

At-sea Habitat Use of Rhinoceros Auklets Breeding in the Shelf Region of Eastern Hokkaido

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At-sea habitat use of breeding seabirds is strongly influenced by marine environmental features that vary over space and time. The use of bio-loggers allows researchers to track fine-scale movements of seabirds and provides opportunities to identify the primary factors affecting their area use for foraging. Using GPS loggers, we tracked chick-rearing rhinoceros auklets (*Cerorhinca monocerata*), which are wing-propelled divers, at Daikoku Island, eastern Hokkaido, Japan. The central phase for foraging activity on birds' trips was determined using a multiple change points model. To examine environmental factors explaining the distribution of the foraging phase, a generalized additive model was used where sea surface temperature, chlorophyll *a* concentration, bathymetry, and distance from the colony were explanatory variables. To obtain information supporting the behavioral tracking, prey items in the bill-loads of adult auklets were collected. We found that auklets foraged over the continental shelf shallower than the 200-m isobath and that distance from the colony was related to the area use. Adult auklets predominately brought back age-0 chum salmon (*Oncorhynchus keta*), which was abundant in coastal waters along southeast Hokkaido during the study period. Our findings indicate that rhinoceros auklets rearing chicks, hence visiting nests frequently, on Daikoku Island can find suitable feeding grounds nearby.

Key words: *Cerorhinca monocerata*, marine habitat, movement, GPS logger, conservation

INTRODUCTION

Marine environments are heterogeneous and vary over space and time (Hays et al., 2005; Mann and Lazier, 2006). Habitat selection of marine top predators is strongly affected by this spatiotemporal heterogeneity (Domalik et al., 2018; McDuire et al., 2018; Lamb et al., 2020). For example, some seabird species forage in areas with high gradients of sea surface temperature (SST) and chlorophyll *a* concentration (chl_a) (Sabarros et al., 2014; Scales et al., 2014). These oceanic gradients shape fronts retaining nutrients and plankton in surface waters, and attract plankton-eaters such as pelagic fish (diet for many seabirds) (Bakun, 2006; Bertrand et al., 2008). In addition, piscivorous seabirds often use complex bathymetric areas where upwelling brings nutrient-rich water to the surface (Yen et al., 2004; Ribic et al., 2008). These marine environments are relevant predictors of habitat use by seabirds because they reflect the distribution of feeding grounds (Bertrand et al., 2014; Prants et al., 2017; Waggitt et al., 2018).

Bio-logging devices, such as a miniaturized GPS data logger with a long-life battery or a solar panel, have been

developed recently. Researchers can track seabirds' behavior for prolonged periods with increased precision of GPS locations (Bouten et al., 2013; Baert et al., 2018) and get opportunities to study the movements of smaller species (Soanes et al., 2015; Fijn et al., 2016; Jakubas et al., 2017). Bio-loggers are now seen as a fundamental tool for understanding environmental factors affecting the area use of seabirds (Wilmers et al., 2015). The rhinoceros auklet, *Cerorhinca monocerata* (hereafter referred to as "auklet"), is a medium-sized, colonial breeding species that is distributed along coastal California, off the west coasts of Canada and Alaska to the Aleutian Islands, and in northern Japan, mainly around Hokkaido (Gaston and Jones, 1998; BirdLife International, 2018). The auklets forage for fishes and large zooplankton species by diving (Gaston and Jones, 1998; Ito et al., 2009), and their behavioral characteristics (e.g., diving ability and time allocation) have been described based on bio-logging techniques (Kato et al., 2003; Kuroki et al., 2003; Watanuki et al., 2006). However, identifying what kinds of seascapes are used as their foraging habitat remains a challenging issue (Cunningham et al., 2018; Wilkinson et al., 2018). Although previous studies examined the at-sea habitat use of the auklets based on direct observation (Davoren, 2000; McGowan et al., 2013), that technique may not track the full range of at-sea behavior. To clarify which environmental factors affect the at-sea habitat use of auklets, it is

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doi:10.2108/zs210014

important to track fine-scale movement patterns using bio-logging devices.

In the Western Pacific, most breeding colonies of auklets are distributed on islands around Hokkaido, Japan (Osa and Watanuki, 2002; Okado et al., 2019). Based on ship-board surveys, auklets in the northern Japan Sea possibly change their feeding area from the south to the north following the seasonal change of the distribution of Japanese anchovy, *Engraulis japonicus* (their main diet) (Deguchi et al., 2010). In contrast, little is known about characteristics of at-sea habitat use of auklets in the Pacific on the eastern side of Hokkaido. The marine environments of this area are influenced by the Oyashio Cold Current, and are characterized by highly nutrient-rich water flowing from the subarctic North Pacific (Sakurai, 2007; Prants et al., 2017). Thus, the primary drivers of at-sea habitat use by the auklets in the Oyashio-dominated area should be different from those in the northern Japan Sea. The auklets breeding in the eastern side of Hokkaido feed on prey species different from those in the northern Japan Sea (Okado et al., 2021), which can serve as a factor to explain foraging site selection (Cunningham et al., 2018).

