

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

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ABSTRACT: How surface-feeding albatrosses feed on deep-sea squids has long been a mystery. We investigated foraging behavior during daylight hours of 20 Laysan albatrosses *Phoebastria immutabilis* breeding in Hawaii using GPS- and camera-loggers. The birds traveled to the North Pacific Transition Zone up to 600 km north of their breeding site. The camera images showed that Laysan albatrosses fed on large (~1 m body length), intact floating dead squids (6 events) and floating fragmented squids (10 events) over deep oceanic water (>2000 m) while they flew in a straight path without sinuous searching. Feeding events on squids were not observed during trips when fishing vessels were photographed and seemed to be distributed randomly and sparsely. Thus, this study suggests that Laysan albatrosses found large, presumably post-spawning, squids opportunistically while they were traveling during daylight hours. Although we did not find cetaceans in our surface pictures, we could not rule out the possibility that birds fed on squids, especially fragmented specimens, in the regurgitates of cetaceans at depth. This study demonstrates the usefulness of combining animal-borne GPS- and camera-loggers on wide-ranging top predators for studying the distribution of little known deep-sea squids and their importance in the diet of marine top predators.

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

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INTRODUCTION

Oceanic deep-sea squids are important prey of marine top predators including fish, marine mammals, and seabirds (Clarke 1996, Croxall & Prince 1996, Klages 1996, Smale 1996). For example, they are a large part of the diet of highly migratory tunas (*Thunnus albacares* from the Indian, Pacific, and Atlantic Oceans, 13% by mass; and *T. obesus* from the Atlantic and Pacific Oceans, 41% by mass) and swordfish *Xiphias gladius* (from the Atlantic Ocean, 60% by mass) (Smale 1996). At least 60 of 67 odontocete species include squids in their diet, and squids

form the main food source (up to >75% of the diet) in at least 28 odontocetes (Delphinidae, Phocoenidae, Physeteridae, and Ziphiidae) (Clarke 1996). Despite the importance of deep-sea squids to the diet of marine top predators, little information is available on the biology and ecology of these squids. This limitation is due to our lack of sampling and observation, and also our limited understanding of when, where, and how large top predators prey on them.

Among seabirds, albatrosses feed by seizing prey while on the surface of the water and feed mainly on squids, including deep-sea dwelling species, which form almost half the food fed to chicks of 5 species

breeding in the southern hemisphere (wandering albatross *Diomedea exulans*, 59% by mass; grey-headed albatross *Thalassarche chrysostoma*, 58%; black-browed albatross *T. melanophrys*, 16%; sooty albatross *Phoebastria fusca*, 42%; and light-mantled sooty albatross *P. palpebrata*, 46%; Croxall & Prince 1996) and 2 species breeding in the Hawaiian Islands (black-footed albatross *Phoebastria nigripes*, 32% by volume; and Laysan albatross *P. immutabilis*, 65%; Harrison et al. 1983). How surface-feeding albatrosses feed on deep-sea squids has long been a mystery. Albatrosses are hypothesized to feed on squids floating dead after spawning (Rodhouse et al. 1987, Lipinski & Jackson 1989), those related to fisheries including discards from fishing vessels and squid baits of longliners (Thompson 1992, Croxall & Prince 1994, Duffy & Bisson 2006), those in the regurgitates of cetaceans (Clarke et al. 1981), those alive when the squids come to the surface at night (Imber & Russ 1975, Imber 1992), or those alive aggregated near the surface at productive oceanic fronts (Xavier et al. 2004, Rodhouse & Boyle 2010). These hypotheses are not exclusive and are still under debate.

Recent development of bio-logging techniques has improved our understanding of the foraging behavior of albatrosses, and have shown that wandering albatrosses feed on widely distributed large prey during the daytime (Weimerskirch et al. 2005, 2007) and that black-browed albatrosses followed a killer whale *Orcinus orca* presumably for a feeding opportunity (Sakamoto et al. 2009a). Simultaneous deployment of GPS- and camera-loggers on albatrosses can provide us with information on when, where, and how these oceanic predators feed on deep-sea squids. They also provide new information on the seasonal patterns and spatial distributions of these squids, and their importance as a food source for albatrosses.

