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SPECIAL FEATURE Bio-logging science in the ecological study of seabirds in Japan

Estimating foraging area of Rhinoceros Auklets by simultaneous sampling of water temperature profiles using bird-borne data-loggers

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ORNITHOLOGICAL SCIENCE

Abstract Alcids are important top predators, consuming substantial amounts of zooplankton and fish in the northern hemisphere. However, studies of their at-sea foraging behaviour are logistically difficult because of their wide foraging range and small body size. We developed a technique to estimate the approximate foraging area for individual birds using water temperature profiles sampled by both diving birds and a research boat. This technique was applied to chick-rearing Rhinoceros Auklets *Cerorhinca monocerata* breeding on Teuri Island, Hokkaido, which feed primarily on Japanese anchovy *Engraulis japonica* in the northern coastal Japan Sea. Annual variations of the warm Tsushima Current may influence the distribution of this prey species. Rhinoceros Auklets foraged mainly in waters with 12–15°C sea surface temperatures (SSTs), which formed in waters north of the breeding colony on 17 June 2002 and in waters south of the breeding colony from 30 May to 3 June 2003. Rhinoceros Auklets dove above or around the thermocline in both years. This indicates that foraging locations and dive depths may be influenced by SSTs and the depth of the thermocline, factors that presumably affect the distribution of their prey.

Key words Alcid, Foraging area, Rhinoceros Auklet, Temperature profile, Thermocline

Alcids are one of the major avian top predators in the northern hemisphere, as they represent 69% of the biomass of breeding seabird populations and consume a variety of zooplankton and fish (Gaston and Jones 1998). Birds breeding on islands commute between their nests (in the colony) and foraging areas. Therefore, their foraging and breeding performance depends on the availability of prey around the colony, while prey distributions often depend on the physical conditions in the surrounding waters (Kitaysky et al. 2000; Bertram et al. 2002). Seasonal and annual variations in at-sea distributions, and the factors affecting these distributions, have been extensively studied using ship-based surveys (Hunt 1996; Davoren and Burger 1999; Davoren 2000; Deguchi et al. 2004). The distribution patterns emerge from the foraging decisions made by each individual. Therefore, to further understand the interaction between the marine environment and alcids, it is important to examine the effects of oceanographic conditions on dive depth and foraging site selection for individual birds (Monaghan et al. 1994; Weimerskirch et al. 1994, 1997; Kitaysky et al. 2000).

It has been logistically difficult to survey individual foraging behaviours of alcids. Because of their long foraging distances (35–164 km: Tremblay et al. 2003; Benvenuti et al. 2001, 2002; Kato et al. 2003) and small body size (<1 kg, Gaston & Jones 1998), the application of radio or satellite transmitters and depth recorders on breeding alcids has been difficult (Hatch et al. 2000). Recently, downsizing of data-log-

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gers has enabled their use with small alcids (Croll et al. 1992; Benvenuti et al. 2001, 2002; Kuroki et al. 2003). By using small bird-borne temperature-depth loggers to collect water temperature profiles from diving Brünnich's Guillemots *Ulia lomvia* and determining additional profiles using a conductivity, temperature, and depth recorder (CTD, deployed from a boat) in potential foraging areas, it is possible to estimate the water masses (distinctive water aggregation having identical temperature and/or salinity features) in which individual birds are foraging (Mehlum et al. 2001; Watanuki et al. 2001).

In a study of breeding Rhinoceros Auklets on Terui Island, Japan Sea, higher chick growth rates were recorded in years when the availability of anchovy around the island was high (Takahashi et al. 2001). The availability of anchovy may be influenced by the northward transportation of the warm Tsushima Current (Deguchi et al. 2004). In this study, we estimated the foraging areas of individual of chick-rearing Rhinoceros Auklets using temperature profiles collected from foraging birds and CTD sampling. After adjustment for the slow response time of the temperature sensor on the data-logger, we evaluated this technique. We then examined the hypothesis that the birds forage in water masses where the sea surface temperature (SST) is suitable for Japanese anchovy *Engraulis japonicus*, the primary prey of Rhinoceros Auklets. We expected that the foraging areas would change among years according to SST changes. Finally, we determined if the depth of the thermocline influenced dive depth of the auklets.

