



Title	Albatross-borne loggers show feeding on deep-sea squids: implications for the study of squid distributions
Author(s)	Nishizawa, Bungo; Sugawara, Takanori; Young, Lindsay C.; Vanderwerf, Eric A.; Yoda, Ken; Watanuki, Yutaka
Citation	Marine ecology progress series, 592, 257-265 https://doi.org/10.3354/meps12482
Issue Date	2018-03-29
Doc URL	http://hdl.handle.net/2115/73339
Type	article (author version)
File Information	MEPS_v592_257-265.pdf



[Instructions for use](#)

1 Title: Albatross-borne loggers show feeding on deep-sea squids: implications for the
2 study of squid distributions

3

4 Running page head: Foraging behavior of Laysan albatrosses

5

6 Authors:

7 Bungo Nishizawa^{1,*}, Takanori Sugawara², Lindsay C. Young³, Eric A. Vanderwerf³,
8 Ken Yoda², Yutaka Watanuki¹

9

10 Author affiliations:

11 ¹Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1, Minato, Hakodate,
12 Hokkaido, 041-8611, Japan

13 ²Graduate School of Environmental Studies, Nagoya University, Furo, Chikusa, Nagoya,
14 Japan

15 ³Pacific Rim Conservation, 3038 Oahu Avenue, Honolulu, HI 96822, USA

16

17 *Corresponding author: nishizawa@salmon.fish.hokudai.ac.jp

18

19 ABSTRACT: How surface-feeding albatrosses feed on deep-sea squids has long been a
20 mystery. We investigated foraging behavior during daylight hours of 20 Laysan
21 albatrosses *Phoebastria immutabilis* breeding in Hawaii using GPS and camera-loggers.
22 The birds traveled to the North Pacific Transition Zone up to 600 km north of their
23 breeding site. The camera images showed that Laysan albatrosses fed on large (~1 m
24 body length), intact floating dead squids (6 events) and floating fragmented squids (10

25 events) over deep oceanic water (> 2000 m) while they flew in a straight path without
26 sinuous searching. Feeding events on squids were not observed during the trip when
27 fishing vessels were photographed and seemed to be distributed randomly and sparsely.
28 Thus, this study suggests that Laysan albatrosses found large, presumably
29 post-spawning, squids opportunistically while they were travelling during daylight
30 hours. Although we did not find cetaceans in our surface pictures, we could not rule out
31 the possibility that birds fed on squids, especially those fragmented, in the vomit of
32 cetaceans in depth. This study demonstrates the usefulness of combining animal-borne
33 GPS and camera-loggers on wide-ranging top predators for studying the distribution of
34 little known deep-sea squids and their importance in the diet of marine top predators.

35

36 KEY WORDS: *Phoebastria immutabilis* • GPS-logger • Camera-logger • *Taningia*
37 *danae* • *Onychia robusta* • Hawaiian Islands • Area-restricted search

38

39

INTRODUCTION

40 Oceanic deep-sea squids are important prey of marine top predators including fish,
41 marine mammal, and seabirds (Clarke 1996, Croxall & Prince 1996, Klages 1996,
42 Smale 1996). For example, they are a large part of the diet of highly migratory tunas
43 (*Thunnus albacares* from Indian, Pacific, and Atlantic Ocean, 13% by mass and *T.*
44 *obesus* from Atlantic and Pacific Ocean, 41% by mass) and swordfish (*Xiphias gladius*
45 from Atlantic Ocean, 60% by mass) (Smale 1996). At least 60 of 67 odontocete species
46 include squids in their diet and, in at least 28 odontocetes (Delphinidae, Phocoenidae,
47 Physeteridae, and Ziphiidae), squids form the main food up to more than 75% of the
48 diet (Clarke 1996). Despite the importance of deep-sea squids to the diet of marine top

49 predators, little information is available on the biology and ecology of these squids. This
50 limitation is due to our lack of sampling and observation, and also our limited
51 understanding of when, where, and how large top predators prey on them.

52

53 Among seabirds, albatrosses feed by seizing prey while on the surface of the water and
54 feed mainly on squids, including deep-sea dwelling species, which form almost half the
55 food fed to chicks of five species breeding in the southern hemisphere (Wandering
56 albatross *Diomedea exulans*; 59% by mass, Grey-headed albatross *Thalassarche*
57 *chrysostoma*; 58%, Black-browed albatross *T. melanophrys*; 16%, Sooty albatross
58 *Phoebastria fusca*; 42%, and Light-mantled sooty albatross *P. palpebrata*; 46%, Croxall
59 & Prince 1996) and two species breeding in the Hawaiian Islands (Black-footed
60 albatross *Phoebastria nigripes*; 32% by volume and Laysan albatross *P. immutabilis*;
61 65%, Harrison et al. 1983). How surface-feeding albatrosses feed on deep-sea squids
62 has long been a mystery. Albatrosses are hypothesized to feed on squids floating dead
63 after spawning (Rodhouse et al. 1987, Lipinski & Jackson 1989), those related to
64 fisheries including discards from fishing vessels and squid baits of longliners
65 (Thompson 1992, Croxall & Prince 1994, Duffy & Bisson 2006), those in the vomit
66 from cetaceans (Clarke et al. 1981), those alive when the squids come to the surface at
67 night (Imber & Russ 1975, Imber 1992), or those alive aggregated near the surface at
68 productive oceanic fronts (Xavier et al. 2004, Rodhouse & Boyle, 2010). These
69 hypotheses are not exclusive and are still under debate.

70

71 Recent development of bio-logging techniques has improved our understanding of the
72 foraging behavior of albatrosses, and have shown that Wandering albatrosses feed on

73 widely distributed large prey during daytime (Weimerskirch et al. 2005, 2007) and that
74 Black-browed albatrosses followed a killer whale *Orcinus orca* presumably for a
75 feeding opportunity (Sakamoto et al. 2009a). Simultaneous deployment of GPS- and
76 camera-loggers on albatrosses can provide us with information on when, where, and
77 how these oceanic predators feed on deep-sea squids. They also provide new
78 information on the seasonal patterns and spatial distributions of these squids, and
79 importance of them as food of albatrosses.

