Diet and Foraging Habitat of Leach's Storm-Petrels Breeding on Daikoku Island, Japan

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ABSTRACT

Leach's Storm-Petrels *Oceanodroma leucorhoa* (LSTP) represent one of the smallest seabirds that feed on small micronektons available only in the surface of the sea. Therefore, they may be sensitive to the change of prey abundance. Daikoku Island (42°52'N, 144°52'E) located in the coast of eastern Hokkaido is known as one of their largest colonies. Samples of diet of LSTPs on the island were collected to examine interannual differences in diet and an at sea census of these birds was conducted in waters adjacent to the island to extract information on feeding habitats. Results of analysis reveal that LSTPs fed mainly on fish, krill, amphipods and squids. Because the change in marine ecosystem derived from 1988/89 climatic regime shift, LSPTs fed on a similar range of prey items throughout the shift. This indicates to high ability of LSTPs to search and forage a range of prey items. But lower diversity of food items in 1995 and 2003 than in 1982 and 1986 points to the potential effects of the 1988/89 climatic regime shift on the variability of prey in LSTPs. Density of LSTPs on the sea surface was significantly greater in slope (200–1000 m depth) and basin (> 1,000 m depth) compared to the shelf (< 200 m depth). Productive and predictable upward water transportation in the slope area observed in this study probably supports the energy requirements of large number of LSTPs breeding on Daikoku Island.

Keywords: Leach's Storm-Petrel, Diet, Climatic regime shift, Sea census

INTRODUCTION

Storm-Petrels *Oceanodroma* spp. breed in waters from high Arctic and Antarctic, and from boreal to tropical waters [1]. They are smallest seabirds and feed on small crustaceans, squids, and fish [2–3] only in the surface of the sea mainly by surface seizing and pattering [1]. Therefore, they may be sensitive to the change of prey abundance. Although there is a report indicating that chick growth of Folk-Tailed Storm-Petrels *O. furcat*a varied with prey abundance among years [4], little information

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is available for interannual variation in their diet. Their distribution in sea and the prey characteristics remain largely unexplored.

Leach's Storm-Petrels *O. leucorhoa* (LSTP) breed on isolated islands in boreal and sub Arctic waters both in Pacific and Atlantic Ocean. Daikoku Island (42°52'N, 144°52'E) located in the coast of eastern Hokkaido has one of the largest colonies [5]. The breeding pairs were estimated to be 1,070,000 in 1972 [6], 415,000 in 1982 [7], and 584,000 in 1994 [8]. They visit the island in mid April, lay egg (one by each pair) in the nest burrow < 1 m deep underground in May, feed chicks from late June until mid October, and then leave the island [7]. They come back to the island only during the night to exchange incubation duties and feed chicks. They feed on small crustaceans including krills, copepods, amphipods, isopods and decapods larva, fish and squids as reported in 1982 [9].

To examine interannual differences in the diet of LSTPs, we carried out further field work on the island. In order to extract information on feeding habitats, we conducted census of LSTPs at sea and performed sampling of krills, regarded as one of their main diets, during the late summer in the waters adjacent to the Daikoku Island.

STUDY AREA AND METHODS

Diet sampling

The diet sampling was carried out on Daikoku Island during April–October 1982, June and July 1986, July–September 1995, and August 2003 under the permits issued by the Ministries of Environment and Education, Japan. In 1982, the birds were caught by hands, with the aide of hand light, when they were landing during the night (between 20:00 and 02:00). In 1986, they were caught using the mist nets [10]. LSTPs often vomit food while they have been trapped in the mist net. In 1986, we caught birds as soon as they hit the nets so as to minimize the possibility to loose a part of the food sample. To avoid sampling the same birds within the sampling night, birds were marked with red paint at their white rump patch. In 1995 and 2003, birds were caught by using one-way traps at the entrance of nest burrows within their chicks. The trap was fitted with a swinging door to the entrance and bendy plastic bag to the other side of exit. The nests were checked every 2 hrs. during the night. Parental birds could not leave the burrow and stayed in the bag calmly once they went through the trap. So we could catch the birds having their stomach contents for their chicks.

Stomach contents of each bird in 1982 and 1986 were pumped 2–3 times using a 10 cm long elastic tube, of 4–5 mm diameter, connected to a 10 ml syringe [9]. During the process, birds sometimes vomited prey items, which were also collected. In 1995 and 2003, birds were forced to swallow approximately 10 ml of warm seawater (38°C) using a syringe, and then the stomach contents of each bird were flushed three times by pushing the belly to facilitate to vomit. The birds sometimes vomited prey items in the bag at the first contact with hands and these items were also collected. Prey items were preserved in 5% formaldehyde or 60% isopropyl alcohol. Samples containing volume of less than 2 ml or only orange oil were excluded from the analyses. These birds were possibly non-breeders or unsuccessful breeders [10].