STUDY AREA AND METHODS

1) Field study

Fieldwork was conducted at Teuri Island (44°25′N, 141°19′E), Hokkaido, Japan, in June 2002 and from May to June 2003 (Fig. 1). Parents that were rearing chicks in nest boxes (modified from Kuroki et al. 1998) were captured by hand at night between 2100 and 0200, 9 parents were captured in 2002 and 11 were captured in 2003. No significant differences in growth or survival rates have been reported between chicks reared in natural nests and those reared in nest boxes (Kuroki et al. 1998). Birds were weighed with Pesola spring balances to the nearest 5 g at the time of capture and recapture. External measurements (total head length and bill depth) were made to the nearest 0.5 mm using a slide caliper when birds were recaptured. Birds were sexed using the total head length and bill depth (Niizuma et al. 1999).

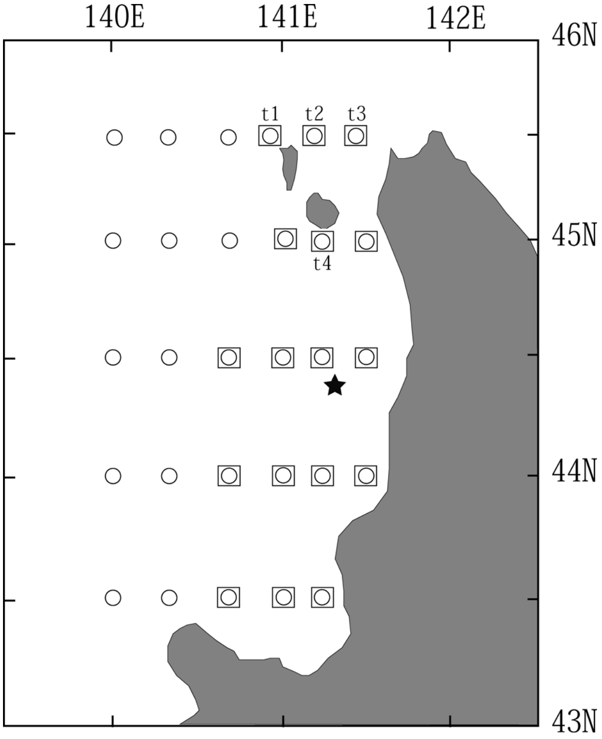

Fig. 1. Spatial distribution of CTD sampling stations in the study area northwest of Hokkaido, Japan Sea, in 2002 (squares) and 2003 (circles). The data-logger and the CTD were cast together at stations t1–t4. A star indicates the location of the Teuri Island breeding colony.

Data-loggers (short and normal types of the M190-DT in cylindrical containers with a domed top: 14 and 16 g weight, 47 and 53 mm length, 15 mm diameter, respectively, or M190-D2GT in the same cylindrical container with 60 mm length, 20 g weight, Little Leonardo, Tokyo) were attached to the backs of birds on 6 and 7 June 2002 and from 28 May to 1 June 2003. A small plastic grid (30×40 mm) was inserted into and glued on the feathers of the lower back with cyanoacrylate adhesive (Loctite 401, Henkel Japan, Yokohama). A data-logger was attached to the grid with adhesive tape (3M 8626; Sumitomo 3M INC) and plastic cable ties (100×2 mm). The birds were released immediately into the entrance of their nest boxes. After 10 days, equipped birds were caught by hand in their nest boxes and the data-loggers were retrieved.

The data-loggers had 16 Mbytes of memory, and were programmed to sample both depth and temperature every second. Depth and temperature was measured by semi-conductor pressure sensor (FPBS-82:

Fujikura) and by a precision thermistor (YSI44000: Nichikisou YSI), respectively. Resolution and accuracy were ±0.1 m and ±0.5 m for depth and ±0.018°C and ±0.1°C for temperature, respectively. After retrieval, data were downloaded onto a laptop computer using purpose-built software (Logger Tools version 3.1, Marine Micro Technology), transformed into text files, and analysed using Igor Pro version 4.04 (Wave Metrics Inc.). Dive depth (m), dive duration (s) and surface time (s) were calculated from recorded depth data. Dives to depths less than 1 m were excluded because they were within the range of potential error.

Birds made successive dives (3 to 127 dives) during periods ranging from 7 s to 115 min, a series of dives was defined as dive bout (see Fig. 1 in Kuroki et al. 2003). The bout-ending criterion (BEC) for each bird was determined as the long surface time at the inflection point of the surface-interval survivorship curve following Gentry and Kooyman (1986). A bout consisted of a series of at least three dives.