80

81 Among the hypotheses mentioned above, we tested the post-spawning floater,
82 fishery-related, and oceanic front hypotheses by investigating foraging behavior of
83 Laysan albatrosses breeding on Oahu, Hawaiian Islands, during daylight hours using a
84 combination of GPS- and camera-loggers. Laysan albatrosses are a suitable marine top
85 predator to test these hypotheses because they feed on both deep-sea dwelling squids
86 and Argentine squids *Illex argentinus* (Harrison et al. 1983, Duffy & Bisson 2006,
87 Walker et al. 2013). Argentine squids are often used as bait in the swordfish longline
88 fishery in Hawaii, which provides an opportunity to test the fishery-related squid
89 hypothesis. Images collected by the bird-borne cameras allow us to identify squid
90 species, whether squids were dead or alive, and whether they were intact or fragmented.
91 Such images also can reveal the presence of fishing vessels (Votier et al. 2013). If
92 Laysan albatrosses feed on floating dead squids without any sign of fishing vessels,
93 these squids may be natural mortalities including post-spawning floaters for resident
94 species or cetacean vomits. Information on whether dead squids are intact or fragmented
95 may be useful to determine post-spawning floater or cetacean vomit hypotheses. If birds
96 feed on dead squids with fishing vessels or squid baits behind the longliners, these

97 squids may be related to fisheries (i.e. discard or bait). If birds feed on squids alive only,
98 post-spawning floater and fishery-related hypotheses would not be supported, and these
99 squids may be associated with specific oceanographic features such as productive
100 oceanic fronts. Finally, we discuss the importance of feeding on squid during daylight
101 hours for the energy requirements of Laysan albatrosses during the chick-rearing period.

102

103

MATERIALS AND METHODS

104

Field study

105 The study was carried out at Kaena Point Natural Area Reserve (21°34'N, 158°16'W)
106 on Oahu, Hawaii, during the early chick-rearing period in February–March 2015. We
107 instrumented 38 birds rearing chicks with a GPS-logger (GiPSy4, TechnoSmart, 23 g)
108 on the back and a camera-logger (Broadwatch, 34 g or Little Leonardo, 20 g) on either
109 the back (for birds brooding chicks) or belly (for birds after brooding chicks) with
110 Tesa[®] tape (Table S1 in the Supplement). To avoid potential negative effect of
111 camera-attachment on small chicks we did not attach cameras on the belly of albatrosses
112 brooding chicks but on the back. We attached cameras on the belly of albatrosses after
113 they finished brooding their chicks. Positions and images were sampled every 1 or
114 3-minutes continuously and 1 to 10-minutes only in daytime (6:00–19:30 in local time),
115 respectively (Table S1 in the Supplement). We captured birds by hand as they were
116 about to leave the colony. The field work was conducted under permits from the State
117 of Hawaii, Department of Land and Natural Resources, Division of Forestry and
118 Wildlife (Permit No. WL18-01), Natural Area Reserves System, and U.S. Geological
119 Survey Bird Banding Laboratory (Permit #23462). Total mass of the equipment was
120 65–70 g (2.7–2.9% of mean body mass of 2.41 kg), which is below the generally

121 accepted 3% threshold for adverse behavioral effects of gliding seabirds (Phillips et al.
122 2003). All birds carrying devices showed no chick desertion during the experiments and
123 they continued rearing chicks after removal of the devices.

124

125

Data processing

126 We used images obtained from camera-loggers to determine prey type including those
127 dead or alive and intact or fragmented, bird activity (i.e. flying or landing on water), and
128 presence of fishing vessels and cetaceans. In cases where the GPS was set to record
129 every 3-minutes (3 of 26 trips, Table S2 in the Supplement), we linearly interpolated
130 positions at 1-minute intervals. We also linearly interpolated positions that would have
131 required unrealistic flying speeds exceeding 80 km h^{-1} (Suryan et al. 2006). We
132 assumed that birds moving slower than 9 km h^{-1} had landed on the sea surface, while
133 those moving faster were flying (Weimerskirch et al. 2002, Guilford et al. 2008,
134 Zavalaga et al. 2010) (Fig. S1 in the Supplement). We defined an “on-water bout” as
135 consecutive landing positions between two flight positions and a “flight bout” as
136 consecutive flight positions between two landing positions. In addition, we defined the
137 “position of on-water bout” as the last position during an on-water bout. Using 23,455
138 images from 26 trips of 20 birds where activity (i.e. flight vs. landing on-water) was
139 determined, 94% of bouts were correctly designated as flight or on-water bouts.

140

141

Data analysis

142 It has been predicted that the movements of foraging animals are adjusted to the
143 hierarchical spatial distribution of prey resources in the environment, and that decisions
144 to modify movement in response to heterogeneous resource distribution are

145 scale-dependent (Fauchald 1999, Pinaud & Weimerskirch 2005). Thus, we explored the
146 relationships between foraging movements of albatrosses and prey distribution (i.e.
147 squid) at a large spatial scale (e.g. 10–100 km) by examining area-restricted search
148 (ARS) behavior, and at a small spatial scale (e.g. < 20 km) by examining changes in
149 azimuth of the movement path 30-minutes before and after squid capture. We examined
150 ARS zones, where sinuosity of movement increased extraordinarily, based on First
151 Passage Time (FPT) analysis (Fauchald & Tveraa 2003). Small scale ARS zones when
152 the bird was landing on the water dramatically inflated the variance in FPT and reduced
153 the ability to detect larger-scale ARS zones (Pinaud 2008). To remove this problem, we
154 considered landing on the water as flying with a constant speed of 34 km h⁻¹ (i.e.
155 average flight speed of this species) by removing locations following Pinaud (2008).
156 FPT was calculated every 5 km for a radius r from 5 to 500 km using with the program
157 Ethographer version 2.03 (Sakamoto et al. 2009b). The plot representing variance in log
158 (FPT) as a function of r allowed us to identify the ARS scales by peaks in the variance.
159 In this calculation, FPT was log transformed to make the variance independent of the
160 magnitude of the mean FPT (Fauchald & Tveraa 2003). The maximum first passage
161 time, at the appropriate ARS spatial scale, was then identified as the most intensively
162 searched foraging area for each individual (Kappes et al. 2010). These analyses were
163 carried out using Igor Pro version 6.3.4.1 and ArcGIS 10.0.