The purpose of this study was to identify the primary drivers of at-sea habitat use of auklets during the chick-rearing period on Daikoku Island, located in a region dominated by the Oyashio Cold Current. First, we tracked the movements of auklets by using GPS data loggers and detected the central phase for foraging activity on birds' trips. We then examined the relationships between the distribution of foraging phase and several marine environmental variables through constructing a generalized additive model. In addition, we assessed the diet composition by collecting prey items from bill-loads of adult auklets.

MATERIALS AND METHODS

Study site

Daikoku Island (42°57'N, 144°52'E) is located 3 km off the Pacific coast of eastern Hokkaido and has an area of approximately 1.0 km² (Fig. 1A, B). The sea area around this island is dominated by the Oyashio Cold Current, which flows southward from the subarctic North Pacific Ocean (Fig. 1A). During breeding season, 77,734 nest burrows and 46,640 pairs of auklets were observed on this island (Okado et al., 2019).

Ethics

All of our fieldwork on Daikoku Island was completed under permission of the Akkeshi Town Board of Education (permissions no. 20 and no. 31-6 for landing on Daikoku Island). The Hokkaido Regional Environmental Office in Kushiro approved our capture procedure, including the attachment of GPS data loggers (permission no. 1906192).

Deployment of GPS data loggers

Our fieldwork was conducted in July 2019 for the deployment and recovery of GPS data loggers. The logger deployment was carried out in early July (4, 7, and 9 July), which coincided with the middle phase of chick rearing. We searched some nest burrows with chicks during the daytime to determine candidate burrows for capturing adult auklets because both parents forage at sea during daytime and return to their nest at night to provide food for their chicks. After sunset, we checked each breeding nest again and captured adult auklets from the nest by hand. In total, six adults were captured. The captured auklets were weighed to the nearest 0.1 g by using a spring balance (Scale Medio Line 41000, PESOLA, Switzerland). A GPS logger (12 g, L35 × W19 × H13 mm with a 28 mm length whip antenna, Gipsy Remote, TechnoSmart, Rome, Italy) was attached to feathers on the back, using tesa tape. The weight of a GPS logger corresponded to 2.0% of the mean body weight of auklets (mean ± SD = 588.0 ± 43.3 g) and 2.2% of that

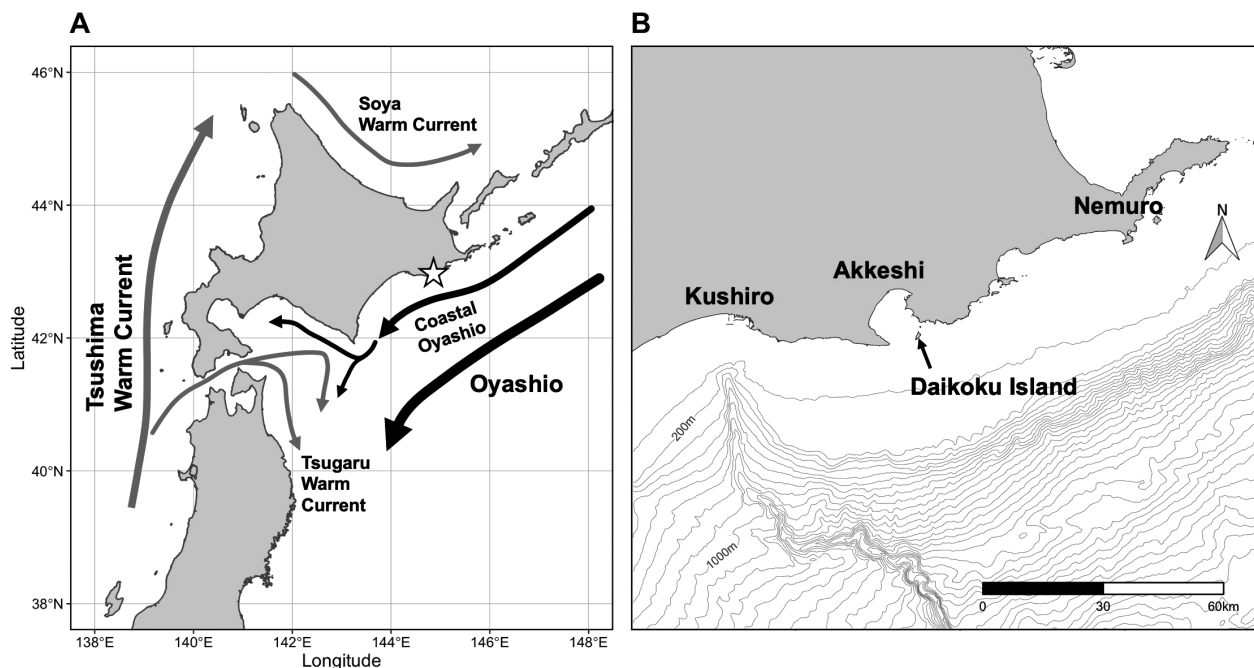


Fig. 1. Location of the study site: Daikoku Island off the eastern Hokkaido, Japan (star in [A]). Arrows in (A) indicate the currents flowing around Hokkaido (black: cold currents, gray: warm currents) (currents were obtained by referring to Isoda and Kishi, 2003). Bathymetric contours in (B) are drawn at 100-m intervals.

of the smallest individual (550 g).