Analyses of prey

The prey items were sorted in laboratory under 8–20x binoculars. The items were usually partly digested but could be categorized into krills, copepods, isopods, amphipods, fish, squids and others using their characteristic parts [11]. Stones and plastics were easily identified. Krills and copepods were identified to the species level whenever possible using reference key. The number of intact crustacean prey was counted. Except for the lantern fish recognized by its scales, most of the fish-prey could not be identified.

In 1986 and 1995, digestion rank of each crustacean prey was classified into 4 categories "intact", "mostly intact" (appendages partly removed), "digested" (ca. 30–70% of appendages removed), "well digested" (ca. 70–100% of appendages removed) and recorded. To get a rough estimate of the time from feeding to sampling of stomach, we force-fed 10 thawed Antarctic krills (*Euphausia superba*) to each of 7 birds and 20 amphipods to each of 16 birds. The stomach contents of these birds were then pumped after 0.5, 2, 3, 5 and 12 hrs.

As prey items were pumped using 4–5 mm diameter elastic tube, large items could not be collected. To evaluate the sampling bias with stomach pumping, we sacrificed 20 birds (in 1986) under the permit from Department of Culture and Environmental Agency. The stomachs of birds were first pumped to extract the samples, and then the birds were killed by dislocation of neck. Upon dissection, proventriculi and gizzards were removed and the contents excluding the liquids (mostly orange oil) were preserved in formaldehyde. Unfortunately, 13 birds were not subjected to gizzard collection. In laboratory, samples were drained using 100 micron mesh and weighed to 0.1 g using the electronic balance. Total length of crustacean prey was measured for "intact" and "mostly intact" items.

At sea survey

A ship-borne survey was carried out by R/V Tankai-maru (Hokkaido Institute of Fisheries) between 25 July and 28 July (summer) and between 26 September and 2 October (autumn) in 2003 in shelf, slope and basin areas in eastern Hokkaido (Fig. 1). Shelf, slope, and basin areas were defined as bottom depth of < 200 m, 200–1000 m and > 1000 m, respectively. Seabirds appeared in the fan shaped area (with ca. 200 m radius) at either left or right side were counted from the upper deck (12 m height from the surface) using 10x binocular while the boat was cruising about 10 kt during the daytime (8:00–17:00). Number, species, behavior (flying, feeding or resting on the sea surface) of seabirds were recorded every 5 min. Only birds on water were used, as the flying birds gave sometimes biased density and may not relate to feeding activity [12].

Krill were sampled using bongo net (from 100 m depth, cruising speed 1.5–2.0 kt) at 6 and 15 stations in the summer and autumn, respectively (Fig. 2). The samples were preserved in 5% formaldehyde before laboratory analysis. Approximately 70–80 ml sub-sample was picked up from each sample using a divider. Then prey items were sorted into species level and then counted. The density of krill was obtained using filtered volume at each sampling station. Plankton was sampled using NORPAC nets from the bottom of the sea (dependent on the depth of water at each station) at 25 stations in autumn (Fig. 3).

