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

Running page head: Foraging behavior of Laysan albatrosses

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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 the trip 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 travelling 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 those fragmented, in the vomit of cetaceans in 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* · *Onykia robusta* · Hawaiian Islands · Area-restricted search

INTRODUCTION

Oceanic deep-sea squids are important prey of marine top predators including fish, marine mammal, 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 Indian, Pacific, and Atlantic Ocean, 13% by mass and *T. obesus* from Atlantic and Pacific Ocean, 41% by mass) and swordfish (*Xiphias gladius* from Atlantic Ocean, 60% by mass) (Smale 1996). At least 60 of 67 odontocete species include squids in their diet and, in at least 28 odontocetes (Delphinidae, Phocoenidae, Physeteridae, and Ziphiidae), squids form the main food up to more than 75% of the diet (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 five 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 *Phoebetria fusca*; 42%, and Light-mantled sooty albatross *P. palpebrata*; 46%, Croxall & Prince 1996) and two 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 vomit from 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 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 importance of them as food of 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, 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. 2013). 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 also can reveal the presence of fishing vessels (Votier et al. 2013). If Laysan albatrosses feed on floating dead squids without any sign of fishing vessels, these squids may be natural mortalities including post-spawning floaters for resident species or cetacean vomits. Information on whether dead squids are intact or fragmented may be useful to determine 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 on squids alive only, 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^{o}34'N, 158^{o}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 (Table S1 in the Supplement). To avoid potential negative effect of camera-attachment on small chicks we did not attach cameras on the belly of albatrosses brooding chicks but on the back. We attached cameras on the belly of albatrosses after they finished brooding their chicks. Positions and images were sampled every 1 or 3-minutes continuously and 1 to 10-minutes only in daytime (6:00–19:30 in local time), respectively (Table S1 in the Supplement). We captured birds by hand as they were about to leave the colony. 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 U.S. Geological Survey Bird Banding Laboratory (Permit #23462). 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.

Data processing

We used images obtained from camera-loggers to determine prey type including those 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-minutes (3 of 26 trips, Table S2 in the Supplement), we linearly interpolated positions at 1-minute 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 9km 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 two flight positions and a "flight bout" as consecutive flight positions between two 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-minutes before and after squid capture. We examined ARS zones, where sinuosity of movement increased extraordinarily, 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 with the program Ethographer version 2.03 (Sakamoto et al. 2009b). The plot representing variance in log (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 first passage time, 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 understand when birds found squid and if they increased searching after finding squid, we calculated changes in azimuth of the movement path 30-minutes before and after prey capture using split moving-window boundary analysis (Cornelius & Reynolds 1991). We used a window size of 5-minutes for trips where positions were obtained every 1-minute (excluded GPS positions at 3-minutes intervals from this analysis), and then calculated change in azimuth between each consecutive GPS position at 1-minute 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 in the Supplement), which allowed us to distinguish on-water bouts with or without prey. Values are presented as means ± SD with their range and the number of sample.

RESULTS

Deep-sea squids fed by albatrosses

Both GPS- and camera data were recovered from 20 birds representing 26 trips to sea. Tracking period was 8.8 ± 9.5 days (range 2.0–39.0 days, 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 ± 66.3 hours (range 5.7–340.0 hours, n = 26 trips, Table S2 in the Supplement) with a mean maximum foraging range of 598.2 ± 569.3 km (range 71.3–2820.7 km, n = 26 trips, Table S2 in the Supplement). A total of 28,068 images were collected from 26 trips of 20 birds (Table S2 in the Supplement), which covered most of duration (87.0 ± 22.0%, range 5.9–100%, n = 26 trips, excluding nighttime, Table S2 in the Supplement) 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 in the Supplement). 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 in the Supplement). 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 in the Supplement). All squids photographed were dead and floating at the sea surface (Fig. 2). Ten of the squids were fragmented (Fig. 2a) and six were intact (Figs. 2b–d). At least two squids were greater than 1-m in total length using size of the birds as a reference, and were identified as *Taningia danae* and *Onykia robusta* (Figs. 2c & 2d). Frequency of trips when birds encountered at least one 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 in the Supplement) than on the back (three squid feeding events during 3 (3 birds) of 21 trips (16 birds), Table S2 in the Supplement) (Chi-squared test, $\chi = 8.864$, df = 1, $p < 0.05$), presumably because the camera on the back sometimes failed to catch images of squids under the water. Birds with a camera on their 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 seven trips of seven birds with camera mounted on their back or belly).