164

165 To understand when birds found squid and if they increased searching after finding
166 squid, we calculated changes in azimuth of the movement path 30-minutes before and
167 after prey capture using split moving-window boundary analysis (Cornelius & Reynolds
168 1991). We used a window size of 5-minutes for trips where positions were obtained

169 every 1-minute (excluded GPS positions at 3-minutes intervals from this analysis), and
170 then calculated change in azimuth between each consecutive GPS position at 1-minute
171 intervals.

172

173 To investigate whether foraging locations of birds were randomly distributed, we
174 carried out a nearest neighbor analysis (Clark & Evans 1954) using the average nearest
175 neighbor tool in ArcGIS 10.0. For this analysis, we used all positions of on-water bouts
176 of 5 trips from 4 birds in which the camera was mounted on the belly (Table S2 in the
177 Supplement), which allowed us to distinguish on-water bouts with or without prey.
178 Values are presented as means \pm SD with their range and the number of sample.

179

180

RESULTS

181

Deep-sea squids fed by albatrosses

182 Both GPS- and camera data were recovered from 20 birds representing 26 trips to sea.
183 Tracking period was 8.8 ± 9.5 days (range 2.0–39.0 days, $n = 20$ birds). Laysan
184 albatrosses foraged mostly over the subtropical and North Pacific Transition Zones (Fig.
185 1). The mean duration of foraging trips was 77.0 ± 66.3 hours (range 5.7–340.0 hours, n
186 = 26 trips, Table S2 in the Supplement) with a mean maximum foraging range of 598.2
187 ± 569.3 km (range 71.3–2820.7 km, $n = 26$ trips, Table S2 in the Supplement). A total
188 of 28,068 images were collected from 26 trips of 20 birds (Table S2 in the Supplement),
189 which covered most of duration ($87.0 \pm 22.0\%$, range 5.9–100%, $n = 26$ trips, excluding
190 nighttime, Table S2 in the Supplement) of the 26 foraging trips. Squids were visible in
191 23 images corresponding to 16 events (i.e. at different positions) from 7 trips of 7 birds
192 (Table S2 in the Supplement). Fishing vessels were visible in 69 images corresponding

193 to 9 events (i.e. different fishing vessels at different positions) from 6 trips of 5 birds
194 (Table S2 in the Supplement). No cetaceans or potential prey other than squids were
195 visible in any images. All images taken during 7 trips of 7 birds that encountered squids
196 during their whole trips did not show any fishing vessels (Table S2 in the Supplement).
197 All squids photographed were dead and floating at the sea surface (Fig. 2). Ten of the
198 squids were fragmented (Fig. 2a) and six were intact (Figs. 2b–d). At least two squids
199 were greater than 1-m in total length using size of the birds as a reference, and were
200 identified as *Taningia danae* and *Onykia robusta* (Figs. 2c & 2d). Frequency of trips
201 when birds encountered at least one squid was greater for those carrying a camera on
202 the belly (13 squid feeding events during 4 (4 birds) of 5 trips (4 birds), Table S2 in the
203 Supplement) than on the back (three squid feeding events during 3 (3 birds) of 21 trips
204 (16 birds), Table S2 in the Supplement) (Chi-squared test, $\chi = 8.864$, $df = 1$, $p < 0.05$),
205 presumably because the camera on the back sometimes failed to catch images of squids
206 under the water. Birds with a camera on their belly landed on the water 71 times and
207 encountered squids 13 times (18%), with on-water duration of 20 ± 17 min (1–70 min, n
208 = 16 squid feeding locations from seven trips of seven birds with camera mounted on
209 their back or belly).

210

211 Birds encountered squids outside of ARS zones (Fig. 1). Birds did not change the speed
212 ($< 55 \text{ km h}^{-1}$, Fig. 3a) and azimuth of movement ($< 20^\circ$, Fig. 3b) of their flight path
213 30-minutes before or after feeding on squids (using 8 foraging events from 5 trips of 5
214 birds that had GPS positions at 1-minute intervals and excluded the other 8 foraging
215 events from 2 trips of 2 birds that had GPS positions at 3-minutes intervals from this
216 analysis, Table S2 in the Supplement, see also MATERIALS AND METHODS),

217 indicating that the birds kept straight flight paths before and after foraging on squids
218 (Fig. S2 in the Supplement).

219

220 **Distribution of deep-sea squids**

221 Locations of squids were widely distributed (Fig. 1). Nearest neighbor analysis
222 indicated that all on-water bouts (i.e. with and without squids) were concentrated
223 around the Hawaiian Islands ($z = -11.48$, $p < 0.05$), while those with squids were
224 randomly distributed within the area covering on-water bouts with squids ($z = -0.17$, $p =$
225 0.86). The average distance between two consecutive squid feeding events was 34 ± 9
226 km (22–46 km, $n = 4$ distances from two birds; one bird provided two squid feeding
227 events within a trip, and the other bird provided three feeding events within one trip and
228 two feeding events within another trip).