Among the hypotheses mentioned above, we tested the post-spawning floater, fishery-related, and oceanic front hypotheses by investigating foraging behavior of Laysan albatrosses breeding on Oahu, Hawaiian Islands (USA), during daylight hours using a combination of GPS- and camera-loggers. Laysan albatrosses are a suitable marine top predator to test these hypotheses because they feed on both deep-sea dwelling squids and Argentine squids *Illex argentinus* (Harrison et al. 1983, Duffy & Bisson 2006, Walker et al. 2012). Argentine squids are often used as bait in the swordfish longline fishery in Hawaii, which provides an opportunity to test the fishery-related squid hypothesis. Images collected by the bird-borne cameras allow us to identify squid species, whether squids were dead or alive, and whether

they were intact or fragmented. Such images can also reveal the presence of fishing vessels (Votier et al. 2013). If Laysan albatrosses feed on floating dead squids with no sign of fishing vessels, these squids may be natural mortalities including post-spawning floaters (for resident species) or those found in cetacean vomit. Information on whether dead squids are intact or fragmented may be useful in assessing the post-spawning floater or cetacean vomit hypotheses. If birds feed on dead squids with fishing vessels or squid baits behind the longliners, these squids may be related to fisheries (i.e. discard or bait). If birds feed only on live squids, the post-spawning floater and fishery-related hypotheses would not be supported, and these squids may be associated with specific oceanographic features such as productive oceanic fronts. Finally, we discuss the importance of feeding on squid during daylight hours for the energy requirements of Laysan albatrosses during the chick-rearing period.

MATERIALS AND METHODS

Field study

The study was carried out at Kaena Point Natural Area Reserve (21° 34' N, 158° 16' W) on Oahu, Hawaii, during the early chick-rearing period in February–March 2015. We instrumented 38 birds rearing chicks with a GPS-logger (GiPSy4, TechnoSmart, 23 g) on the back and a camera-logger (Broadwatch, 34 g; or Little Leonardo, 20 g) on either the back (for birds brooding chicks) or belly (for birds after brooding chicks) with Tesa® tape (for details, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m592p257_supp.pdf). To avoid potential negative effects of camera attachment on small chicks, we did not attach cameras to the bellies of albatrosses brooding chicks, but rather on their backs. We attached cameras to the bellies of albatrosses after they finished brooding their chicks. Positions were recorded every 1 or 3 min continuously and images were taken every 1 to 10 min only in daytime (06:00–19:30 h local time) (Table S1). We captured birds by hand as they were about to leave the colony. Total mass of the equipment was 65–70 g (2.7–2.9% of mean body mass of 2.41 kg), which is below the generally accepted 3% threshold for adverse behavioral effects of gliding seabirds (Phillips et al. 2003). All birds carrying devices showed no chick desertion during the experiments and they continued rearing chicks after removal of the devices. The field work

was conducted under permits from the State of Hawaii, Department of Land and Natural Resources, Division of Forestry and Wildlife (permit no. WL18-01), Natural Area Reserves System, and US Geological Survey Bird Banding Laboratory (permit no. 23462).

Data processing

We used images obtained from camera-loggers to determine prey type (including dead or alive and intact or fragmented), bird activity (i.e. flying or landing on water), and presence of fishing vessels and cetaceans. In cases where the GPS was set to record every 3 min (3 of 26 trips, Table S2), we linearly interpolated positions at 1 min intervals. We also linearly interpolated positions that would have required unrealistic flying speeds exceeding 80 km h^{-1} (Suryan et al. 2006). We assumed that birds moving slower than 9 km h^{-1} had landed on the sea surface, while those moving faster were flying (Weimerskirch et al. 2002, Guilford et al. 2008, Zavalaga et al. 2010) (Fig. S1 in the Supplement). We defined an 'on-water bout' as consecutive landing positions between 2 flight positions and a 'flight bout' as consecutive flight positions between 2 landing positions. In addition, we defined the 'position of on-water bout' as the last position during an on-water bout. Using 23 455 images from 26 trips of 20 birds where activity (i.e. flight vs. landing on water) was determined, 94 % of bouts were correctly designated as flight or on-water bouts.

