pelagic resources brought to the reef by grey reef sharks.

245 **Discussion**

246 Reef sharks transfer a significant amount of nitrogen to and within an isolated atoll,
247 but the degree of connectivity differs between the sexes, with females utilising a
248 higher number of routes throughout the nearshore ecosystem. Thus, in doing so,
249 females, which are also typically larger than males, transfer nutrients more broadly
250 across the atoll. Enhancing the understanding of these habitat linkages within reef
251 ecosystems is critical to assist management and conservation strategies, protect
252 movement corridors and respond to potential changes in nutrient dynamics [7].

253 Higher coverage of N distribution across the atoll by female sharks is likely
254 due in part to female grey reef sharks being larger than males [35], as well as having
255 higher movement rates within nearshore waters. By calculating kernel utilisation
256 distributions of acoustically tagged grey reef sharks at Palmyra Atoll, Bradley et al.

257 [24] found that, compared to females, the activity space of male sharks was slightly
258 larger, something which is supported here by the distribution of dynamic residency
259 scores (Fig. 3). Along with our results, this suggests that males may disperse more
260 than females, potentially spending more time offshore, beyond the receiver array.
261 Sexual segregation in the nearshore and offshore environment has been recorded in
262 other populations of grey reef sharks, as well as other carcharhinids, and is
263 suggested to be due to differential reproductive or foraging strategies [8]. The
264 difference in routes utilised between sexes and their differing role in nutrient transfer
265 needs to be incorporated into conservation plans, so areas important to or preferred
266 by males and females are managed appropriately, ensuring each sex maintains their
267 role in fostering connections throughout the ecosystem. Although male sharks
268 utilised fewer routes, they also increased the proportion of routes they used over the
269 years, even though the number of males detected decreased after 2012. This
270 suggests the movement corridors utilised are not consistent over time for subsets of
271 the population. This also demonstrates that measuring the efficacy of management
272 strategies such as marine protected areas will require ongoing monitoring, because
273 as animal movement patterns change, spatial strategies may need to be modified to
274 ensure movement corridors remain protected. This may become even more
275 important as marine ecosystems experience rapid effects of climate change.

276 There were no differences between seasons in the proportion of routes
277 utilised. Grey reef shark movements on the Great Barrier Reef were not driven by
278 environmental factors such as water temperature, rainfall or wind speed, and more
279 likely related to biotic factors such as reproduction [38]. These results either reflect a
280 resilience to change in environmental conditions within the movement network, or
281 that environmental conditions experienced in these tropical systems were not

282 variable enough to have an impact (average temperature for each season ranged
283 from 27.2°C (in March to May 2012) to 29.5°C (in September to November 2014)).
284 Due to reef sharks potentially being isolated from alternative suitable habitat, they
285 may have higher tolerances to the range in local environmental conditions to avoid
286 changing movement patterns [38].

287 Due to an extensive eight year, tag-recapture program at Palmyra that has led
288 to accurate estimates of population size [24], we were in a unique position to be able
289 to quantify population level estimates of N distribution. The within-geographic-zone
290 movements are potentially assisting nutrient recycling, as sharks may be egesting
291 nutrients in the same habitat in which they were consumed [28]. For instance, from
292 our analyses it can be seen that in some cases there was a high level of connectivity
293 between nearby receivers (such as between acoustic receivers 10 and 16); this is
294 also reflected in the high proportion of within-geographic-zone movements (Fig. 3).
295 Moreover, it has recently been shown that grey reef sharks demonstrate strong
296 residency within specific areas at the sub-habitat level [27]. In addition, grey reef
297 sharks demonstrate vertical movement [27,39]; thus, the predators may be
298 transporting nutrients vertically within habitats as well [9]. Some routes and receiver
299 locations along which the largest inputs of N were estimated to have occurred by the
300 tagged sharks crossed between reef zones, demonstrating the potential for grey reef
301 sharks to contribute to nutrient translocation. For example, just over 35% of
302 movements by the tagged grey reef sharks that were recorded by the receiver array
303 occurred between the forereef and backreef (Fig. 3).