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^{o}, Fig. 3b) of their flight path 30-minutes before or after feeding on squids (using 8 foraging events from 5 trips of 5 birds that had GPS positions at 1-minute intervals and excluded the other 8 foraging events from 2 trips of 2 birds that had GPS positions at 3-minutes intervals from this analysis, Table S2 in the Supplement, see also MATERIALS AND METHODS), indicating that the birds kept straight flight paths before and after foraging on squids (Fig. S2 in the Supplement).

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 distributed within the area covering on-water bouts with squids ($z = -0.17$, $p = 0.86$). The average distance between two consecutive squid feeding events was 34 ± 9 km (22–46 km, n = 4 distances from two birds; one bird provided two squid feeding events within a trip, and the other bird provided three feeding events within one trip and two 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 living squids during daytime. However, we still have possibility that our camera with 1–10 min sampling interval 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 squid species staying at depths of 250–900 m during daytime (Kubodera et al. 2007, Jereb & Roper 2010) and are previously recorded in the regurgitations of Laysan albatrosses and black-footed albatrosses breeding in Hawaii

Islands (Harrison et al. 1983, Walker et al. 2013). 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).

Considering that many species of squids, including deep-sea dwelling species, are semelparous (i.e. spawning happens during a single reproductive cycle) and die at 1–2 years of age after spawning (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). 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 spawning grounds and spawning season for *T. danae* are still unknown, this species is cosmopolitan with the exception of polar regions, and small-sized specimens (62 mm in mantle length) were 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 periodically 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 vomited by a sperm whale have been observed on the sea surface, and a wandering albatross has been 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 the vomit of them 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 unlikey that cetaceans regurgitate intact squids, 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 periods, we cannot rule out the possibility that Laysan albatrosses feed on squid regurgitations from cetacean, especially for fragmented squids, because our bird-borne still cameras with 1–10 min sampling intervals only during daylight hours may have failed to catch images of cetaceans underwater, especially when they might regurgitate food.

Laysan albatrosses are known to feed on squid baits (*Illex argentinus*, < 400 mm in mantle length) used in the Hawaiian swordfish longline fishing (Duffy & Bisson 2006, Jereb & Roper 2010), but feeding events on squids were not observed during the trip 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 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 fed by our birds may not be related to fisheries in this region.

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

How does this feeding strategy meet with daily energy demand? We explored daily food consumption of Laysan albatrosses during the brooding periods as follows. Energy contents of ommastrephid squids per wet gram is 4.26 kJ (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 in the Supplement), hence, 26 times during 13.5 hours 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 RESULTS), Laysan albatrosses encountered floating squids 4.7 times per day on average. Laysan albatrosses, one-third the body mass of Wandering albatrosses, might ingest 108 g of prey per encounter event (Wandering albatrosses ingested 324 ± 518 g prey in a foraging event, Weimerskirch et al. 2005). From these values, the energy gain from dead floating squid per day is estimated as follows: 4.26 (kJ/g) × 108 (g) × 4.7 × 0.744 = 1608.81 (kJ). Daily energy expenditure of foraging (and also chick rearing) Laysan albatross is 2072.3 kJ (Pettit et al. 1988). Which is to say, 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 camera 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 sit-and-wait searching strategy (Imber 1992, Weimerskirch et al. 1997, 2005). Laysan albatrosses feed small-sized (< 144 mm) ommastrephidae squids, fish, and crustaceans to their chicks (Harrison et al. 1983). These small-sized squids and other micronekton stay in deep water during 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, though both species relied mainly on foraging in daytime (Conners et al. 2015). Moreover, both species strongly increased drift forage at night when the lunar phase was the darkest, suggesting they feed on diel vertically-migrating micronekton including small-sized squids to some extent (Conners 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 an opportunistic feeder not to concentrate their foraging effort at specific places, which might be related to spatial pattern of their main prey of squids (i.e. random distribution with low predictability). Zollner & Lima (1999), using a generic model, predicted that straighter movements are probably the most efficient way to search for randomly distributed prey over large scales. Indeed, 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 their stomach for unpredictable periods, sometimes more than nine months (Xavier et al. 2005), the temporal and spatial resolution 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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FIGURE LEGENDS