Data analysis

It has been predicted that the movements of foraging animals are adjusted to the hierarchical spatial distribution of prey resources in the environment, and that decisions to modify movement in response to heterogeneous resource distribution are scale-dependent (Fauchald 1999, Pinaud & Weimerskirch 2005). Thus, we explored the relationships between foraging movements of albatrosses and prey distribution (i.e. squid) at a large spatial scale (e.g. 10–100 km) by examining area-restricted search (ARS) behavior, and at a small spatial scale (e.g. <20 km) by examining changes in azimuth of the movement path 30 min before and after squid capture. We examined ARS zones, where sinuosity of movement increased markedly, based on first passage time (FPT) analysis (Fauchald & Tveraa

2003). Small-scale ARS zones when the bird was landing on the water dramatically inflated the variance in FPT and reduced the ability to detect larger-scale ARS zones (Pinaud 2008). To remove this problem, we considered landing on the water as flying with a constant speed of 34 km h^{-1} (i.e. average flight speed of this species) by removing locations following Pinaud (2008). FPT was calculated every 5 km for a radius r from 5 to 500 km using the program Ethographer v. 2.03 (Sakamoto et al. 2009b). The plot representing variance in $\log(\text{FPT})$ as a function of r allowed us to identify the ARS scales by peaks in the variance. In this calculation, FPT was log transformed to make the variance independent of the magnitude of the mean FPT (Fauchald & Tveraa 2003). The maximum FPT, at the appropriate ARS spatial scale, was then identified as the most intensively searched foraging area for each individual (Kappes et al. 2010). These analyses were carried out using Igor Pro version 6.3.4.1 and ArcGIS 10.0.

To determine when birds found squid and whether they increased searching after finding squid, we calculated changes in azimuth of the movement path 30 min before and after prey capture using split moving-window boundary analysis (Cornelius & Reynolds 1991). We used a window size of 5 min for trips where positions were obtained every 1 min (with GPS positions at 3 min intervals excluded from this analysis), and then calculated change in azimuth between each consecutive GPS position at 1 min intervals.

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

RESULTS

Deep-sea squids consumed by albatrosses

Both GPS and camera data were recovered from 20 birds representing 26 trips to sea. The mean tracking period was $8.8 \pm 9.5 \text{ d}$ (range 2.0–39.0 d, $n = 20$ birds). Laysan albatrosses foraged mostly over the subtropical and North Pacific Transition Zones (Fig. 1). The mean duration of foraging trips was $77.0 \pm 66.3 \text{ h}$