304 With approximately 86% of grey reef shark biomass derived from pelagic
305 resources [7], these sharks may be distributing large quantities of nutrients onto the
306 reef that could not have been produced within the atoll itself. Coral reefs are located

307 in nutrient-limited oceanic waters, yet often support very high biodiversity and
308 productivity [40]. While previous focus has been on tight nutrient cycling, research
309 has shown that within coral reefs, fish are an important nutrient reservoir; both coral
310 growth and primary production are enhanced by fish storing nutrients (in biomass)
311 and egesting them [41–43]. New research indicates that, within reef systems, these
312 fish derived nutrients may play an important role in the maintenance of ecosystem
313 dynamics [44]. Just how important might these shark-derived nutrient subsidies be in
314 Palmyra? Palmyra Atoll has been recorded to have an average of 1.75 μM of
315 dissolved inorganic nitrogen (ammonium, nitrates and nitrites) [45], which
316 corresponds to between 32 and 109 μg of nitrogen containing compounds per litre of
317 water. In addition, during *in situ* nutrient sampling at locations around Palmyra Atoll
318 (from 2006 to 2012) of nitrate and nitrite, a combined maximum of 15.21 μM was
319 recorded ($n = 125$, range 0.08 – 15.21 μM ; [46]), corresponding to 942 μg of nitrate
320 and nitrite per litre of water. Therefore, our estimations of an average-sized individual
321 male and female grey reef shark subsidising the reef with as much as $0.008 \pm$
322 0.00004 and 0.011 ± 0.00005 kg d^{-1} , respectively, of pelagic-derived N into the atoll,
323 potentially provides a substantial contribution to reef primary productivity. While the
324 precise effects of this nutrient subsidy on Palmyra's benthic communities remain to
325 be explored, changes in grey reef shark population size will likely lead to disruptions
326 in nutrient transport dynamics on this typical, nutrient-limited coral reef. Interspecific
327 interactions between grey reef sharks and blacktip reef sharks may also alter nutrient
328 dynamics, due to strong spatial partitioning between the two species [27]. Removal
329 or reduction of one species may change the degree of among-habitat movements by
330 the other, potentially altering nutrient deposition. For example, a loss of blacktip reef

331 sharks may cause increased deposition of pelagic N into the lagoons by the grey
332 reef sharks [27].

333 We recognise that these results should be interpreted with caution due to the
334 fact that we do not know exactly where sharks go once they leave one receiver and
335 arrive at another, and that not all egested material will be deposited within Palmyra
336 Atoll; hence, we stress that these are estimates of *potential* nutrient flow. However,
337 this is the first study to explicitly attempt to measure shark-derived nutrient transfer
338 using a model that incorporates both the movement dynamics and residency
339 patterns of free-ranging sharks. With the current available data and limited
340 knowledge on shark daily rations, absorption and faecal production rates, this study's
341 method enhances our understanding of the role grey reef sharks may play in nutrient
342 connectivity.

343 Acoustic telemetry data and network theory are emerging as particularly
344 useful tools for exploring habitat use and animal movements [6]. However, acoustic
345 telemetry does have limitations. For example, here, as in many telemetry studies, the
346 number of individuals with active tags was not consistent over the entire study
347 period. This was partly due to some individuals being tagged after the beginning of
348 2011. In addition, by focusing on movements between different receivers, if sharks
349 left Palmyra Atoll's forereef to feed within pelagic waters and then were next
350 detected on the forereef by the same receiver (i.e. self-loops), the movement would
351 not have been included within the analyses. Therefore, the number of movements
352 made by the tagged individuals is likely to be on the conservative side. In addition,
353 acoustic tagging of sharks was spatially non-uniform due to weather-dependent
354 access to sampling sites. This will not affect the quantitative estimates of total N
355 transferred, but it needs to be stressed that the visual representation of N

356 redistribution (Fig. 3) is a spatial estimation for our tagged sharks only, not the
357 population. Despite the limitations, acoustic telemetry can serve as a powerful
358 instrument to quantify the movements of marine predators, particularly in remote or
359 challenging environments, as well as over large areas [3,6,47].

360 In light of the fundamental influence that marine predators have on the
361 functioning of ecosystems, understanding how these animals foster within- and
362 cross-system connections is crucial to produce effective conservation and
363 management strategies [7,48]. Palmyra Atoll, one of a limited number of near-
364 pristine atolls, offered a valuable opportunity to assess unrestricted within-system
365 connectivity fostered by grey reef shark movements and their potential role in
366 nutrient transport [7,23]. This study offers a useful comparison for assessments of
367 predator-initiated connections within exploited reefs, to predict the effects of
368 exploitation on undisturbed reefs [49]. Further, it extends our understanding of grey
369 reef shark movements across various reef systems, which is crucial for developing
370 effective conservation approaches and species vulnerability assessments. Finally, it
371 provides the first quantitative estimate, to our knowledge, of population-level nutrient
372 transport in marine predators with implications for the long-term resilience of the
373 coral reef ecosystems.

374

375 **Competing interests:** We have no competing interests.