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

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

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

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

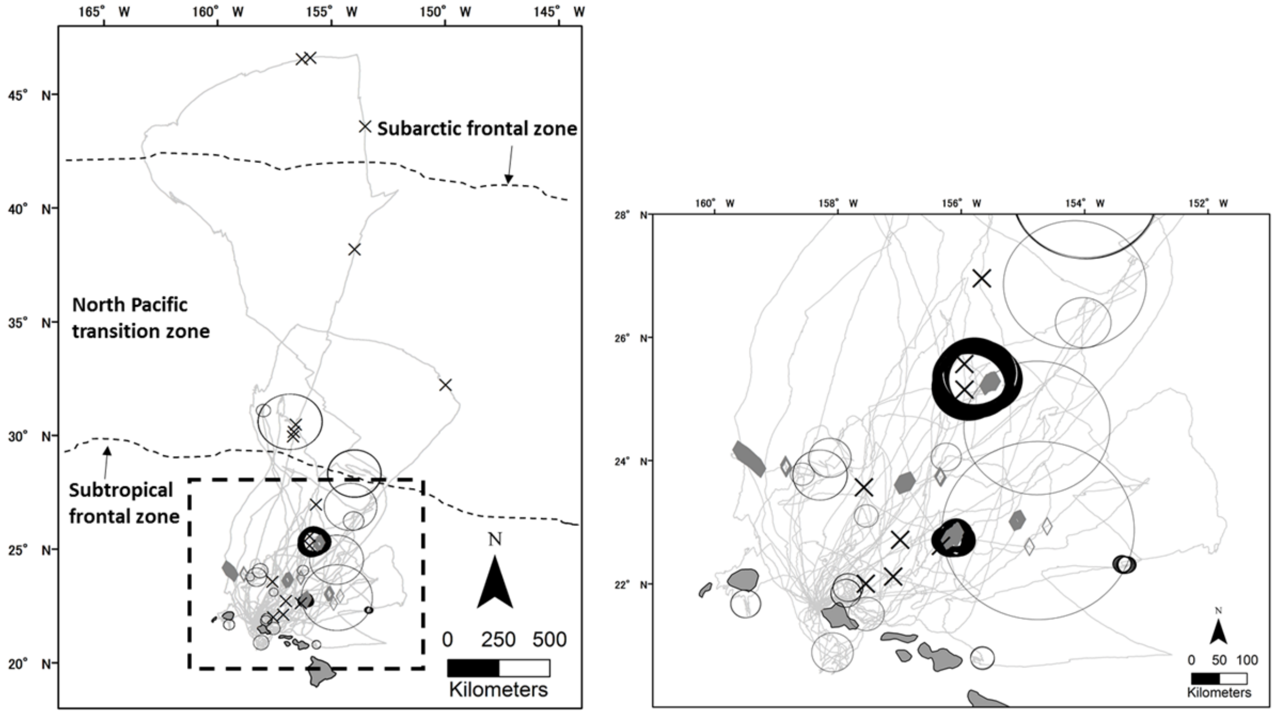
165° W
160° W
155° W
150° W
145° W
45° N
40° N
35° N
30° N
25° N
20° N
Subarctic frontal zone
North Pacific transition zone
Subtropical frontal zone
N
0 250 500
Kilometers
160° W
158° W
156° W
154° W
152° W
28° N
26° N
24° N
22° N
N
0 50 100
Kilometers