We programmed the loggers to get a positional fix every 15 min between 03:00 and 21:00 h, because chick-rearing auklets stay in their nest or rest on the water surface at night (Kato et al., 2003). To examine a tendency of movement of auklets during the chick-rearing period, we aimed to track birds over multiple days until late July. An automatic data-downloading device (base station, TechnoSmart) was placed near the location of the breeding colony during 4–29 July and powered by an external battery. Data recorded by the loggers can remotely download to the base station when logger-equipped auklets get close. According to the manufacturer's specifications (TechnoSmart), the downloading link is about several hundred meters in the line of sight, depending on land features and weather. This system allows us to collect data from birds without recapture, especially from species that are sensitive to frequent handling (Cunningham et al., 2018; Sun et al., 2020). We checked the base station every several days and downloaded any accumulated data to a laptop PC.

We attempted to retrieve the loggers and checked burrows five–six times per night on 26–28 July. However, we could not recapture birds carrying devices. In the later chick-rearing period, as adult birds might spend less time in their nest, we were not able to confirm whether the loggers came off or remained on the backs of birds. It is presumed that the loggers would come off when birds molt back feathers after leaving the breeding area.

Effects of logger deployment

Sun et al. (2020) reported that deploying similar weight loggers on auklets (~2.3%) can increase the breeding abandonment. To confirm whether logger attachment to parent birds increased the risk of breeding abandonment, we checked the nests for the presence of chicks again during the daytime on 26–29 July (19–23 days after the deployment). Furthermore, to examine the influence of logger deployment on the growth of chicks, we also compared wing length and body weight of chicks on the date of logger deployment (before the deployment) with those after the deployment.

We found chicks in four of the six nests on 26–29 July. In the two burrows where no chicks were found, the chicks were relatively large (wing length = 96–99 mm) before logger deployment. Wing length of > 130 mm is considered to be a criterion for fledging in auklets (Deguchi et al., 2004). Assuming the basic growth rate of wing length (approximately 3.0 mm day⁻¹; Takenaka et al., 2005), the wing length of the two chicks would have reached the fledging size at 10–12 days after the date of the first measurement. It has also been shown that the abandonment rate of auklets is lowest

during chick rearing (Sun et al., 2020). Thus, it is suggested that they had already fledged when we checked their nests again (26–29 July). The wing length and body weight in four of the six chicks were able to be measured both before and after the deployment (Table 1). We confirmed increased wing length in these four chicks after the deployment (mean ± SD: 65 ± 28 mm vs. 109 ± 47 mm, paired *t*-test: *t* = -0.36, *P* = 0.04). This wing growth rate (mean = 2.6 mm day⁻¹, range = 0.8–4.4 mm day⁻¹) was slightly lower than the basic growth rate. Furthermore, there was no significant difference in body weight before and after the deployment (mean ± SD: 212.0 ± 79.0 g vs. 220.8 ± 115.9 g, paired *t*-test: *t* = -0.34, *P* = 0.76), and we confirmed decreased body weight in two of the four chicks after the deployment (Table 1). These findings suggest that the feeding rate or mass of deployed birds might have been decreased, although we have no information about those in non-deployed birds. Our logger deployment might have affected the growth of chicks, because they did not gain weight during the deployment.

Movement data analysis

In this study, a foraging trip was defined as the movement trajectory of an auklet from departure to arrival back on the colony. The number of foraging trips was counted for each auklet for the tracking period. Since auklets rarely fly at night (Kato et al., 2003), we assumed that tracked birds were resting on the sea at night when both the last point of a day (around 21:00 h) and the first point of the next day (around 03:00 h) were recorded on the sea. We regarded that case as a 2-day foraging trip. Total travelled distance of each trip was measured and averaged for each tracked auklet, and the maximum distance from the colony was also measured for each bird.

Foraging trips of most seabird species can be divided into a transit phase (departure from and returning to nesting site) and a central phase for foraging activity (Weimerskirch, 2007; Rey et al., 2010; Michelot et al., 2021). In order to focus on the foraging phase of auklets' trips in our analysis, we detected and excluded the transit phases. First, we calculated the following variables: (1) the distance from the colony for each location and its percentage of the maximum distance reached in each trip (hereafter referred to as "percentage of max. distance"), and (2) the duration from the departure for each location and its percentage of the total duration of each trip (hereafter referred to as "percentage of trip duration"). Secondly, to define the foraging phase and the transit phases on the trips, we estimated multiple changing points using the package "mcp" (Lindeløv, 2020) in R (R Core Team, 2020). This method can

Table 1. Summary of GPS tracking of auklets, and difference in chicks' size before and after logger deployment.