376 **Ethical approval:** This project has been certified by the Institutional Animal Care and Use
377 Committee (IACUC), University of California, Santa Barbara, Protocol no. 856. Sharks were
378 captured at Palmyra Atoll, which has been a U.S. National Wildlife Refuge since 2001 and
379 part of the Pacific Remote Islands Marine National Monument since 2009, under U.S. Fish
380 and Wildlife Service special use permits (Permit numbers #12533–14011, #12533–13011,

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383 **Authors' contributions:** JJW, YPP and DMPJ conceived the project, JJW and DMPJ
384 analysed the telemetry data and wrote the manuscript, with DB conducting the nitrogen flux
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402 **Data accessibility:**

- 403 • Raw acoustic telemetry data: https://github.com/JJWilliams24/Palmyra_Atoll

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555 **Tables**

556 **Table 1** Summary of the tagged grey reef sharks and their movements detected by the
 557 acoustic receivers in Palmyra Atoll; mean values displayed in the table are presented with
 558 one standard deviation.

	All sharks	Female	Male
Number of individuals detected			
2011	27	20	7
2012	38	25	13
2013	33	22	11
2014	30	20	10
Entire study period	41	28	13
Number of movements \leq110 hours			
2011	16,665	13,559	3,106
2012	21,750	17,177	4,573
2013	29,639	24,648	4,991
2014	31,288	24,933	6,355
Entire study period	99,342	80,317	19,025
Days at liberty between 2011 and 2014^a			
Min	21	21	40
Max	1,439	1,437	1,439
Mean (SD)	985 (396)	977 (410)	1,001 (380)
Fork length (m)			
Min	0.86 ^b	0.86 ^b	1.03
Max	1.47 ^b	1.47 ^b	1.31
Mean (SD)	1.18 (0.15) ^b	1.21 (0.17) ^b	1.13 (0.10)

^a Days at liberty are the number of days between an individual's first and last detection in the dataset.

^b The fork length for one female was missing, thus for the measurements of all sharks, n = 40, and for females, n = 27.

559 **Table 2** The five nodes around which the greatest quantity of nitrogen (N) is estimated to
 560 have been distributed by the tagged male or female grey reef sharks per day, based on the
 561 dynamic residency score of each node. See Fig. 1 for location of nodes.

Acoustic receiver (geographic zone ^a)	Node strength	Residency index (%)	Dynamic residency score	Quantity of nitrogen potentially distributed by the tagged grey reef sharks (g d ⁻¹)
Females				
18 (FR)	11,674	89.73	10,474.62	15.66
40 (BR)	9,023	81.23	7,329.64	10.96
16 (FR)	7,360	84.11	6,190.47	9.26
10 (FR)	7,122	79.66	5,673.21	8.48
60 (FR)	4,094	92.19	3,774.33	5.64
Males				
16 (FR)	1,704	82.26	1,401.72	5.24
60 (FR)	1,702	75.55	1,285.83	4.80
10 (FR)	1,567	55.34	867.22	3.24
18 (FR)	1,727	39.11	675.43	2.52
40 (BR)	1,413	32.26	455.84	1.70

^a Geographic zones include the fore-reef (FR), back-reef (BR) and lagoon.

562 **Figure legends**

563 **Fig. 1** Spatial array of acoustic receivers at Palmyra Atoll; only receivers included within the
564 analyses performed in this study are shown; the colour version of this figure is available
565 online. Satellite image from Google Earth.

566 **Fig. 2** The monthly edge densities of movement networks for male and female grey reef
567 sharks (*Carcharhinus amblyrhynchos*) over each year of the study period; these differed
568 significantly between the sexes ($P < 0.01$); the boxplots present the median and quartile
569 values, the circles denote outliers.

570 **Fig. 3** The four-year movement networks of (a) female ($n=28$) and (b) male ($n=13$) grey reef
571 sharks overlaid on kernel densities that represent dynamic residency at each receiver.
572 Networks include only movements that took ≤ 110 hours and have been filtered to show the
573 75 most frequently used routes by each sex. Edge thickness represents the frequency of
574 movements (M range = 36-2711; F range = 129-13131). The dynamic residency score was
575 calculated as the node strength (S_i) of each receiver divided by 100 and multiplied by a
576 standard residency index, R (M range = 1-1401; F range = 2-10474). The size of each node
577 represents the potential N redistribution by the tagged grey reef sharks (see Table 2). The
578 inset habitat networks illustrate the relative frequency of shark movements within and
579 between geographic zones, with the size of the nodes representing the relative detection
580 frequencies in each habitat; the left-hand nodes represent the zone the sharks moved into
581 after last being detected in the habitat depicted by the right-hand node. The base map of
582 Palmyra Atoll was acquired from [50].