2) Diet sampling

Food loads were collected during the night using a landing net by catching birds returning to the island with fish. Food collections were made during logger-recording periods in 2002 and 2003. To examine the prey brought back by birds carrying data-loggers, their mates were caught and kept in nest boxes with closed entrances for 10 days in 2003. The head of the chick was covered with a nylon-net. The foods that remained in the nest were collected on the following morning (Hatch 1984). These chicks were artificially fed with 30–60 g of Japanese sand lance *Ammodytes personatus*. Fish species in the food samples were identified and weighed to the nearest 0.1 g with an electronic balance in our laboratory after collecting.

3) Temperature profiles sampled using data-loggers and CTD

Temperatures recorded by our data-loggers should be biased because of the slow response time (around 10–20 s with 90% time constancy). To overcome this problem, we used the following equation, which is basically the same as the one used by Daunt et al. (2003):

$$T_n = t_{n+1}/(1-e^a) - e^a t_n/(1-e^a) \qquad (1)$$

where T_n is the ambient temperature (°C) at time n (S), and t_n+1 and t_n are the recorded temperatures at the times $n+1$ and n, respectively. The value of a is equal to $-1/\tau$ (τ is the time constant of the data-logger).

To evaluate equation (1), we simulated bird dives at four CTD stations (t1–t4) using the R/V Hokuyo-maru (Wakkanai Fisheries Experimental Station, Hokkaido) in May and June 2002 (Fig. 1). A data-logger (M190-DT) was placed in a small nylon pouch (80×120×10 mm) and attached to the CTD. The casting speed of the CTD (0.4–0.7 m/s) was similar to the descent rate (0.5 m/s) of diving Rhinoceros Auklets (Kuroki et al. 2003). The response time of the CTD temperature sensor was very quick (0.1 s). The values of τ for each data-logger were calculated in the laboratory. Data-loggers were kept in 0°C water for 5 min, then moved quickly into +20°C water. This procedure was repeated three times for each data-logger. The mean values of τ of each data-logger were substituted into equation (1).

The CTD observations were carried out with the R/V Hokuyo-maru at 17 stations in the area surrounding the colony from 15 to 19 June 2002 and at 29 stations from 28 May to 3 June 2003 (Fig. 1). Temperature-depth profiles sampled by birds were corrected using equation (1), and compared to the CTD profiles collected at each station. The most likely CTD station was defined as the site that gave the smallest sum of squares of the temperature difference (SSD) between the bird and CTD samples at 1 m intervals through the range of 5 to 20 m depth.

4) SST and chlorophyll-*a* distribution

To investigate the relationship between the spatial distribution of bird diving activity, SST and chlorophyll *a* concentrations (Chl-*a*), weekly satellite SST and Chl-*a* data during the deployment period of the data-loggers were used. SST and Chl-*a* data were obtained from the NOAA/NASA AVHRR Pathfinder and SeaWiFS (distributed by NASA), respectively, and processed using SeaDAS software (version 5.0; NASA). Chl-*a* data with 9 km resolution centred on each CTD station were used in the analyses.

5) Statistics

We used Mann-Whitney U-tests, Wilcoxon signed rank tests, chi-squared tests, and regression analysis for statistical tests using Stat View (version 5.0; SAS Institute Inc.). Dive depth and duration data for Rhinoceros Auklets often had bi-modal distributions (Kato et al. 2003, in this study), therefore, median values were used as the average value for individual birds for dive depth and duration data. Results are presented as mean±SD with sample size.

RESULTS

1) Dive depth and bout

Five (four for females and one for male) of nine and six (four for females and two for males) of 11 data-loggers were recovered in 2002 and 2003, respectively (Table 1). The data-loggers recorded dive depth and temperature for 14.8±3.3 days (10–18 days). In these data, only dive data that corresponded to CTD sampling periods were analysed. In total, 7736 dives were recorded. The birds made 198.2±63.2 dives d^{-1} on average (Table 1). Median dive depth and duration were 20.4±7.2 m and 71.2±30.9 s, and maximum dive depth and duration were 51.9±8.9 m (37.5–69.1 m) and 184±60.8 s (110–276 s), respectively. The BEC was 88.2±12.5 s (60–110 s). The birds made 15.4±5.5 diving bouts per day and 13.3±3.6 dives per bout on average. The bout duration was 19.8±5.4 min.

2) Diet

The mass of food loads carried by parents without data-loggers was 37.2±9.0 g (n=20 loads) and 36.1±12.9 g (n=20 loads) in 2002 and 2003, respectively. The mass of food loads brought back by parents with data-loggers in 2003 (17.7±10.7 g, n=16 loads from 6 birds) was smaller than those carried by parents without data-loggers (U=14.0, P=0.005). The mass proportion of Japanese anchovy in the prey was 100% in 2002. In 2003, the mass proportions of prey for birds with and without data-loggers were 75 and 73% for Japanese anchovy, 20 and 17% for Japanese sand lance, and 5 and 10% for Japan Sea greenling *Pleurogrammus azonus*, respectively. There was no significant difference in diet composition between birds with and without data-loggers in 2003 ($\chi^2=1.94$, P=0.380).