229

230 **DISCUSSION**

231 We found that Laysan albatrosses fed on large intact floating dead squids including
232 *Onykia robusta* and *Taningia danae* which are resident species in Hawaiian waters
233 (Wakabayashi et al. 2007, Jereb & Roper 2010), and on unidentified floating
234 fragmented squids during daytime. Our Laysan albatrosses did not feed on living squids
235 during daytime. However, we still have possibility that our camera with 1–10 min
236 sampling interval failed to catch images of living squids that could easily escape from
237 the birds. Sampling of images at a higher rate would help to confirm this. *O. robusta*
238 and *T. danae* are deep-sea dwelling squid species staying at depths of 250–900 m during
239 daytime (Kubodera et al. 2007, Jereb & Roper 2010) and are previously recorded in the
240 regurgitations of Laysan albatrosses and black-footed albatrosses breeding in Hawaii

241 Islands (Harrison et al. 1983, Walker et al. 2013). Three sources of these dead floating
242 squids have been suggested: post-spawning mortality of squids (Rodhouse et al. 1987),
243 vomit of odontocete cetaceans (Clarke et al. 1981), and fishery-related squids including
244 squid baits for longliners and discards from fishing vessels (Thompson 1992, Duffy &
245 Bisson 2006).

246

247 Considering that many species of squids, including deep-sea dwelling species, are
248 semelparous (i.e. spawning happens during a single reproductive cycle) and die at 1–2
249 years of age after spawning (Hoving et al. 2014), if mating/spawning migrations
250 towards the surface followed by mass mortalities do occur, then these aggregations
251 would represent considerable, but sporadic, opportunities for surface-foraging seabirds
252 such as albatrosses (Rodhouse et al. 1987). Presence of paralarvae of *O. robusta* in
253 northern Hawaiian waters indicates that this species spawns there during fall and winter
254 (Wakabayashi et al. 2007). Although spawning grounds and spawning season for *T.*
255 *danae* are still unknown, this species is cosmopolitan with the exception of polar
256 regions, and small-sized specimens (62 mm in mantle length) were captured by nets in
257 northern Hawaiian waters during fall (Roper & Vecchione 1993). Thus, it is possible
258 that Laysan albatrosses feed on floating dead squids after they spawn.

259

260 Deep-sea squids might also become available to albatrosses through marine
261 mammal-seabird interactions. For example, sperm whales *Physeter macrocephalus*,
262 which feed on deep-sea squids, vomit periodically to empty their stomachs of
263 indigestible items including squid beaks which do not pass further down the gut (Clarke
264 1980, Clarke et al. 1981). Deep-sea squids recently vomited by a sperm whale have

265 been observed on the sea surface, and a wandering albatross has been observed feeding
266 on these during daylight hours in the south Atlantic (Clarke et al., 1981). Also, sperm
267 whales and other odontocetes in Hawaiian waters feed on deep-sea squids including *O.*
268 *robusta* and *T. danae* (Clarke & Young 1998), thus the vomit of them may also be
269 available to surface-foraging seabirds such as Laysan albatrosses in the region. Our
270 birds fed on intact squids, including *O. robusta* and *T. danae*, and fragmented squids. It
271 is unlikely that cetaceans regurgitate intact squids, therefore, the cetacean vomit
272 hypothesis is not supported at least for intact dead squids (*O. robusta* and *T. danae*).
273 Although no cetaceans were photographed during our study periods, we cannot rule out
274 the possibility that Laysan albatrosses feed on squid regurgitations from cetacean,
275 especially for fragmented squids, because our bird-borne still cameras with 1–10 min
276 sampling intervals only during daylight hours may have failed to catch images of
277 cetaceans underwater, especially when they might regurgitate food.

278

279 Laysan albatrosses are known to feed on squid baits (*Illex argentinus*, < 400 mm in
280 mantle length) used in the Hawaiian swordfish longline fishing (Duffy & Bisson 2006,
281 Jereb & Roper 2010), but feeding events on squids were not observed during the trip
282 when fishing vessels were photographed in our study. Considering that fishing vessels
283 can be easily found by albatrosses and albatrosses can be attracted to the fishing vessels
284 from long distances up to 30 km (Collet et al. 2015), fishery-related squids (i.e. discards
285 or baits) can potentially be consumed by albatrosses soon after (probably within a few
286 hours) when they are available. In addition, squids fed on by our birds were much larger
287 than bait species. Thus, squids fed by our birds may not be related to fisheries in this
288 region.

289

290 We therefore suggest that Laysan albatrosses feed on large floating dead, probably
291 post-spawning, squids in daytime at least. We could not, however, rule out the
292 possibility that Laysan albatrosses also feed on squids, especially fragmented squids,
293 from cetacean vomits. All identifiable albatross prey during daytime were squids in this
294 study. Sampling of images at a higher rate, and at night, would help to confirm this
295 conclusion.

296

297 How does this feeding strategy meet with daily energy demand? We explored daily food
298 consumption of Laysan albatrosses during the brooding periods as follows. Energy
299 contents of ommastrephid squids per wet gram is 4.26 kJ (Pettit et al. 1984). The
300 assimilation efficiency of seabirds fed on squid is 0.744 (Jackson 1986). In the present
301 study, Laysan albatrosses landed on the water 1.9 ± 0.8 times h^{-1} (range 0.9–3.8 times
302 h^{-1} , $n = 26$ trips, Table S2 in the Supplement), hence, 26 times during 13.5 hours in
303 daytime. Using the encounter rate of floating squids (18%, ratio of the number of
304 on-water bouts with squids to all on-water bouts, see RESULTS), Laysan albatrosses
305 encountered floating squids 4.7 times per day on average. Laysan albatrosses, one-third
306 the body mass of Wandering albatrosses, might ingest 108 g of prey per encounter event
307 (Wandering albatrosses ingested 324 ± 518 g prey in a foraging event, Weimerskirch et
308 al. 2005). From these values, the energy gain from dead floating squid per day is
309 estimated as follows: $4.26 \text{ (kJ/g)} \times 108 \text{ (g)} \times 4.7 \times 0.744 = 1608.81 \text{ (kJ)}$. Daily energy
310 expenditure of foraging (and also chick rearing) Laysan albatross is 2072.3 kJ (Pettit et
311 al. 1988). Which is to say, the energy gain from dead floating squid has the potential to
312 provide 77.6% of the daily energy expenditure for foraging Laysan albatrosses. This

313 estimate, though crude, suggests that foraging on dead floating squids during daytime
314 might be an important energy source for Laysan albatrosses.