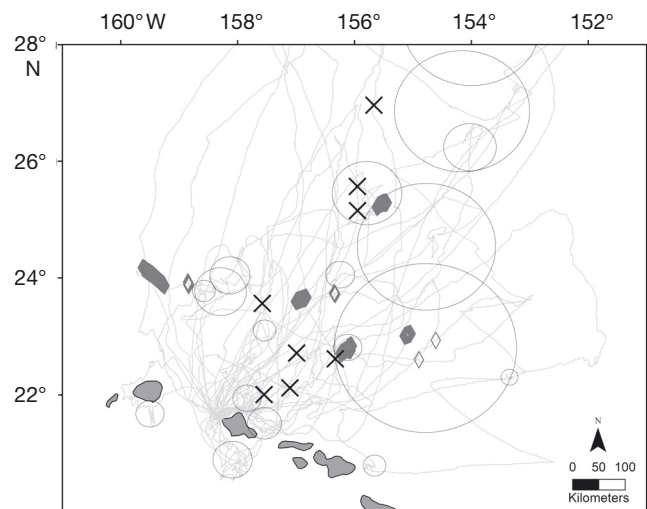
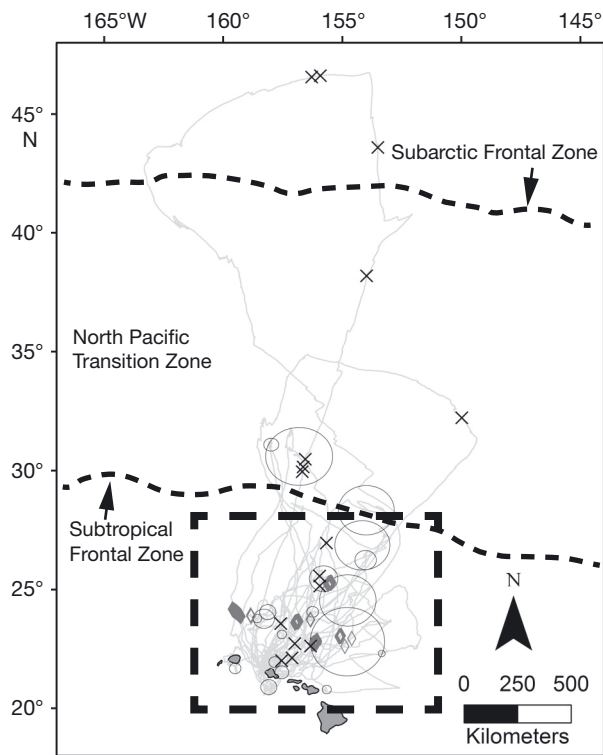


Fig. 1. Movements during 26 foraging trips made by 20 Laysan albatrosses. Locations of encounters with squids (x) and fishing vessels (◇) that were determined with images are shown. Area-restricted search zones (circles) are also indicated. Right panel shows enlargement of dashed rectangle. Hawaiian Islands are also shown (gray with black outlines). Subtropical frontal zone and subarctic frontal zone follow Roden (1991)

(5.7–340.0 h, $n = 26$ trips; Table S2) with a mean maximum foraging range of 598.2 ± 569.3 km (71.3–2820.7 km, $n = 26$ trips, Table S2). In total, 28 068 images were collected from 26 trips of 20 birds (Table S2), which covered most of the duration ($87.0 \pm 22.0\%$, range 5.9–100%, $n = 26$ trips, excluding nighttime, Table S2) of the 26 foraging trips. Squids were visible in 23 images corresponding to 16 events (i.e. at different positions) from 7 trips of 7 birds (Table S2). Fishing vessels were visible in 69 images corresponding to 9 events (i.e. different fishing vessels at different positions) from 6 trips of 5 birds (Table S2). No cetaceans or potential prey other than squids were visible in any images. All images taken during 7 trips of 7 birds that encountered squids during their whole trips did not show any fishing vessels (Table S2). All squids photographed were dead and floating at the sea surface (Fig. 2). Ten of the squids were fragmented (Fig. 2a) and 6 were intact (Fig. 2b–d). At least 2 squids were >1 m in total length using size of the birds as a reference, and were identified as *Taningia danae* and *Onykia robusta* (Fig. 2c,d). The frequency of trips when birds encountered at least 1 squid was greater for those carrying a camera on the belly (13 squid feeding events during 4 [4 birds] of 5 trips [4 birds], Table S2) than on the back (3 squid feeding events during 3 [3 birds] of 21 trips [16 birds], chi-squared test, $\chi =$

8.864, $df = 1$, $p < 0.05$; Table S2), presumably because the camera on the back sometimes failed to catch images of squids under the water. Birds with a camera on the belly landed on the water 71 times and encountered squids 13 times (18%), with on-water duration of 20 ± 17 min (1–70 min, $n = 16$ squid feeding locations from 7 trips of 7 birds with cameras mounted on their backs or bellies).