3) Temperature profiles

Solar irradiation can quickly warm black data-loggers that are attached to birds' backs while the birds are flying or resting on the water surface. Within a dive bout, water temperature recorded during the first and second dives was warmer than during subsequent dives (Fig. 2). Thus, only water temperature data recorded after the third dive were used to calculate SSD in our study. The SSD was calculated every dive bout. Only a single dive deeper than 20 m (required depth to calculate SSD) was sampled from each bout.

Table 1. Diving parameters and results of estimation of foraging sites of 11 Rhinoceros Auklets during chick-rearing period in 2002 and 2003.

Year	Bird ID	Sex	Analysed data period (day)	No. of dives	Descent rate ($m\,s^{-1}$)	Ascent rate ($m\,s^{-1}$)	Median dive depth (m)	Median dive duration (s)	No. of bouts per day	No. of dives in a bout	Bout duration (min)	% of dive bouts containing only <20 m depth dives	% of dive bouts outside of CTD sampling area	% of dive bouts estimated foraging sites
2002	D67	F	1	162	0.8±0.2	0.9±0.4	27.9	93	15	11.0±0.71	22.2±14.6	7	6	87
2002	D88	M	1	121	0.8±0.2	0.8±0.3	33.0	109	8	14.6±11.5	22.1±22.4	0	2	98
2002	G09	F	1	188	0.6±0.2	0.9±0.2	26.5	112	8	17.5±8.5	24.8±15.9	13	39	48
2002	G13	F	1	214	0.6±0.3	1.1±0.3	20.0	87	19	10.4±6.4	17.7±12.9	31	16	53
2002	G27	F	1	109	0.6±0.3	0.9±0.3	30.1	119	17	7.9±4.1	20.9±13.4	0	23	77
2003	52	F	5	1225	0.9±0.2	1.2±0.3	15.6	55	19.2±7.2	12.9±14.9	20.0±18.9	22	0	78
2003	98	M	5	1274	1.0±0.2	1.2±0.4	5.8	26	22.6±9.5	10.0±13.4	10.7±11.8	17	6	77
2003	128	M	5	770	1.0±0.2	1.1±0.3	20.3	66	14±6.9	10.0±7.5	13.9±12.3	1	6	93
2003	L69	M	5	1004	1.0±0.1	1.4±0.4	26.6	62	7.8±3.0	18.3±15.9	30.7±28.7	4	0	96
2003	L86	M	5	1020	0.9±0.2	1.2±0.3	5.8	27	17.2±8.2	17.3±12.6	15.9±15.0	33	3	64
2003	L107	F	5	1649	0.7±0.2	1.2±0.3	12.3	42	22.0±5.3	15.9±20.6	18.7±19.5	11	0	89

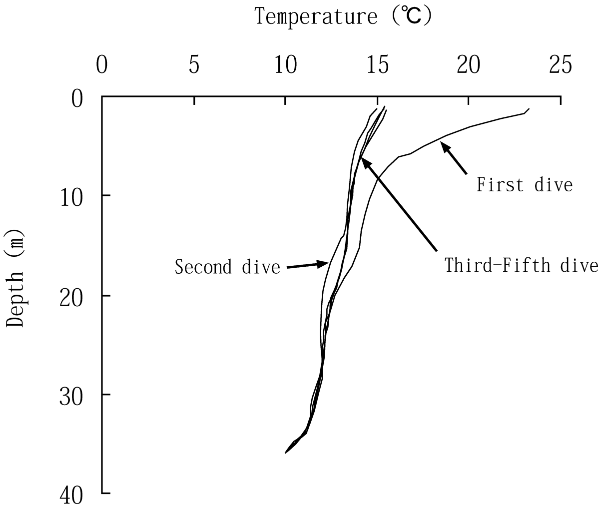

Fig. 2. Uncorrected water temperature profiles recorded by the data-logger during the descent phases of five consecutive dives contained in a dive bout.

Thus, seven to 92 dive bouts for each bird were used in the analysis.