ID of auklet	Adult						Chick			
	Body weight (g)	Tracking duration (days)	Number of trips	Number of located positions	Mean of total distance ^a (km)	Maximum distance ^b (km)	Before deployment		After deployment	
							Weight (g)	Wing length (mm)	Weight (g)	Wing length (mm)
1214	590	7	7	485	85.1	47.6	355	99	n.a.	n.a.
1215	560	10	9	629	87.5	63.4	290	96	n.a.	n.a.
1216	568	15	14	794	68.7	56.0	240	68	262	134
1217	550	20	19	1233	79.6	50.5	280	79	355	142
1218	590	17	17	1023	73.5	59.8	98	25	82	39
1219	670	16	15	994	54.6	85.3	230	87	184	121
Mean ± SD	588 ± 43.3	14.2 ± 4.8	13.5 ± 4.6	859.7 ± 276.4	74.8 ± 12.1	60.4 ± 13.5	248.8 ± 78.7	75.7 ± 27.3	220.8 ± 115.9	109.0 ± 47.5

^a Total movement distance of each trip was measured and averaged for each auklet

^b Maximum distance from the colony reached by each tracked auklet

n.a., not applicable (absence in the nest)

identify two inflection points on the relationship between the percentage of max. distance and the percentage of trip duration based on Bayesian inference (Michelot et al., 2021). By the *mcp* function, we identified the two changing points at 11.1% and 84.3% of the trip duration, and three phases of the trips were detected (see Supplementary Figure S1). Thirdly, in order to confirm that the estimated central phase (11.1–84.3% of the trip duration) corresponds to foraging activity, we also calculated the mean speed and the total movement distance in each phase for each trip. These variables were compared among phases by the Steel–Dwass test. Auklets moved significantly longer distances at lower speeds during the central phase, and in contrast, shorter distances at higher speeds during both the first and the last phases (see Supplementary Figure S2). Previous research showed that auklets stayed on the sea surface with little flying during most of the daytime (Kato et al., 2003). Thus, we considered that the central phase of birds' trips was likely to be foraging activity (also including resting on the sea surface).

Prey species identification

During the chick-rearing period, parent birds collect fishes in their bills (1–30 items) and deliver them to chicks at night (Davoren and Burger, 1999). The bill-loads (all prey items brought back by a single adult in its bill) are a reliable sampling of prey items, thus allowing us to assess the diet composition (Cunningham et al., 2018). On 11 and 16 July 2019, we caught 20 adult auklets at night and collected all of the prey items in the bill-loads. In order to avoid a risk of capturing partners of the logger-deployed birds, the food sampling was conducted in an area 50 m from the nests of tracking birds. The collected prey items were identified to the species level, and fork-length and body mass of each item were measured to determine the age class. We then calculated the frequency of occurrence and percentage of mass of each identified prey species.

Statistical analysis

To clarify the effect of marine environmental variables on the distribution of auklets' foraging activity, we fitted a generalized additive model (GAM) in the R package "mgcv" (Wood, 2017). Within the maximum movement range of tracked auklets, we counted the number of locations that corresponded to the foraging phase in each grid at a 500×500 m spatial resolution. This was used as a response variable in the model. SST, chl_a, bathymetry (sea depth), and distance from the colony were included as explanatory variables. These environmental variables are known to affect the foraging habitat selection of seabirds (McGowan et al., 2013; Sabarros et al., 2014; Domalik et al., 2018). Remotely sensed satellite data of SST and chl_a were downloaded from the Japan Aerospace Exploration Agency (JAXA SGLI, 250×250 m resolution; https://www.eorc.jaxa.jp/cgi-bin/jasmes/sgli_nrt/index.cgi). The obtained SST and chl_a

data were averaged for a month (July 2019) because there were no images for some dates and times due to cloudy weather conditions. Bathymetric data were downloaded from the Japan Oceanographic Data Center (JODC, 500×500 m resolution; https://www.jodc.go.jp/jodcweb/JDOSS/index_j.html). The SST and chl_a data were resampled at the 500×500 m grid size to set them at the same resolution as the bathymetric data. We used these environmental data within the maximum movement range of auklets for our model analysis. All of the explanatory variables were used as nonlinear predictors (chl_a was log-transformed). The degree of smoothing for explanatory variables was set to the default method of the *mgcv* function. Before fitting the model, we confirmed that explanatory variables were not correlated with each other.