315

316 Our camera could not take images at night, so it is possible that albatrosses feed on
317 squids and other prey under different circumstances at night, similar to Wandering
318 albatrosses that feed on small prey at night using sit-and-wait searching strategy (Imber
319 1992, Weimerskirch et al. 1997, 2005). Laysan albatrosses feed small-sized (< 144 mm)
320 ommastrephidae squids, fish, and crustaceans to their chicks (Harrison et al. 1983).
321 These small-sized squids and other micronekton stay in deep water during daytime but
322 come to the surface at night (Roper & Young 1975, Jereb & Roper 2010). Laysan
323 albatrosses have relatively high levels of rhodopsin, a light-sensitive pigment that is
324 typically found in high levels in nocturnal birds (Harrison & Seki 1987). A recent study
325 on foraging movements using GPS indicated that Laysan albatrosses relied on foraging
326 at night to a greater extent than black-footed albatrosses, though both species relied
327 mainly on foraging in daytime (Conners et al. 2015). Moreover, both species strongly
328 increased drift forage at night when the lunar phase was the darkest, suggesting they
329 feed on diel vertically-migrating micronekton including small-sized squids to some
330 extent (Conners et al. 2015).

331

332 Despite the importance of deep-sea squids in trophic connectivity between top predators
333 such as whales, seabirds and tuna and their prey such as zooplankton and small fish
334 (Rodhouse & Nigmatullin 1996), information on the biology and ecology of deep-sea
335 squids is quite limited. Deep-sea squids are widely distributed over the world's oceans,
336 and they are considered semelparous (Hoving et al. 2014). Our results suggest that

337 deep-sea squids such as *O. robusta* and *T. danae* spawn in the Pacific basin during our
338 winter periods and are distributed randomly and sparsely in the deep oceanic basin.

339

340 Our Laysan albatrosses fed on large floating dead squids outside of ARS zones and
341 opportunistically found them with straight flight paths over oceanic water without
342 sinuous searching. These findings indicate that Laysan albatrosses may be an
343 opportunistic feeder not to concentrate their foraging effort at specific places, which
344 might be related to spatial pattern of their main prey of squids (i.e. random distribution
345 with low predictability). Zollner & Lima (1999), using a generic model, predicted that
346 straighter movements are probably the most efficient way to search for randomly
347 distributed prey over large scales. Indeed, similar searching pattern occurs in Wandering
348 albatrosses; they follow long curvilinear search routes over oceanic waters where they
349 encounter larger prey at an average of every 64 km (Weimerskirch et al. 2005).

350

351 Squid beaks in the regurgitations of albatrosses provide information on cephalopod
352 distribution and biology (Cherel & Weimerskirch 1995, 1999). However, because squid
353 beaks remain in their stomach for unpredictable periods, sometimes more than nine
354 months (Xavier et al. 2005), the temporal and spatial resolution of these data are coarse.
355 Our study demonstrates the usefulness of combining animal-borne GPS and
356 camera-loggers on highly mobile seabird species to collect information on the spawning
357 area and distribution of little known deep-sea squids and their importance to marine top
358 predators.

359

360 *Acknowledgements.* We thank Dr. Toshie Wakabayashi for identifying squids in the

361 images. This study was supported by Japan Society for the Promotion of Science
362 (#26304029 to Y.W.).

363

364

LITERATURE CITED

365 Cherel Y, Weimerskirch H (1995) Seabirds as indicators of marine resources:
366 Black-browed albatrosses feeding on ommastrephid squids in Kerguelen waters. Mar
367 Ecol Prog Ser 129: 295–300

368 Cherel Y, Weimerskirch H (1999) Spawning cycle of onychoteuthid squids in the
369 southern Indian Ocean: new information from seabird predators. Mar Ecol Prog Ser
370 188: 93–104

371 Clark PJ, Evans FC (1954) Distance to nearest neighbor as a measure of spatial
372 relationships in populations. Ecology 35: 445–453

373 Clarke M (1980) Cephalopoda in the diet of sperm whales of the southern hemisphere
374 and their bearing on sperm whale biology. Discovery Reports, pp. 1–324

375 Clarke M, Young R (1998) Description and analysis of cephalopod beaks from
376 stomachs of six species of odontocete cetaceans stranded on Hawaiian shores. J Mar
377 Biol Assoc UK 78: 623–641

378 Clarke MR (1996) Cephalopods as prey. III. Cetaceans. Phil Trans R Soc Lond B 351:
379 1053–1065

380 Clarke MR, Croxall JP, Prince PA (1981) Cephalopod remains in regurgitations of the
381 wandering albatross *Diomedea exulans* L at South Georgia. Brit Antarct Surv B 54:
382 9–21

383 Collet J, Patrick SC, Weimerskirch H (2015) Albatrosses redirect flight towards vessels
384 at the limit of their visual range. Mar Ecol Prog Ser 526: 199–205

385 Connors MG, Hazen EL, Costa DP, Shaffer, SA (2015) Shadowed by scale: Subtle
386 behavioral niche partitioning revealed at the individual and species level in two
387 sympatric, tropical, chick-brooding albatross species. *Mov Ecol* 3: 28

388 Cornelius JM, Reynolds JF (1991) On determining the statistical significance of
389 discontinuities within ordered ecological data. *Ecology* 72: 2057–2070

390 Croxall JP, Prince PA (1994) Dead or alive, night or day: how do albatrosses catch
391 squid? *Antarct Sci* 6: 155–162