The τ (s) of the data-loggers used in our study was 14.3±4.6 s (range 8–20 s). The temperature profiles derived from equation (1) using the temperatures recorded by the data-loggers and τ corresponded well to temperature profiles collected by CTD (Fig. 3), indicating that corrected temperature profiles were appropriate. The vertical casting speed of the CTD through the water column was $<1.0\,\mathrm{m\,s^{-1}}$. Therefore, we used temperature data when the birds descended at rates slower than $1\,\mathrm{m\,s^{-1}}$. Because the ascent rate was greater than the descent rate (ascent: $1.1\pm0.2\,\mathrm{m\,s^{-1}}$, descent: $0.8\pm0.2\,\mathrm{m\,s^{-1}}$, n=11 birds, 2914 dives, $Z=-2.93$, $P=0.003$) and often exceeded $1\,\mathrm{m\,s^{-1}}$ (Kuroki et al. 2003), we only used data collected during the descent phase.

4) Estimation of foraging sites

We assumed that the birds foraged at sites with the smallest SSD within our study area. This produces

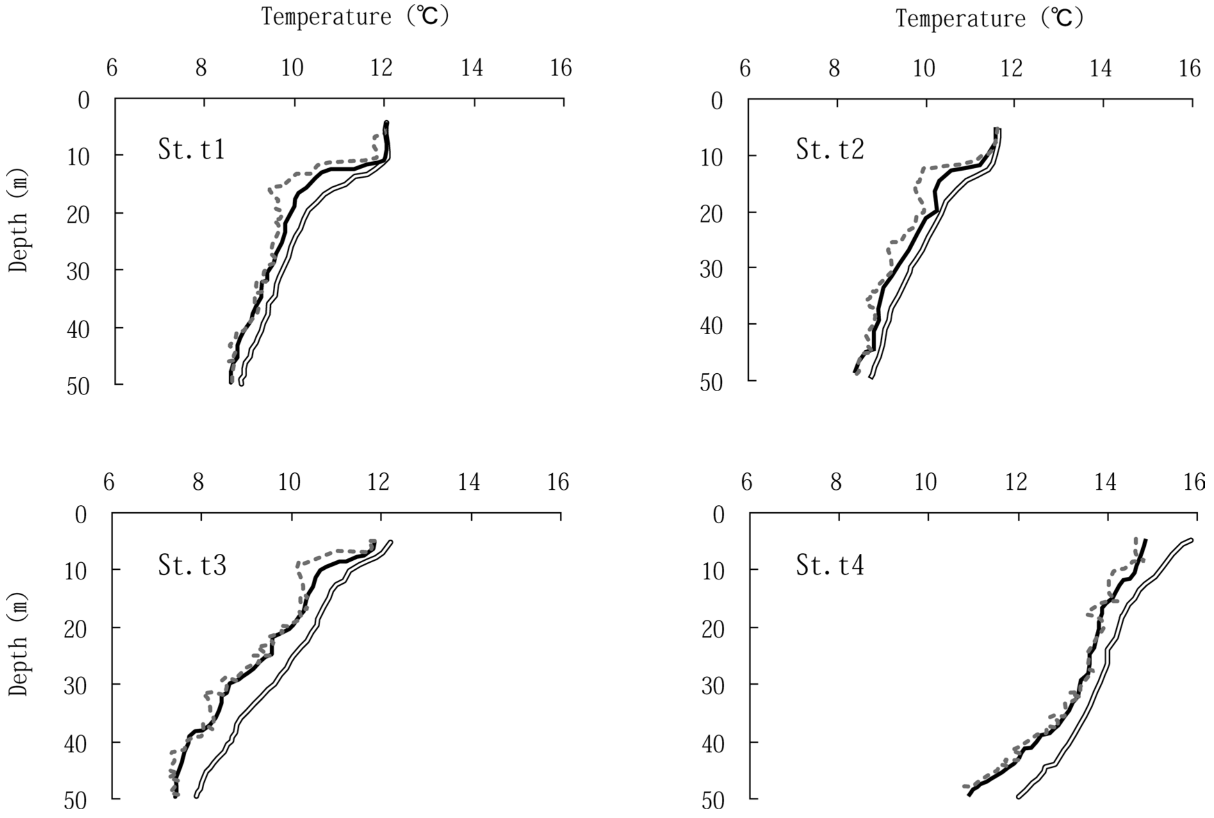

Fig. 3. Comparison between water temperature profiles obtained by CTD (black line), uncorrected temperature profiles simultaneously recorded by data-logger (open line), and those corrected using equation (1) (broken line). Data were collected at CTD stations t1–t4 in 2002 (also see Fig. 1). Only temperature data collected during the descent phase were used.