RESULTS

Movement

We successfully obtained tracking data from all of the

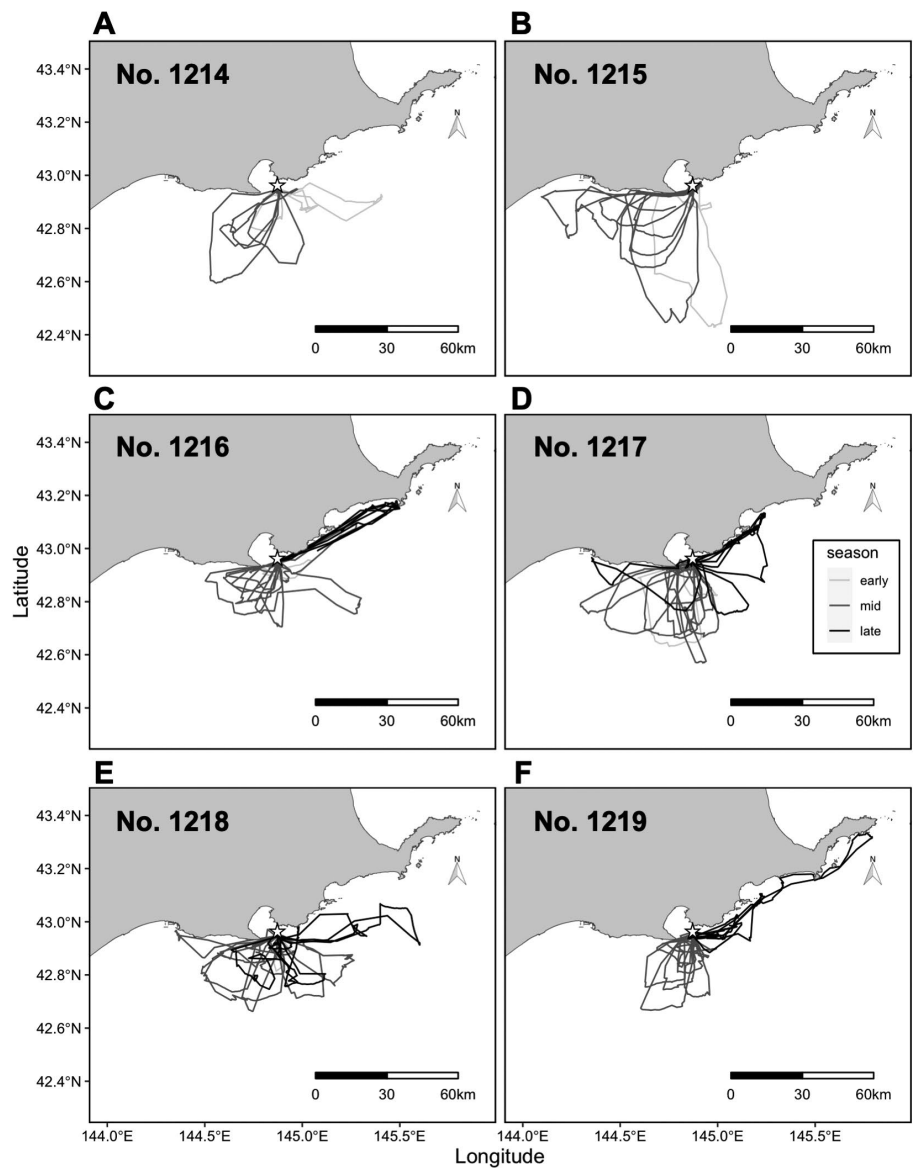


Fig. 2. Foraging trips of six auklets tracked by GPS loggers. The number in the upper left of each panel is the ID of the bird. The trajectories recorded in early (1–9), mid (10–19), and late (20–31) July are shown in different colors. The star in each panel indicates the location of the colony.

logger-deployed auklets ($n = 6$) by the base station. Three of the six devices recorded the data until late July, and thereafter no data were downloaded on the base station. The other three devices stopped recording in mid-July, probably because the logger came off and/or the battery ran out, or the birds abandoned their nests. Tracking duration ranged from 7 to 20 days (mean = 14.2 days), with 485–1233 GPS locations (including those located on the island) and a mean of 13.5 trips per auklet (range = 7–19 trips; Table 1). One-day trips accounted for 95% of all 81 trips.

Auklets travelled off the south–west of Daikoku Island in early and mid July (Fig. 2). In late July, four of the six auklets also travelled to coastal waters on the eastern side of the island (Fig. 2C–F). The mean total movement distance was 74.8 km per trip per auklet (range = 54.6–87.5 km) and the mean maximum distance from the colony was 60.4 km per auklet (range = 47.6–85.3 km; Table 1). The foraging phase locations on the trips were distributed on the continental shelf < 200-m isobath (Fig. 3A), and most of them moved in the east–west direction along the isobath lines. The foraging phase was also found at an area over the edge of the shelf slope and the submarine canyon off the southern side of the island (Fig. 3A).

Foraging activity and environmental variables

Both SST and chl a (monthly average) showed spatially uniform distribution for the most part of the waters around Daikoku Island (Fig. 3B, C), except for off the southwest part of the island with partly higher chl a concentration (Fig. 3C). GAM results showed that distribution of the foraging phase was significantly related to all of the explanatory variables (Table 2, Fig. 4). Foraging activity of auklets reached maximum at SST of approximately 9°C, and decreased linearly

with increasing chl a concentration (Fig. 4A, B). A small peak on the curve was observed at bathymetry of 200–300 m (Fig. 4C). However, it should be noted that the changes of the curve observed for those variables (SST, chl a , and bathymetry) were relatively small. Foraging activity was higher at closer proximity to the colony, and a slight increase was also confirmed beyond approximately 70 km (Fig. 4D).