To compare density of LSTPs, krill and plankton,

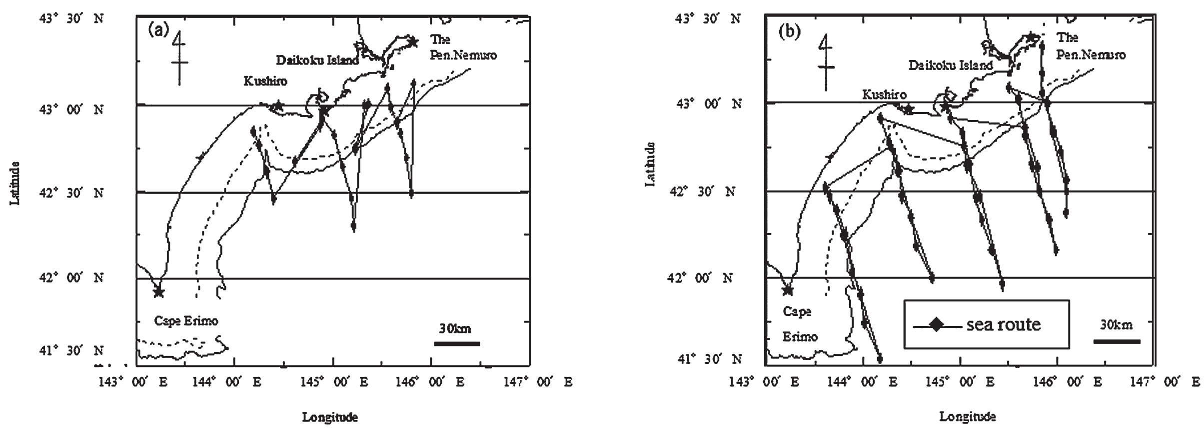

Fig. 1 Sea route used for at sea survey by R/V Tankai Maru in summer (a) and autumn (b). A dotted line and faint solid line are shown in 200 m and 1000 m of bottom depth, respectively. Horizontal and vertical axes show the longitude and latitude, respectively.

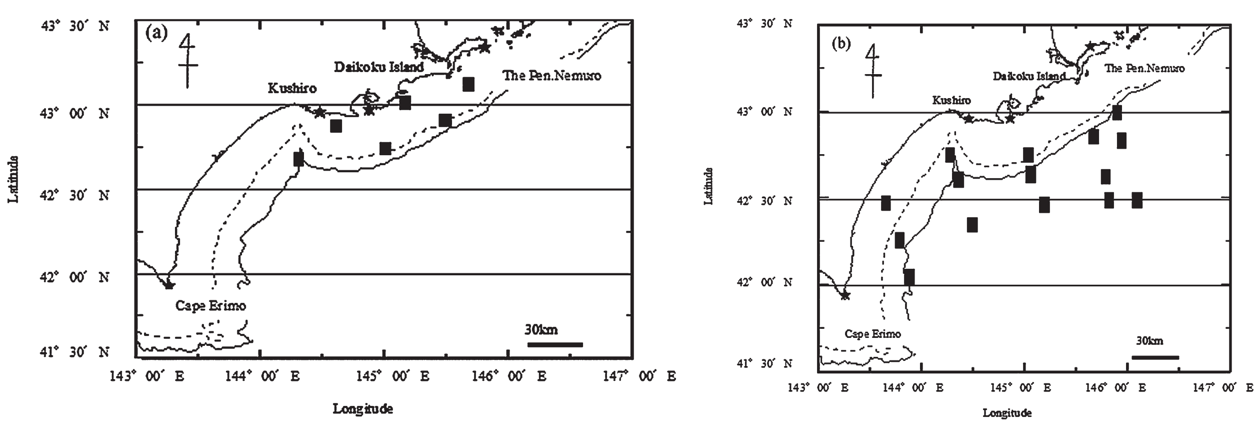

Fig. 2 Stations (closed squares) sampled krills by using bongo net in summer (a) and autumn (b).

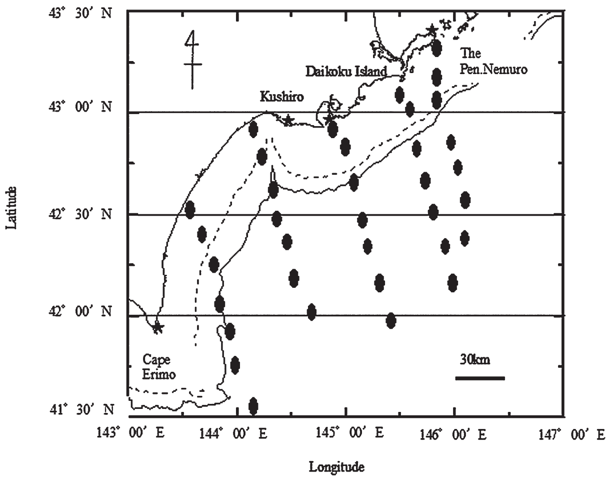

Fig. 3 Stations (closed circles) sampled for planktons by using NORPAC net in autumn.

survey areas were divided into categories of shelf, slope and basin (Fig 1). Effects of month (summer and autumn) and areas (shelf, slope and basin) were examined by general linear model using log-transformed value.

RESULTS

Evaluation of stomach pumping

In 1986, twenty birds were sacrificed to evaluate the accuracy of stomach pumping technique. In 20 prey samples collected by the pump, 4 contained mostly orange oil (> 90% mass by eye) and were not weighed. Excluding these, mass of food items collected by the pump (1.4 ± 0.8 g) was 74% of the total mass of food items, which remained in the proventriculi (1.9 ± 1.4 g), meaning that 42% of diet was sampled by pumping. The percentage of occurrence of prey items did not differ much between pump and proventriculi samples (Table 1). Hard parts (squid beaks and eye lenses) occurred more frequently in gizzard, though crustaceans and fish bones were not found in it.