Birds encountered squids outside of ARS zones (Fig. 1). Birds did not change the speed (<55 km h^{-1} , Fig. 3a) and azimuth of movement ($<20^\circ$, Fig. 3b) of their flight path 30 min before or after feeding on squids (using 8 foraging events from 5 trips of 5 birds that had GPS positions at 1 min intervals and excluding the other 8 foraging events from 2 trips of 2 birds that had GPS positions at 3 min intervals from this analysis, Table S2; see also the Materials and Methods), indicating that the birds kept straight flight paths before and after foraging on squids (Fig. S2).

Distribution of deep-sea squids

Locations of squids were widely distributed (Fig. 1). Nearest-neighbor analysis indicated that all on-water bouts (i.e. with and without squids) were concentrated around the Hawaiian Islands ($z = -11.48$, $p < 0.05$), while those with squids were randomly dis-

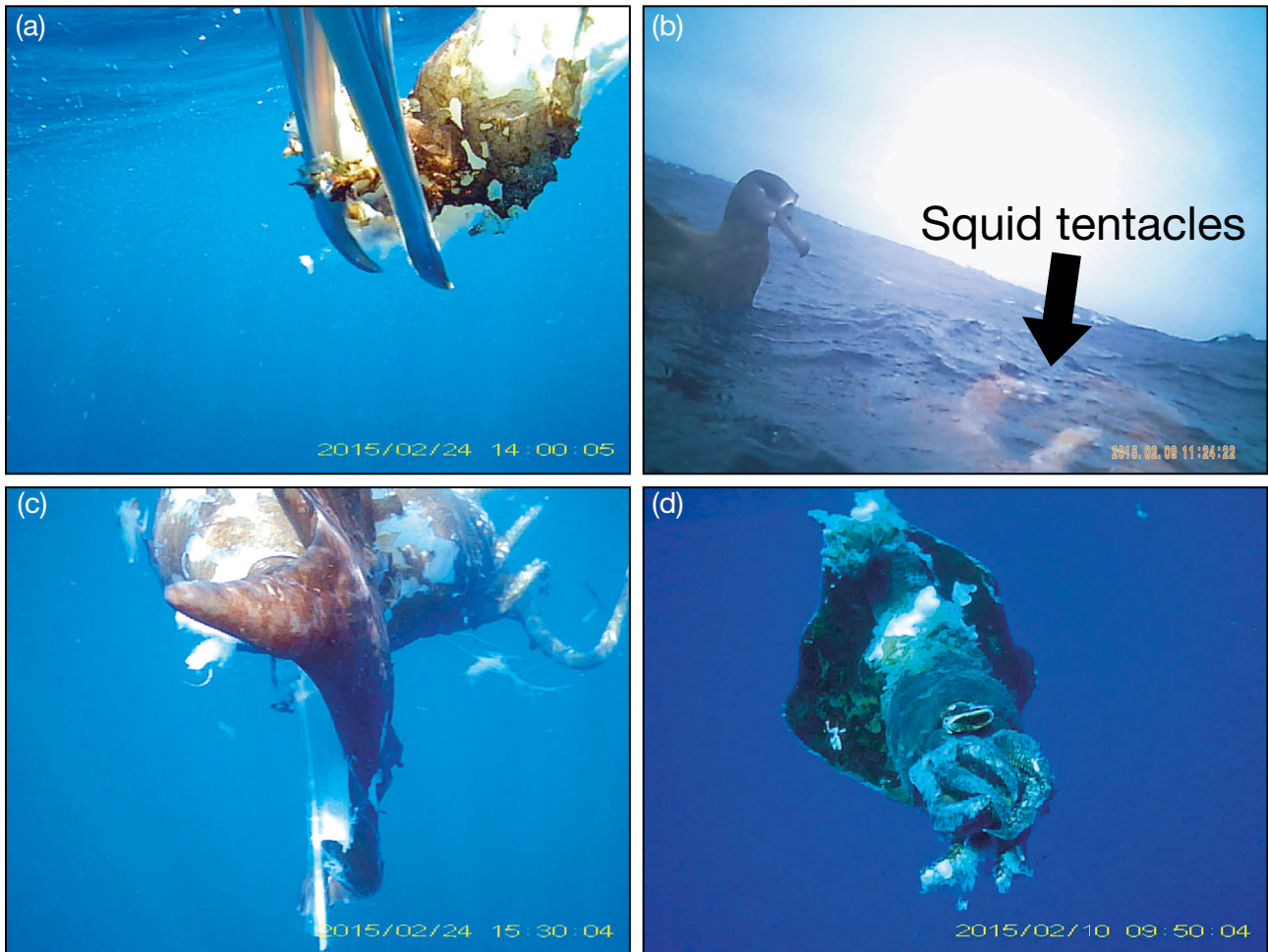


Fig. 2. Images of squids taken by camera-loggers on the (a,c,d) belly and (b) back of Laysan albatrosses. (a) Squid tentacle photographed by the camera on bird O357P_1, (b) large squid with a black-footed albatross (photographed by O453P_1), (c) *Onykia robusta* (photographed by O357P_1), and (d) *Taningia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