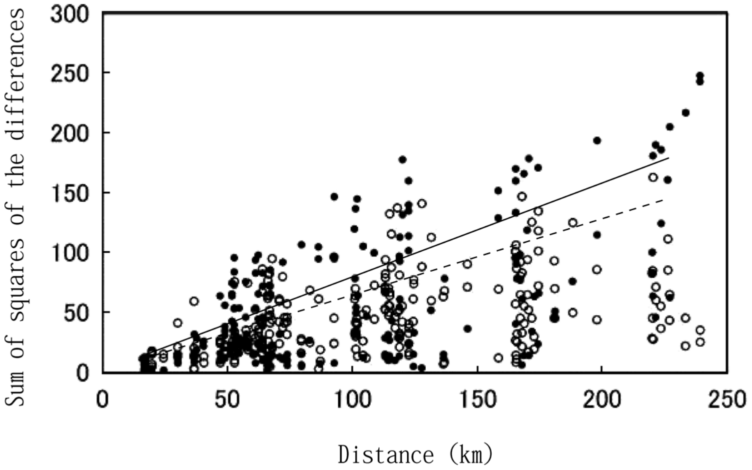

Fig. 4. Sum of squares of the differences (SSD) in the temperature recorded at 1 m intervals in the range from 5 to 20 m depth in relation to distance between all pairs of CTD stations in 2002 (closed circles) and 2003 (open circles). Solid and broken lines show regression lines for 2002 and 2003, respectively.

serious errors if more than two sites have similar temperature profiles. In each study year, SSDs were calculated between the temperature profile at each CTD station (17 and 29 stations in 2002 and in 2003, respectively) and those at all other CTD stations, and increased with the distance between locations (Fig. 4; 2002; $Y=0.85X$, $r^2=0.69$, $P<0.01$, 2003; $Y=0.68X$, $r^2=0.73$, $P<0.01$). The smallest SSD at each CTD station was given by the nearest CTD station, so that there was a small possibility of misidentifying the site where a bird was diving as the nearest CTD station.

If the birds forage outside of the study area and distant from the marginal CTD station, any estimated foraging sites will correspond to the nearest CTD station at the edge of the study area without any other criteria. Therefore, we needed to determine the SSD criteria required to determine foraging sites that were outside of the study area. We defined the SSD criteria as half of the value of the average SSDs for the nearest CTD location. This implied that foraging sites outside of the study area could not be estimated if their distance from the CTD station along the outer edge was longer than half of the average distance between the nearest CTD stations (22.1±6.9 km [n=17 stations] and 28.1±13.1 km [n=28 stations], for 2002 and 2003, respectively). We estimated that 0 to 39% of the dive bouts occurred in waters outside of the study area (Table 1). Finally, foraging sites were determined for 48 to 97% of dive bouts.

5) Between-year differences in foraging sites and oceanographic variables

Birds foraged in waters north of the 44°25′N line crossing the breeding colony (northern sector) and dove frequently near the colony in 2002, whereas diving mainly occurred in waters south of the 44°25′N line crossing the breeding colony (southern sector) in 2003 (Fig. 5). As a whole, SSTs in the study area in mid-June 2002 were 2 to 5°C higher than those during early June 2003. The SSTs in the foraging area (northern sector in 2002 and southern sector in 2003) did not differ between 2002 (13.1±0.8°C, n=10 sites) and 2003 (13.1±0.5, n=11 sites, U=48.0, P=0.622).

Thermoclines were found at depths shallower than the maximum dive depths of birds (69 m; Fig. 6). The tendency for a warm upper layer overlaying a cold bottom layer was found almost everywhere in the study area. Birds mostly dove above or around the depth of the thermocline. We assumed the index of thermocline depth was the depth at which the temperature was 2°C lower than the SST. Those depths at foraging sites where birds dove did not differ between 2002 and 2003 (median 30.0 m, n=26, U=66.0, P=0.572). Birds made shallower and shorter dives in 2003 (median dive depth: 14.0 m, n=6 birds; median dive duration: 48.5 s, n=6 birds) compared to 2002 (median dive depth: 27.9 m, n=5 birds, U=3.0, P=0.028; median dive duration: 109 s, n=5 birds, U=0.00, P=0.006, Table 1). In 2003, birds also made conspicuously shallow (≦5 m) dives in the warm upper layer above the shallow thermo-