Digestion rank of crustacean prey shown by the number did not differ significantly between pump (intact, 2; partly intact, 7; digested, 18; well digested, 25) and proventriculi samples (intact, 1; partly intact, 6; digested, 14; well digested, 18). Size of intact and partly intact crustacean prey was larger for proventriculi (14.4 ± 0.4 mm, n = 7) than pump samples (6.3 ± 0.4 mm, n = 10, $Z = -2.714$, $P < 0.001$, *U*-test).

Digestion rank

In 1986, 79% and 78% of krill and amphipods prey collected in 20:00–23:00 and 23:00–02:00, respectively, were categorizes as "digested" or "well digested". In 1995, 83% of krill and amphipods prey collected between 20:30 and 01:00 were "digested" or "well digested". In the digestion experiment, intact or mostly intact prey was recovered 0.5–3 hrs. after feeding, and "digested" and "well digested" prey was recovered 3–12 hrs. after feeding.

Between year changes of diet in summer

To minimize the effects of seasonal change of the diet only July and August samples were used. The greatest number of decapods and barnacles were recovered from the sample taken in 1986 (including pump samples of 16 birds sacrificed). Squids occurred frequently in 1995. LSTP fed mainly on fish, krill, amphipods and squids (Table 2). Diversity of food items seemed to be lower in 1995 and 2003 than in 1982 and 1986 (Table 2).

In 1982 and 2003, *E. pacific* represented all the krill species in the diet. Although not recorded, most of krill found in 1995 sample was also *E. pacifica*. Most of fish and squids were not identified, though Myctophids were found from 4 samples in 2003. Five lower beaks of squids collected in 1982 were identified as Gonatus spp. LSTPs fed on both Hyperiidae and Gammariidae amphipods.

Table 1 Evaluation of stomach pumping. Percent occurrence of prey items in the pump sample, proventriculi and gizzard of 16 LSTPs on Daikoku Island in 1986.

Prey item	Pump sample	Stomach sample	
		Proventriculi	Gizzards
Fish	65	70	0
Krill	30	35	0
Amphipods	30	25	0
Decapods	10	15	0
Squids	10	30	71

Table 2 Percent occurrence of prey items in the stomach of LSTPs on Daikoku Island.

Year Prey items	1982	1986	1995	2003
Fish	23	58	46	39
Krill	22	34	57	79
Amphipod	13	39	43	0
Decapods	3	19	0	4
Barnacle	0	14	0	0
Squid	13	5	85	0

Table 3 Density of LSTP (birds/km^2), krill (inds/m^3) and plankton (inds/m^3) on the sea in summer and autumn. Sample sizes are given in parentheses and means are provided with standard deviation (SD).

Species	Season	Area		
		Shelf	Slope	Basin
Leach's Storm-Petrel	Summer	1.02 ± 1.83 (8)	20.22 ± 21.86 (5)	27.22 ± 40.97 (6)
	Autumn	0.05 ± 0.12 (6)	0.65 ± 1.71 (7)	0.14 ± 0.26 (17)
Krill	Summer	0.03 ± 0.01 (3)	0.14 ± 1.10 (3)	-
	Autumn	0.00 ± 0.00 (3)	0.13 ± 0.09 (5)	0.10 ± 0.11 (7)
Plankton	Autumn	0.22 ± 0.07 (9)	0.37 ± 0.08 (8)	0.40 ± 0.07 (18)

At sea density of LSTPs and their prey

Density of LSTPs on the sea surface was significantly higher in summer than in autumn ($F_{1, 43} = 31.9$, $P < 0.0001$, Table 3) and it was higher in slope and basin than in shelf ($F_{2, 43} = 5.9$, $P < 0.01$, Table 3). Krill density did not differ significantly between summer and autumn ($F_{1, 21} = 0.14$, $P < 0.71$, Table 3). Krill density seemed to be in the order of slope > basin > shelf, though the effect was marginal ($F_{2, 21} = 0.3.58$, $P < 0.052$, Table 3). Among krill species, *E. pacifica* (0.067 ± 0.084 inds/m^3, n = 21) was more abundant than *Tysanoessa inermis* (0.002 ± 0.005 inds/m^3, n = 21) and *T. longepes* (0.019 ± 0.024 inds/m^3, n = 21). Plankton density was significantly greater in slope and basin than in shelf in autumn ($F_{2, 32} = 22.7$, $P < 0.0001$, Table 3).