Fig. 1

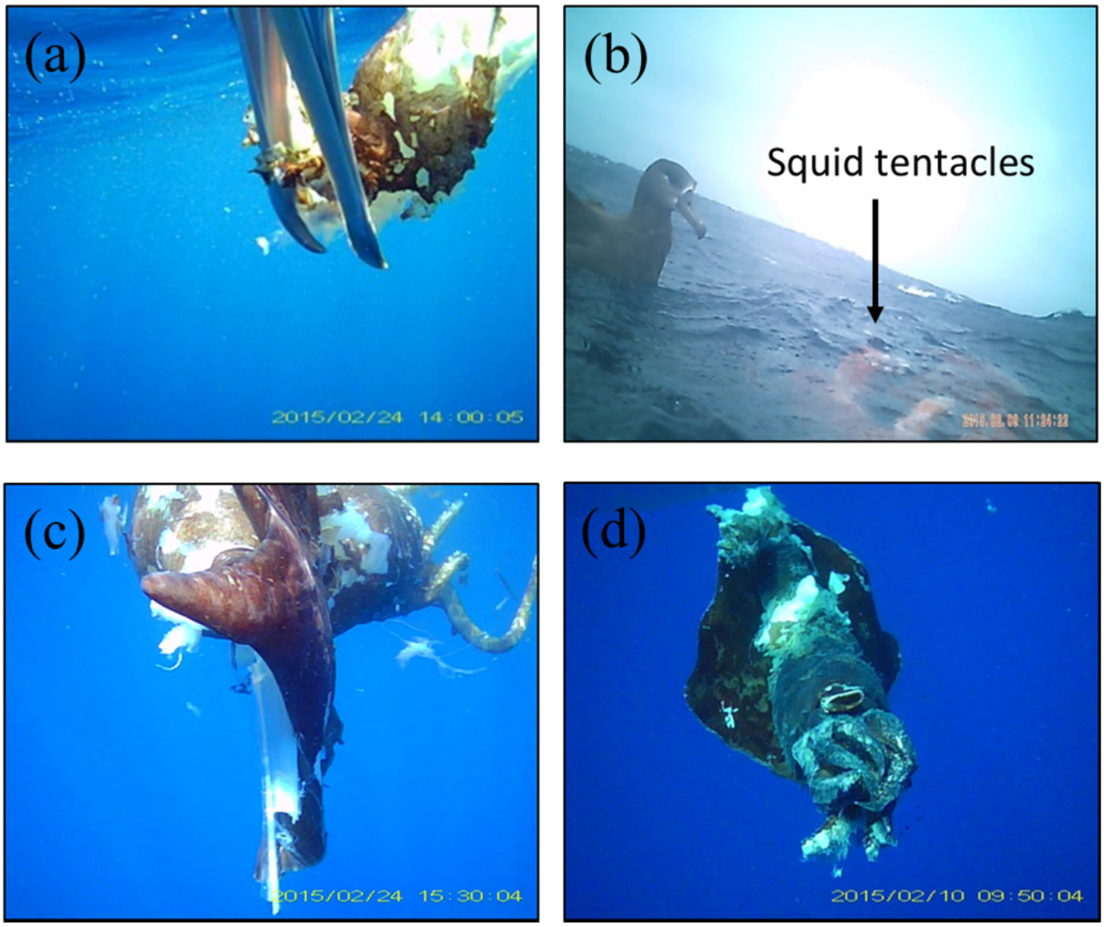
(a)
2015/02/24 14:00:05
(b)
Squid tentacles
(c)
015/02/24 15:30:04
(d)
2015/02/10 09:50:04