392 Croxall JP, Prince PA (1996) Cephalopods as prey: seabirds. *Philos Trans R Soc B:*
393 *Biol Sci* 351: 1023–1043

394 Duffy D, Bisson J (2006) The effect of pelagic longline fishing on Laysan and
395 Black-footed Albatross diets. *Pelagic Fish Res Prog* 11: 1–3

396 Fauchald P (1999) Foraging in a hierarchical patch system. *Am Nat* 153: 603–613

397 Fauchald P, Tveraa T (2003) Using first-passage time in the analysis of area-restricted
398 search and habitat selection. *Ecology* 84: 282–288

399 Guilford TC, Meade J, Freeman R, Biro D, Evans T, Bonadonna F, Boyle D, Roberts S,
400 Perrins CM (2008) GPS tracking of the foraging movements of Manx Shearwaters
401 *Puffinus puffinus* breeding on Skomer Island, Wales. *Ibis* 150: 462–473

402 Harrison CS, Hida TS, Seki MP (1983) Hawaiian seabird feeding ecology. *Wildl*
403 *Monogr* 85: 1–71

404 Harrison CS, Seki MP (1987) Trophic relationships among tropical seabirds at the
405 Hawaiian Islands. In Croxall, JP (ed) *Seabirds: feeding ecology and role in marine*
406 *ecosystems*. Cambridge University Press, Cambridge, Great Britain 305–326

407 Hoving HJT, Perez JAA, Bolstad KSR et al. (2014) The study of deep-sea cephalopods.
408 *Adv Mar Biol.* 67: 235–359

- 409 Imber MJ (1992) Cephalopods eaten by wandering albatrosses (*Diomedea exulans* L.)
410 breeding at six circumpolar localities. J Royal Soc New Zealand 22: 243–263
- 411 Imber MJ, Russ R (1975) Some foods of the wandering albatross (*Diomedea exulans*).
412 Notornis 22: 27–36
- 413 Jackson S (1986) Assimilation efficiency of white-chinned petrel (*Procellaria*
414 *aequinoctialis*) fed different preys. Comp Biochem Physiol 85A: 301–303
- 415 Jereb P, Roper CFE (2010) Cephalopods of the world: An annotated and illustrated
416 catalogue of cephalopod species known to date. Volume 2. Myopsid and Oegopsid
417 Squids. FAO, Rome, 605 pp
- 418 Kappes MA, Shaffer SA, Tremblay Y, Foley DG, Palacios DM, Robinson PW, Bograd
419 SJ, Costa DP (2010) Hawaiian albatrosses track interannual variability of marine
420 habitats in the North Pacific. Prog Oceanogr 86: 246–260
- 421 Klages NTW (1996) Cephalopods as prey. II. Seals. Phil Trans R Soc Lond B 351:
422 1045–1052
- 423 Kubodera T, Koyama Y, Mori K (2007) Observations of wild hunting behaviour and
424 bioluminescence of a large deep-sea, eight-armed squid, *Taningia danae*. Proc R Soc
425 B 274: 1029–1034
- 426 Lipinski MR, Jackson S (1989) Surface-feeding on cephalopods by procellariiform
427 seabirds in the southern Benguela region, South Africa. J Zool 218: 549–563
- 428 Pettit TN, Nagy KA, Ellis HI, Whittow GC (1988) Incubation energetics of the Laysan
429 Albatross. Oecologia 74:546–550
- 430 Pettit TN, Whittow GC, Ellis HI (1984) Food and energetic requirements of seabirds at
431 French Frigate Shoals, Hawaii. In: Grigg RW, Tanoue KY (eds) Proceedings of the
432 2nd Symposium on Resource Investigations in the Northwestern Hawaiian Islands,

433 25-27 May 1983. Univ. of Hawaii Sea Grant Office, Honolulu, pp 265-282

434 Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses
435 and petrels. *Auk* 120: 1082–1090

436 Pinaud D (2008) Quantifying search effort of moving animals at several spatial scales
437 using first-passage time analysis: effect of the structure of environment and tracking
438 systems. *J Appl Ecol* 45: 91–99

439 Pinaud D, Weimerskirch H (2005) Scale-dependent habitat use in a long-ranging central
440 place predator. *J Anim Ecol* 74: 852–863

441 Roden GI (1991) Subarctic-subtropical transition zone of the North Pacific: large-scale
442 aspects and mesoscale structure. In Wetherall JA (ed) *Biology, oceanography, and*
443 *fisheries of the NPTZ and subarctic frontal zone*. NOAA Technical Report NMFS
444 105, Honolulu, HI, USA, pp 1–38

445 Rodhouse PG, Boyle PR (2010) Large aggregations of pelagic squid near the ocean
446 surface at the Antarctic Polar Front, and their capture by grey-headed albatrosses.
447 *ICES J of Mar Sci* 67: 1432–1435

448 Rodhouse PG, Nigmatullin CM (1996) Role as consumers. *Philos Trans R Soc Lond B*
449 *Biol Sci* 351: 1003–1022

450 Roper CFE, Vecchione M (1993) A geographic and taxonomic review of *Taningia*
451 *danae* Joubin, 1931 (Cephalopoda: Octopoteuthidae), with new records and
452 observations on bioluminescence. In *Recent advances in fisheries biology* (eds T.
453 Okutani, R. K. O’Dor & T. Kubodera), pp. 441–456. Kanagawa, Japan: Tokai
454 University Press

455 Roper CFE, Young RE (1975) Vertical distribution of pelagic cephalopods.
456 *Smithsonian Contribution to Zoology* 209: 1–51

457 Sakamoto KQ, Takahashi A, Iwata T, Trathan PN (2009a) From the eye of the
458 albatrosses: A bird-borne camera shows an association between albatrosses and a
459 killer whale in the Southern Ocean. PLoS ONE 4: e7322

460 Sakamoto KQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, Wanless S
461 (2009b) Can ethograms be automatically generated using body acceleration data
462 from free-ranging birds? Plos ONE 4: e5379