DISCUSSION

Sampling bias

Size of the crustacean prey in pump sample was smaller than that remained in proventriculi, apparently because of the limitation of diameter of tube of the pump. However, the occurrence of the prey items and the digestion status did not differ between these pumps and proventiriculi; indicating that the pumping give unbiased sample of prey occurrence in the stomach. Many LSTPs contain hard items (stones etc) in gizzard that is located at the end of stomach, and may use it to reduce buoyancy in species that feed by pursuit diving; the actual purpose of its use, however, is unclear [13]. Similarly, LSTPs kept hard parts in it (Table 1). High occurrence of squid beak and eye lenses in 1995 (Table 2) might indicate that birds vomited a part of the contents of gizzard with water flushing technique.

Prey

Most prey species found in the diet of LSTPs show daily vertical migration [14–16]. As LSTPs feed on items on the surface layer of the sea, it is hypothesized that LSTPs feed mainly during the night [17]. The proportion of LSTPs giving pump samples containing > 2 ml contents decreased rapidly during 22:00–23:00 and became less than 10% after 24:00 on Daikoku Island [10]. Most of crustacean prey found in the stomach was "digested" or "well digested", being similar to the digestion status of crustaceans 2–12 hrs. after feeding. Therefore, prey items collected in this study certainly fed well before the sampling during the night, presumably in the daylight hours or the evening as implied in Watanuki (2002) [10]. The patch of euphausiids is sometimes observed near surface during daylight hours [18].

LSTPs on Daikoku Island feed on *T. longipes* and *T. inermis* and copepods (*Neocalanus cristatus*) in spring and on *E. pacifica* and fish in summer (see also Ref. 9). In our survey at sea, *E. pacifica* was dominant krill species in summer and autumn. *T. longipes* and *T. inermis* were infrequent in summer and autumn in this area.

Climatic regime shifts occurred in 1976/77 and 1988/89 [19–21]. Sea surface temperature (SST) decreased after the 1976/77 climatic regime shift but increased after the 1988/89 climatic regime shift in the Oyashio waters [22]. During the cold regime after the 1976/77 climatic regime shift, sardine was dominant in the Pacific waters off eastern Hokkaido while the stock of sardine almost disappeared in the waters during the warm regime after the 1988/89 climatic regime shift [23–24]. In contrast to this substantial decrease in sardine stock, mesozooplankton, dominated by *Neocalanus* copepods, biomass tended to increase after the 1988/89 climatic regime shifts [22, 25]. The abundance of myctophid fishes do not change with the 1988/89 climatic regime shift [26]. Although no data are available on krills, the communities of mesozooplankton, myctophid fishes and krills might have less change with the 1988/89 climatic regime in the Oyashio waters.

Through the change in marine ecosystem derived from 1988/89 climatic regime shift, LSTPs similarly fed on a range of prey items. This indicates high ability of LSTPs to search and forage the range of prey items. But the diversity of food items seemed to be lower in 1995 and 2003 than in 1982 and 1986, indicating the potential effects of the regime shift on the variability of prey in LSTPs.

Distribution at the sea

Census of birds was conducted during day light hours (8:00–17:00). As discussed, LSTPs might not feed mainly during dark time. Thus LSTPs observed at the sea surface possibly reflected their feeding activity to some extent.

Main prey item in the summer of 2003 was *E. pacifica* as found in other study years. Density of both LSTPs and *E. pacifica* was highest in the slope area off Kushiro, though the density of LSTPs was low in the slope area off Erimo where *E. pacifica* was sometimes abundant. LSTPs possibly forage in areas close to the Daikoku Island where prey density is high. Daikoku Island is located in an area affected by the cold Oyashio current [27]. Narrow and steep sloped area along the coast of eastern Hokkaido (Fig. 1) affects the Oyashio current flow; it could produce upward transportation of nutrient rich water, as observed in the area of Aleutian Archipelago [28]. In 2003, SST along the slope area was 11°C being colder than that in the shelf (14°C) and basin (14°C) areas in late September; indicating upward water transportation along the slope [29]. This upward water transportation would result in high primary production [30], and high density of euphasiids and myctophids including *Diaphus theta* and *Stenobrachius leucopsarus* [31] attract marine mammals [32]. The energy rich area, such as shelf area, is highly productive [30].

In conclusion, LSTPs feed on the fixed range of prey both in cold and warm regimes. Productive and predictable upward water transportation in the slope area may support the energy requirements of large number of LSTPs breeding on Daikoku Island.

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