tributed within the area covering on-water bouts with squids ($z = -0.17$, $p = 0.86$). The average distance between 2 consecutive squid feeding events was 34 ± 9 km (22–46 km, $n = 4$ distances from 2 birds; 1 bird provided 2 squid feeding events within a trip, and the other bird provided 3 feeding events within 1 trip and 2 feeding events within another trip).

DISCUSSION

We found that Laysan albatrosses fed on large intact floating dead squids including *Onykia robusta* and *Taningia danae*, which are resident species in Hawaiian waters (Wakabayashi et al. 2007, Jereb & Roper 2010), and on unidentified floating fragmented squids during daytime. Our Laysan albatrosses did

not feed on live squids during the daytime. However, it is possible that our cameras, with 1–10 min sampling intervals, failed to catch images of living squids that could easily escape from the birds. Sampling of images at a higher rate would help to confirm this. *O. robusta* and *T. danae* are deep-sea dwelling species that stay at depths of 250–900 m during the daytime (Kubodera et al. 2007, Jereb & Roper 2010) and have previously been recorded in the regurgitations of Laysan and black-footed albatrosses breeding in the Hawaiian Islands (Harrison et al. 1983, Walker et al. 2012). Three sources of these dead floating squids have been suggested: post-spawning mortality of squids (Rodhouse et al. 1987), vomit of odontocete cetaceans (Clarke et al. 1981), and fishery-related squids including squid baits for longliners and discards from fishing vessels (Thompson 1992, Duffy & Bisson 2006).