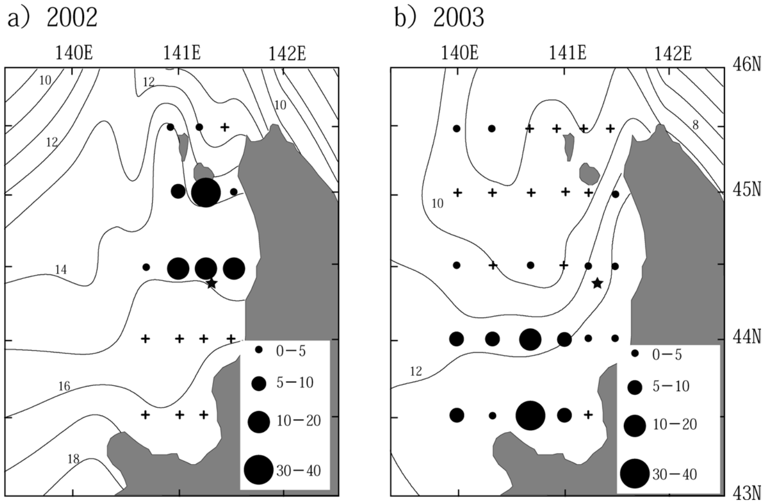

Fig. 5. Spatial distribution of the number of dives shown as the percentage of absent (crosses) and present (black circles) and SST contours surrounding the breeding colony in 2002 (a) and 2003 (b).

cline (14 m at 44°00′N, 6 m at 43°30′N). Chl-*a* concentrations (mg m^{-3}) at CTD sampling stations did not differ between northern and southern sectors in 2002 (median 0.4, n=10, U=5.0, P=0.117) and 2003 (median 0.4, n=24, U=38.0, P=0.079).

DISCUSSION

1) Evaluation of the technique

Deployment of data-loggers potentially affects animal behaviour (Wilson et al. 1986; Croll et al. 1992). In a study of Common Murres *Uria aalge*, parents carrying 6–8 g radio-transmitters (<1% of body mass) were likely to increase the duration of their foraging trips and therefore decrease the meal delivery rate (Wanless et al. 1988; Hamel et al. 2004). Kuroki et al. (2003) also found that the meal delivery rate by Rhinoceros Auklets carrying 20 g data-loggers (3.6% of body mass) was slower than those without loggers. Similarly, the mass of the food load brought back by parents carrying data-loggers was smaller than that of parents without data-loggers in our study, although there was no significant difference in diet composition between them. Foraging behaviours of birds carrying data-loggers might be influenced to some degree in this study. However, the foraging area estimated in this study was approximately similar to that observed by ship-based surveys in June 2002 (Tomohiro Deguchi et al. unpublished), indicating that our results were not seriously biased.

It was difficult to determine foraging sites when 1) the birds made dives shallower than 20 m during the bout, 2) more than two sites had similar temperature profiles, and 3) the birds made dives outside the study area. Dive bouts occasionally (0–33% of bouts) consisted of dives shallower than 20 m (Table 1). We did not find more than two CTD stations with the same temperature profiles. Dive bouts were occasionally (0–39% of bouts) made outside the study area. Thus we could estimate the foraging sites for 48–98% of the dive bouts for each bird. These values are comparable to those determined by land-based radio tracking (71–87% in Common Guillemot, Monaghan et al. 1994) and satellite tracking (35–44% in large alcids: Common Murre, Thick-billd Murre and Tufted Puffin *Fratercula cirrhata*, Hatch et al. 2000). Therefore, our technique is useful for estimating the approximate foraging area of small alcids.

2) Factors affecting foraging area and dive depth

Our results indicated that SST and thermocline depth affected the foraging behaviour of birds, but Chl-*a* concentrations did not. Birds foraged mainly in the northern sector from the colony in mid-June 2002, whereas birds foraged mainly in the southern sector in early June 2003 (Fig. 5). Despite this between-year difference in foraging area, SSTs ranged between 12 and 15°C in both years. In both years, the main diet of Rhinoceros Auklets was anchovy. Anchovy shoals occur in the surface layer (<60 m) in areas with SSTs between 12 and 15°C (Ohshimo 1996; Mihara 1998). Therefore, the between-year differences in foraging area might reflect changes in the distribution of prey.