Diet

In total, 90 prey items (total mass of 550.6 g) were collected from 20 auklets. These items consisted of a total of four species of fish: Pacific saury (*Cololabis saira*), Japanese anchovy (*Engraulis japonicus*), chum salmon (*Oncorhynchus keta*), and Japanese sardine (*Sardinops melanostictus*). The number of fish in a single bill-load ranged from one to 10 items (mean \pm SD = 4.5 \pm 3.0 items), and each bill-load consisted of one–three species (mean \pm SD = 1.7 \pm 0.7 species). The most frequently found diet was chum salmon, followed by Pacific saury (Table 3). The percentage of mass was highest for Japanese sardine, followed

Table 2. Statistics for generalized additive model explaining distribution of the foraging phase.

Variables	Estimate	SE	t	edf	F	P
Intercept	0.163	0.004	38.69			
s (sea surface temperature)				3.44	7.12	< 0.0001
s (\log_{10} (chlorophyll a + 0.00001))				1.00	9.58	0.002
s (bathymetry)				6.51	9.73	< 0.0001
s (distance from colony)				8.36	133.79	< 0.0001

edf , estimated degrees of freedom

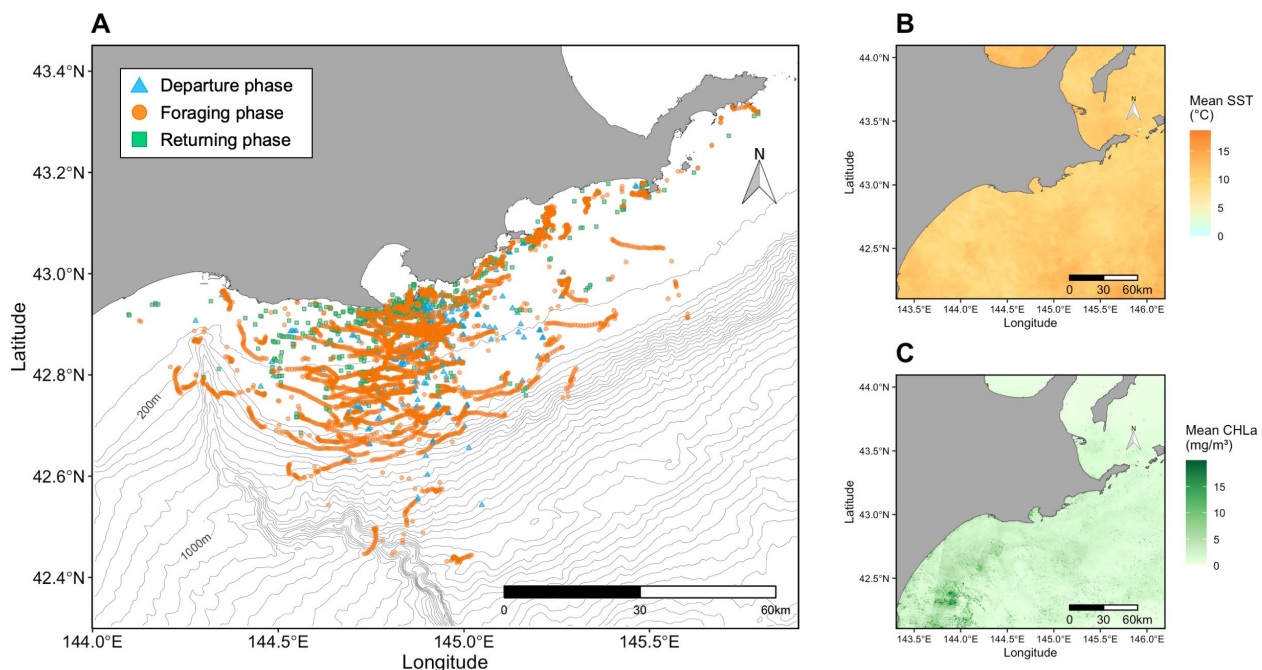


Fig. 3. Distribution of the foraging phase (A) and oceanography: (B) sea surface temperature and (C) chlorophyll a concentration off eastern Hokkaido. Each phase on the trips was determined by the mcp (multiple change points) method. Bathymetric contours in (A) are drawn at 100-m intervals.