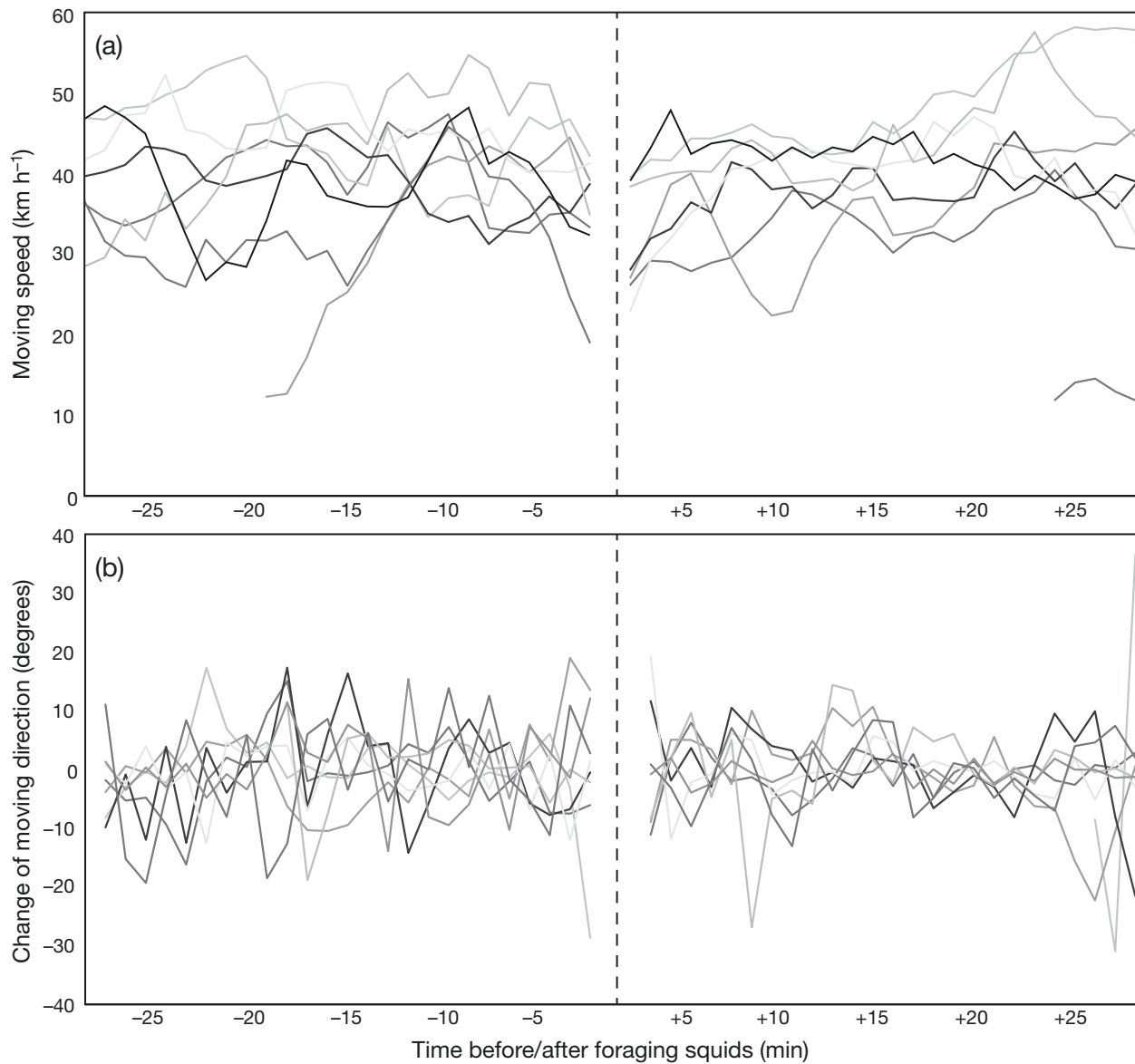


Fig. 3. (a) Changes in the moving speed during flight and (b) azimuth 30 min before and after on-water bouts with squids (8 foraging events from 5 trips of 5 birds equipped with GPS at 1 min intervals). Vertical broken lines show the time birds landed on the water with squid. Each line represents one bird

Considering that many squids, including deep-sea dwelling species, are semelparous (i.e. spawning happens during a single reproductive cycle) and die after spawning at 1–2 yr of age (Hoving et al. 2014), if mating/spawning migrations towards the surface followed by mass mortalities do occur, then these aggregations would represent considerable, but sporadic, opportunities for surface-foraging seabirds such as albatrosses (Rodhouse et al. 1987). The presence of paralarvae of *O. robusta* in northern Hawaiian waters indicates that this species spawns there during fall and winter (Wakabayashi et al. 2007).

Although the spawning grounds and spawning season of *T. danae* are still unknown, this species is cosmopolitan with the exception of polar regions, and small-sized specimens (62 mm in mantle length) have been captured by nets in northern Hawaiian waters during fall (Roper & Vecchione 1993). Thus, it is possible that Laysan albatrosses feed on floating dead squids after they spawn.