463 Smale MJ (1996) Cephalopods as prey. IV. Fishes. Phil Trans R Soc Lond B 351:
464 1067–1081

465 Suryan RM, Sato F, Balogh GR, Hyrenbach KD, Sievert PR, Ozaki K (2006) Foraging
466 destinations and marine habitat use of short-tailed albatrosses: A multi-scale
467 approach using first-passage time analysis. Deep-Sea Res Part II 53: 370–386

468 Vaske Jr. T (2011) Are deep-sea cephalopods really common preys for oceanic
469 seabirds? Biota Neotrop 11: (1)

470 Votier SC, Bicknell A, Cox SL, Scales KL, Patrick SC (2013) A bird's eye view of
471 discard reforms: bird-borne cameras reveal seabird/fishery interactions. PLoS ONE
472 8: e57376

473 Wakabayashi T, Kubodera T, Sakai M, Ichii T, Chow S (2007) Molecular evidence for
474 synonymy of the genera *Moroteuthis* and *Onykia* and identification of their
475 paralarvae from northern Hawaiian waters. J Mar Biol Assoc UK 87: 959–965

476 Walker WA, Pitman RL, Ballance LT (2013) Wanted: dead or alive? Hawaiian
477 albarosses feed mainly by scavenging on mesopelagic cephalopods. Poster presented
478 at the 40th Annual Pacific Seabird Group Meeting

479 Weimerskirch H, Bonadonna F, Bailleul F, Mabile G, Dell'Omo G, Lipp HP (2002)
480 GPS tracking of foraging albatrosses. Science 295: 1259–1259

- 481 Weimerskirch H, Gault A, Cherel Y (2005) Prey distribution and patchiness: Factors in
482 foraging success and efficiency of wandering albatrosses. *Ecology* 86: 2611–2622
- 483 Weimerskirch H, Pinaud D, Pawlowski F, Bost CA (2007) Does prey capture induce
484 area-restricted search? A fine-scale study using GPS in a marine predator, the
485 wandering albatross. *Am Nat* 170: 734–743
- 486 Weimerskirch H, Wilson RP, Lys P (1997) Activity pattern of foraging in the
487 wandering albatross: a marine predator with two modes of prey searching. *Mar Ecol*
488 *Prog Ser* 151: 245–254
- 489 Xavier JC, Cherel Y, Roberts J, Piatkowski U (2013) How do cephalopods become
490 available to seabirds: can fish gut contents from tuna fishing vessels be a major food
491 source of deep-dwelling cephalopods? *ICES J Mar Sci* 70: 46–49
- 492 Xavier JC, Croxall JP, Cresswell KA (2005) Boluses: An effective method for assessing
493 the proportions of cephalopods in the diet of albatrosses. *Auk* 122: 1182–1190
- 494 Xavier JC, Trathan PN, Croxall JP, Wood AG, Podesta G, Rodhouse P (2004) Foraging
495 ecology and interactions with fisheries of wandering albatrosses (*Diomedea exulans*)
496 breeding at South Georgia. *Fish Oceanogr* 13:324–344
- 497 Zavalaga CB, Halls JN, Mori GP, Taylor SA, Dell'Omo G (2010) At-sea movement
498 patterns and diving behavior of Peruvian boobies *Sula variegata* in northern
499 Peru. *Mar Ecol Prog Ser* 404: 259–274
- 500 Zollner PA, Lima SL (1999) Search strategies for landscape-level interpatch movements.
501 *Ecology* 80: 1019–1030

502

503 **FIGURE LEGENDS**

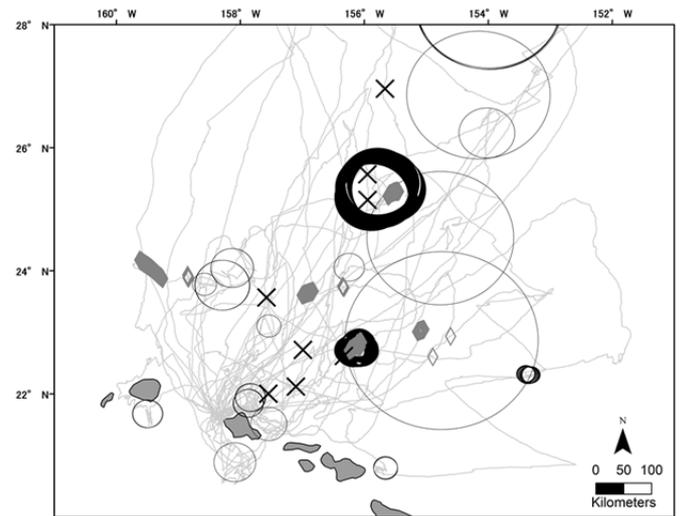
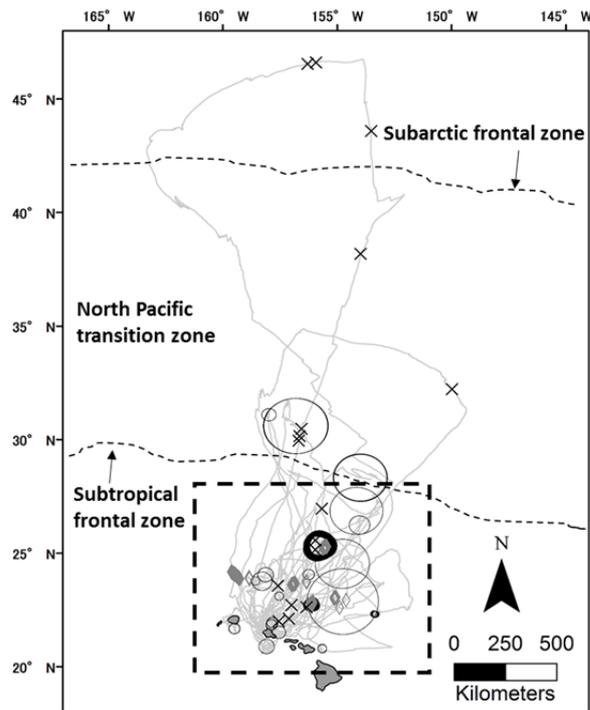
504 Fig. 1. Movements during 26 foraging trips made by 20 Laysan albatrosses. Locations

505 of encounters with squids (×) and fishing vessels (◇) that were determined with
506 images are shown. Area-Restricted Search zones (○) are also indicated. Hawaiian
507 Islands are shown in gray polygon. Subtropical frontal zone and subarctic frontal
508 zone are following Roden (1991).