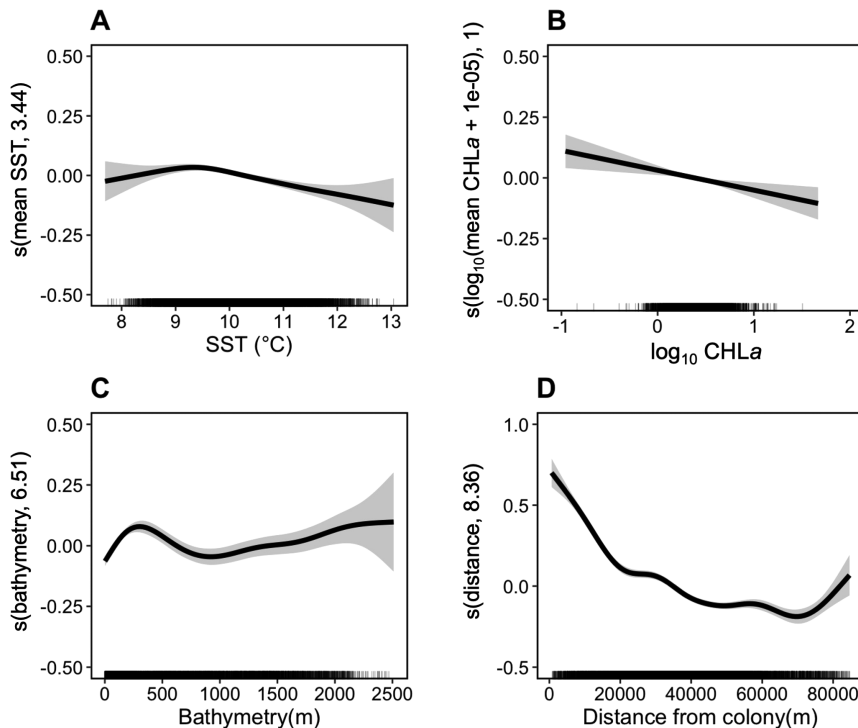


Fig. 4. Relationships between distribution of the foraging phase and explanatory variables: **(A)** sea surface temperature, **(B)** chlorophyll a concentration, **(C)** bathymetry, **(D)** distance from the colony. Response curves, shown with 95% confidence intervals (shaded), were predicted by using a generalized additive model.

Table 3. Prey species in bill-loads brought back to chicks by adult auklets in July 2019.

Prey species	% of auklets	% of mass	Fork-length ^a (mm)
<i>Sardinops melanostictus</i>	40.0	53.4	150.4 ± 34.4 (94–185, <i>n</i> = 9)
<i>Oncorhynchus keta</i>	70.0	34.6	86.1 ± 9.7 (65–112, <i>n</i> = 34)
<i>Cololabis saira</i>	55.0	8.8	69.3 ± 15.9 (43–116, <i>n</i> = 36)
<i>Engraulis japonicus</i>	5.0	3.1	140 (<i>n</i> = 1)

Frequency of occurrence (% of auklets) and percent of mass (% of mass) of each prey species were calculated. Total number of auklets = 20, total number of collected items = 90, total mass of prey items = 550.6 g.

^a Mean ± SD (range, sample size), fishes lacking head were excluded from measurement.

by chum salmon (Table 3). The fork-length of Japanese sardine was the largest among the four species of fish (mean ± SD = 150.4 ± 34.4 mm, Table 3) and its number was one–two individuals per bill-load. Mean ± SD of the fork-length of chum salmon and Pacific saury was 86.1 ± 9.7 and 69.3 ± 15.9 mm, respectively (Table 3).

DISCUSSION

We found that tracked auklets intensively used areas over the continental shelf, including around the shelf edge

(Figs. 2, 3A). During the foraging phase on the trips, auklets moved at lower speeds in the east–west direction (Fig. 3A, and see Supplementary Figure S2). These results suggest that auklets search a feeding ground along the current of the coastal Oyashio flowing on the continental shelf. From early to mid-July, chum salmon, the dominant item in the bill-loads (Table 3), are widely distributed in coastal waters of eastern Hokkaido (Irie, 1990; Ueno and Ishida, 1996). On the other hand, Japanese sardine (the largest diet item of auklets, Table 3) are distributed in waters farther off the south of Daikoku Island in early July, and move to inshore waters around the shelf edge from mid to late July (Inagake and Hirano, 1984). Chick-rearing auklets may be able to reach a suitable feeding ground without travelling long distances because diet animals (chum salmon) are sufficiently available near the colony. And it is likely that auklets also occasionally travel to distant feeding patches to obtain a larger prey item (Japanese sardine). To meet the highest energetic demands for chick rearing and to encourage rapid growth of chicks (Drent and Daan, 1980; Hamer et al., 2002), foraging closer to the colony would be energetically efficient (Jakubas et al., 2013).

Intensive at-sea use around the colony may also be related to breeding colony size. In colonial seabirds, the foraging areas increase with the number of breeding pairs via density-dependent competition for food resources (Lewis et al., 2001; Corman et al., 2016; Lamb et al., 2017). The largest breeding colony of auklets in Japan has been recorded on Teuri Island, the Japan Sea side (290,000 pairs; Osa and Watanuki, 2002). In contrast, the number of breeding auklets on Daikoku Island is relatively small (46,640 pairs; Okado et al., 2019). The maximum distance from the colony recorded in our study (mean = 60.4 km, Table 1) was shorter than that previously estimated at Teuri Island (mean = 87 km, maximum = 164 km; Kato et al., 2003). Due to the small colony size, effects of density-dependent competition on the movement range may be limited in the Daikoku Island colony.