Deep-sea squids might also become available to albatrosses through marine mammal–seabird interactions. For example, sperm whales *Physeter macrocephalus*, which feed on deep-sea squids, vomit peri-

odically to empty their stomachs of indigestible items including squid beaks which do not pass further down the gut (Clarke 1980, Clarke et al. 1981). Deep-sea squids recently regurgitated by a sperm whale have been observed at the sea surface, and a wandering albatross was observed feeding on these during daylight hours in the south Atlantic (Clarke et al. 1981). Also, sperm whales and other odontocetes in Hawaiian waters feed on deep-sea squids including *O. robusta* and *T. danae* (Clarke & Young 1998), thus their vomit may also be available to surface-foraging seabirds such as Laysan albatrosses in the region. Our birds fed on intact squids, including *O. robusta* and *T. danae*, and fragmented squids. It is unlikely that cetaceans regurgitate intact specimens; therefore, the cetacean vomit hypothesis is not supported at least for intact dead squids (*O. robusta* and *T. danae*). Although no cetaceans were photographed during our study, we cannot rule out the possibility that Laysan albatrosses feed on squid regurgitated by cetaceans, especially for fragmented squids, because our bird-borne still cameras with 1–10 min sampling intervals only during daylight hours may have failed to capture images of cetaceans underwater, especially when they might regurgitate food.

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

We therefore suggest that Laysan albatrosses feed on large floating dead, probably post-spawning, squids, at least during the daytime. However, we cannot rule out the possibility that Laysan albatrosses also feed on squids, especially fragmented specimens, from cetacean regurgitates. All identifiable albatross prey collected during the daytime in this study were squids. Sampling of images at a higher rate, and at night, would help to confirm this conclusion.

How does this feeding strategy contribute to meeting the daily energy demand? We explored daily food consumption of Laysan albatrosses during the brood-

ing periods as follows. The energy content of ommatrephid squids is 4.26 kJ g^{-1} wet weight (Pettit et al. 1984). The assimilation efficiency of seabirds fed on squid is 0.744 (Jackson 1986). In the present study, Laysan albatrosses landed on the water 1.9 ± 0.8 times h^{-1} (range 0.9–3.8 times h^{-1} , $n = 26$ trips, Table S2), hence, 26 times during 13.5 h in daytime. Using the encounter rate of floating squids (18%, ratio of the number of on-water bouts with squids to all on-water bouts, see the Results), Laysan albatrosses encountered floating squids 4.7 times d^{-1} on average. Wandering albatrosses ingested $324 \pm 518 \text{ g}$ prey in a foraging event (Weimerskirch et al. 2005); thus Laysan albatrosses, which are one-third the body mass of wandering albatrosses, might ingest 108 g of prey per encounter event. From these values, the daily energy gain from dead floating squid is estimated as follows: $4.26 (\text{kJ g}^{-1}) \times 108 (\text{g}) \times 4.7 \times 0.744 = 1608.81 \text{ kJ}$. The daily energy expenditure of foraging (and also chick rearing) of Laysan albatross is 2072.3 kJ (Pettit et al. 1988). Thus, the energy gain from dead floating squid has the potential to provide 77.6% of the daily energy expenditure for foraging Laysan albatrosses. This estimate, though crude, suggests that foraging on dead floating squids during daytime might be an important energy source for Laysan albatrosses.

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

Despite the importance of deep-sea squids in trophic connectivity between top predators such as whales, seabirds, and tuna and their prey such as

zooplankton and small fish (Rodhouse & Nigmatullin 1996), information on the biology and ecology of deep-sea squids is quite limited. Deep-sea squids are widely distributed over the world's oceans, and they are considered semelparous (Hoving et al. 2014). Our results suggest that deep-sea squids such as *O. robusta* and *T. danae* spawn in the Pacific basin during our winter periods and are distributed randomly and sparsely in the deep oceanic basin.

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

Squid beaks in the regurgitations of albatrosses provide information on cephalopod distribution and biology (Cherel & Weimerskirch 1995, 1999). However, because squid beaks remain in the stomach for unpredictable periods, sometimes more than 9 mo (Xavier et al. 2005), the temporal and spatial resolutions of these data are coarse. Our study demonstrates the usefulness of combining animal-borne GPS- and camera-loggers on highly mobile seabird species to collect information on the spawning area and distribution of little known deep-sea squids and their importance to marine top predators.

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