Fig. 2

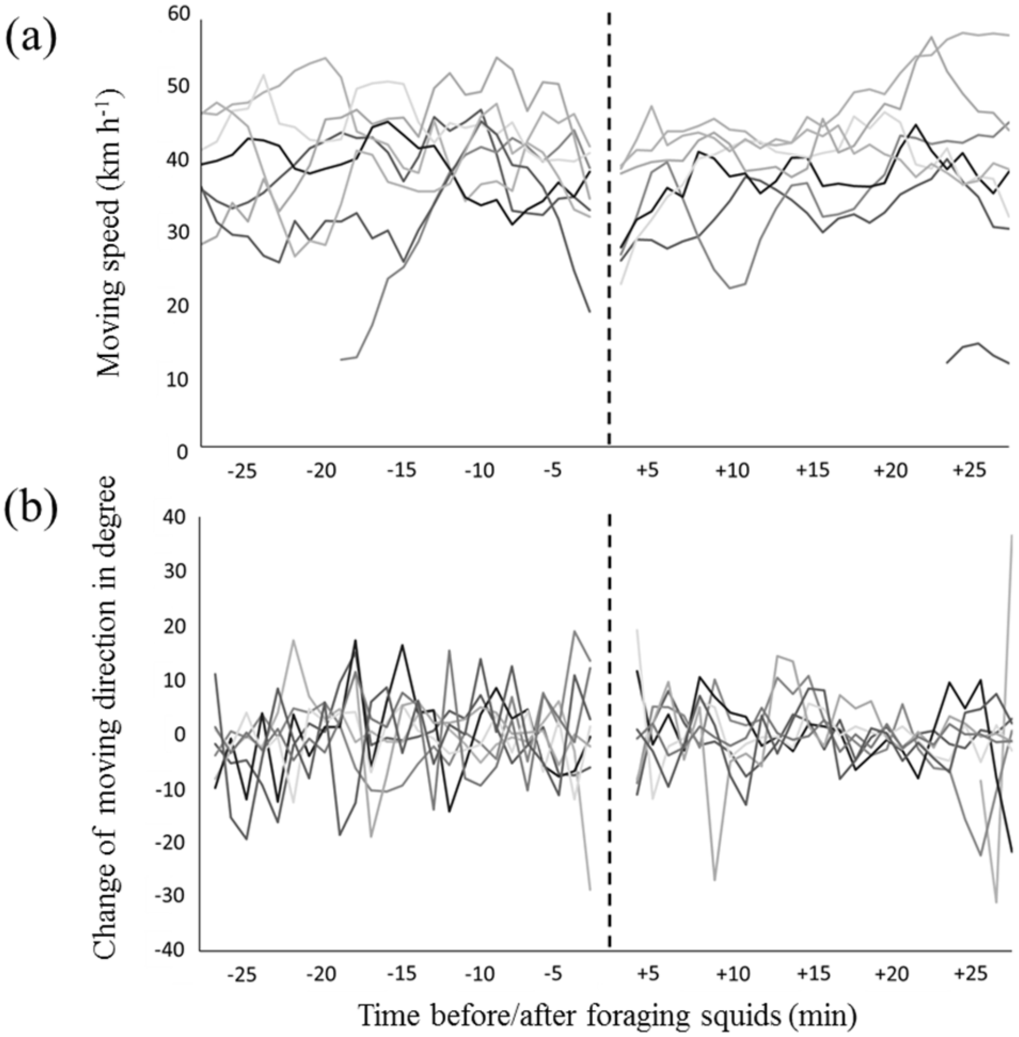
(a)
(b)
Moving speed (km h-1)
Change of moving direction in degree
60
50
40
30
20
10
0
40
30
20
10
0
-10
-20
-30
-40
-25
-20
-15
-10
-5
+5
+10
+15
+20
+25
Time before/after foraging squids (min)

Fig. 3