Although auklets often travelled to areas distant from the colony (e.g., around the submarine canyon south of the island), GAM results suggest that auklets foraged closer to the colony (Fig. 4D). On the other hand, there was no clear relationship between foraging activity and oceanographic (SST and chl_a) or bathymetric variables (Fig. 4A–C). This suggests that the effects of seascapes on the distribution of auklets' foraging area might not be very strong, at least around Daikoku Island. In the area off the Pacific coast of eastern Hokkaido, water mass distributions in July are predominantly formed by the Coastal Oyashio Water flowing southwestward from off Kuril Island and/or the Okhotsk Sea (Kusaka et al., 2009, 2013). This feature makes distributions of SST and chl_a widely uniform during the chick-rearing

period of auklets. In the California Current System, breeding auklets forage at waters not only near the colony on the continental shelf but also distant beyond the shelf edge (Wilkinson et al., 2018). In this system, deep-sea upwelling brings nutrient-rich water to the surface and forms oceanic fronts (SST and chl_a), which affect foraging site selection of auklets (Wilkinson et al., 2018). It is likely that the habitat utilization of auklets found in this study is different from that of other regions. Auklets' response to seascapes might be determined by area-specific mechanisms creating feeding grounds, but further research, including at other breeding areas, is needed.

We also found that some tracked auklets shifted the destination of their foraging trips from south to east of the colony in late July (Fig. 2). In the breeding population of the Japan Sea (Teuri Island), the auklets' foraging area changes seasonally, reflecting the migration of their main prey item, Japanese anchovy (Deguchi et al., 2010). Our diet sampling showed that chum salmon most frequently occurred in the bill-loads (Table 3), matching the findings of Okado et al. (2020), who also studied breeding auklets on Daikoku Island. All salmon were age-0 class since the fork-length was smaller than 240 mm (Ishida et al., 1998). Age-0 chum salmon migrate northward along the coast of southeast Hokkaido to the Okhotsk Sea during the chick-rearing period of auklets (Irie, 1990; Ueno and Ishida, 1996). Therefore, auklets may respond to the seasonal migration of age-0 chum salmon. Alternatively, it is also possible that auklets explored other foraging patches because prey availability around the colony was depleted by the high intensity of use.

Most of the 20 parent birds (70%) brought age-0 chum salmon to their chicks (Table 3). On the other hand, the mass in the bill-loads was dominated by Japanese sardine (53.4%, Table 3). Japanese sardine was not found in the bill-loads in previous research conducted at the same breeding colony in 2014 and 2015 (Okado et al., 2020), suggesting that the diet composition of auklets on Daikoku Island has changed over the past few years. Diet composition of auklets often varies among years (Takahashi et al., 2001; Cunningham et al., 2018). In addition, the inter-annual variations of diet composition likely reflect the change of prey availability (Deguchi et al., 2004). The appearance of Japanese sardine in the bill-loads in this study indicates that this species is available in the coastal Oyashio Cold Current in the summers of recent years. Furthermore, the diet of auklets changes not only among years but also within a breeding season. The auklets breeding on Teuri Island switched their diet from cold water-living age-0 Japan Sea greenling (*Pleurogrammus azonus*) and sand lance *Ammodytes* spp. to warm-water living anchovy in a 2-week period (Takahashi et al., 2001). Thus, it is also possible that the difference in the diet composition between 2019 (this study) and 2014–2015 (Okado et al., 2020) may reflect a seasonality of the availability of sardines in the coastal Oyashio Cold Current in the summer. With the limited diet sampling in July in this study and Okado et al. (2020), the seasonal change of their diet is still unknown.

In the coastal area of eastern Hokkaido where the productive coastal Oyashio Cold Current dominates (Kusaka et al., 2013), more than $\sim 10^6$ birds, including three–four species of alcids (including rhinoceros auklets), two species of

gulls, two species of cormorants, and one species of storm-petrel, breed at least at three islands, several islets, and several locations along the coast (Osa and Watanuki, 2002). The region also provides important feeding or nursery grounds to both pelagic and demersal fishes (Honda et al., 2004; Sakurai, 2007; Yatsu, 2019), and consequently provides important fishing grounds for humans. Knowledge about the distribution of important marine habitats in the region is still sparse, however. Our results may give some clues about which features of marine habitats are important to breeding seabirds in this region.

ACKNOWLEDGMENTS

This research was funded by the Environment Research and Technology Development Fund (JPMEERF20184003) of the Environmental Restoration and Conservation Agency of Japan.

COMPETING INTERESTS

The authors have no competing interests to declare.

AUTHOR CONTRIBUTIONS

YY and YK designed this study. YY, JO, YW, AY, and YK conducted field research for tracking rhinoceros auklets at Daikoku Island. TS and YY analyzed data. TS wrote the manuscript. All authors contributed to the final manuscript.

SUPPLEMENTARY MATERIALS

Supplementary materials for this article are available online. (URL: <https://doi.org/10.2108/zs210014>)

Supplementary Figure S1. Determination of two change points by mcp model.

Supplementary Figure S2. Differences in mean speed and total movement distance on each trip phase.

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(Received March 6, 2021 / Accepted December 16, 2021 /

Published online February 17, 2022)