509 Fig. 2. Images of squids taken by camera-loggers on the belly (a, c, d) and back (b) of
510 Laysan albatrosses. (a) squid tentacle photographed by bird (O357P_1), (b) large
511 squid with a black-footed albatross photographed by bird (O453P_1), (c) *Onykia*
512 *robusta* photographed by bird (O357P_1), and (d) *Taningia danae* pictured by bird
513 (O168P_1).

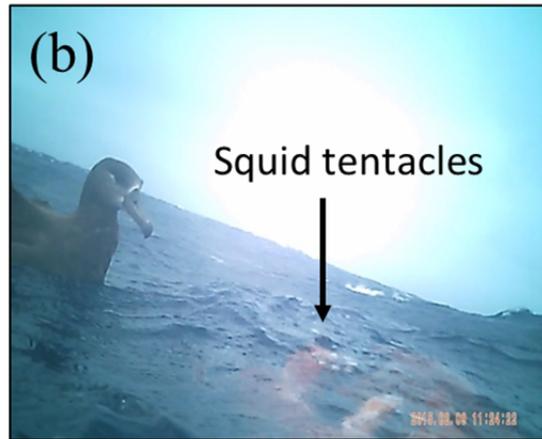
514 Fig. 3. Changes in the moving speed during flight (km h^{-1}) (a) and azimuth ($^{\circ}$) (b)
515 30-minutes before and after on-water bouts with squids (8 foraging events from 5
516 trips of 5 birds equipped with GPS at 1-minute intervals). Vertical broken lines show
517 the time birds landed on the water with squid. Each line represents one bird.

518



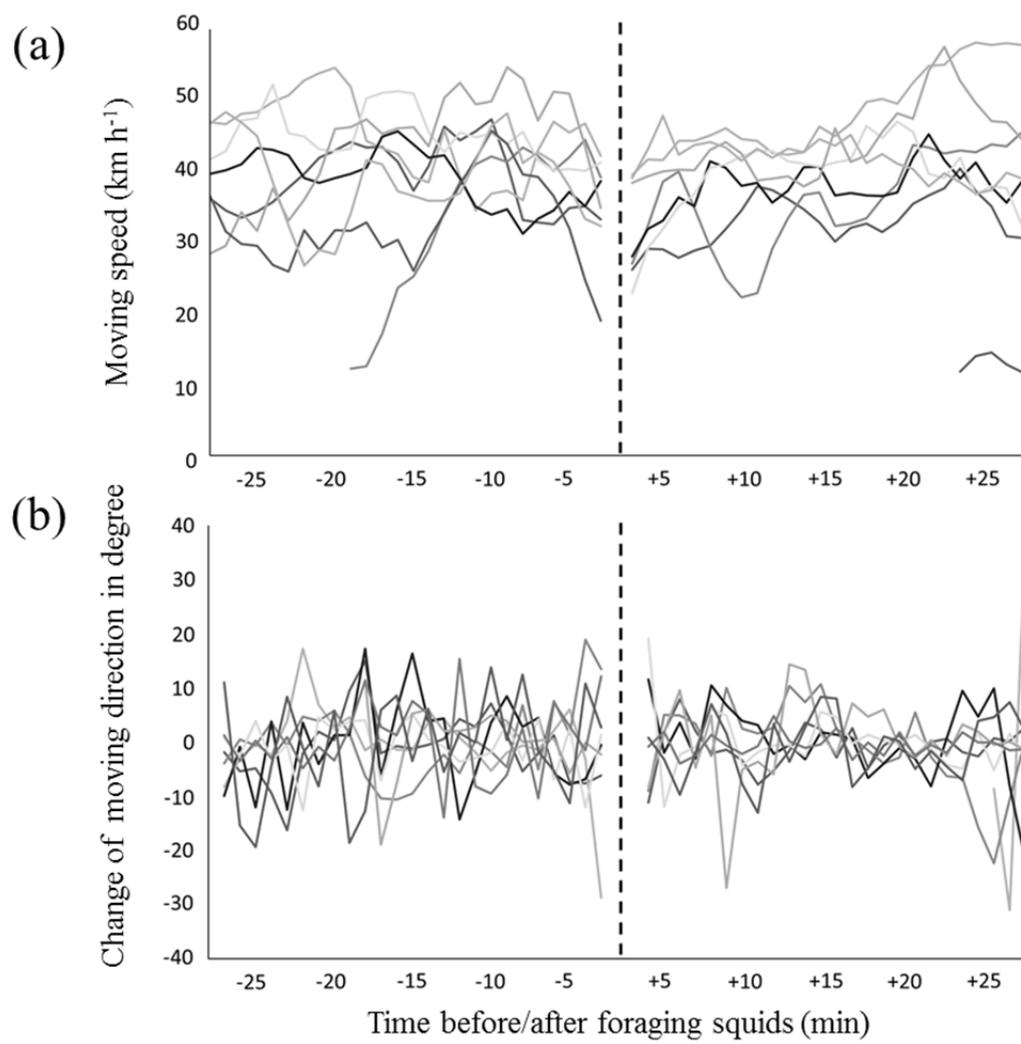
519

520 **Fig. 1**



521

522 **Fig. 2**



523

524 **Fig. 3**