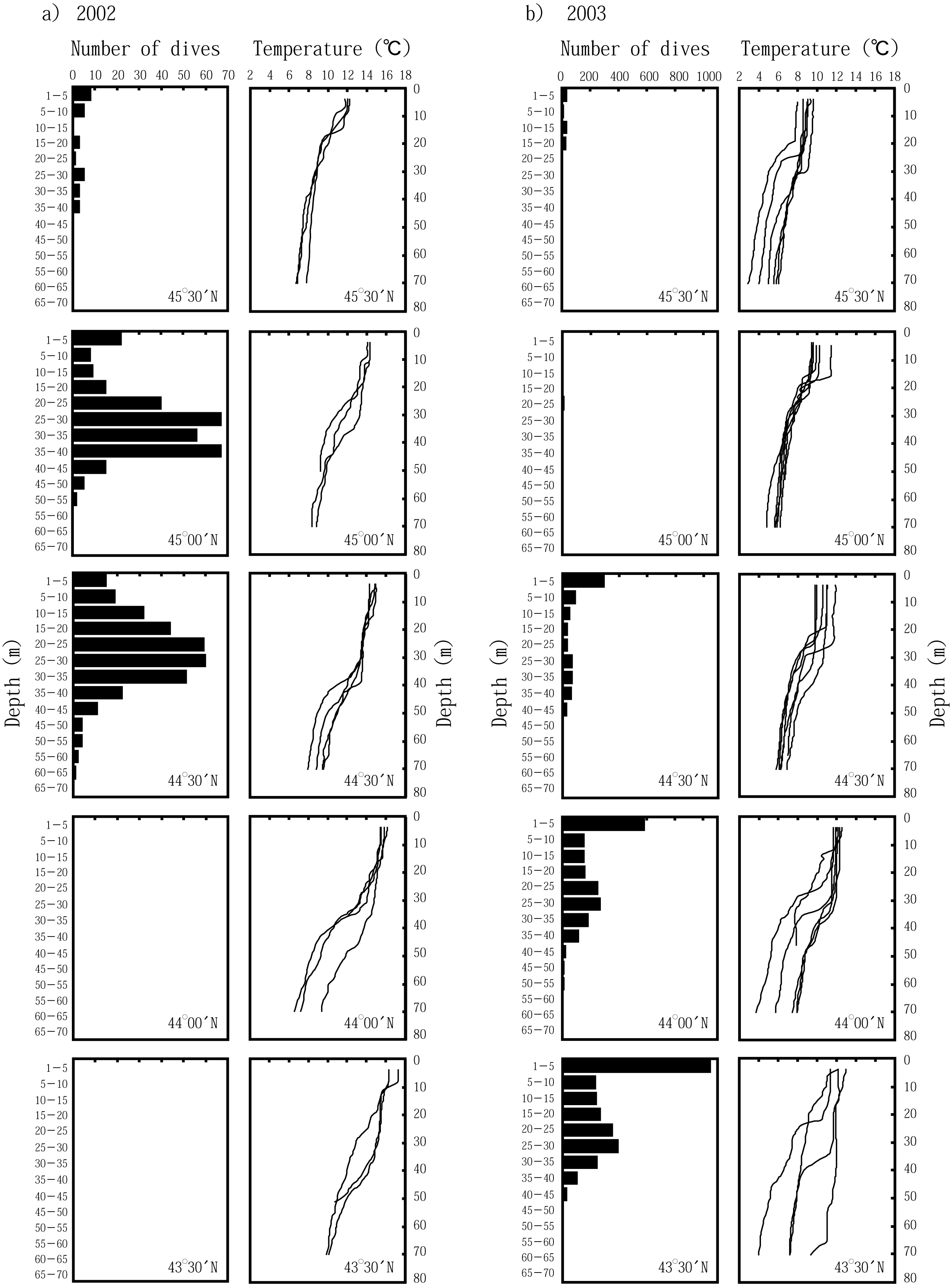

Fig. 6. Frequency distribution of dive depth (left) and water temperature profiles of CTD stations (right) along the latitudinal zone in 2002 (a) and 2003 (b).

It is unclear why Chl-*a* concentrations did not affect foraging site selection. In our study area, Chl-*a* concentrations were low compared to observations in the frontal area (1.2–1.5 mg m^{-3}) and were similar to values from July (0.3 mg m^{-3}) when the lowest Chl-*a* concentrations was observed (Yamada et al. 2004). We did not find a strong front in terms of gradients in SST and Chl-*a* concentrations. Therefore, the low Chl-*a* concentrations observed in this study might not affect the foraging area.

Rhinoceros Auklets primarily dove to the depth of the thermocline. Dive depth was shallower in 2003 than in 2002 because the birds made very shallow dives (≦5 m; Fig. 6). The reason for so many shallow dives in 2003 is unclear, but many of these shallow dives occurred in sites where the thermocline occurred at a very shallow depth (Fig. 6). Thus, the depth of the thermocline may have largely influenced dive depth for Rhinoceros Auklets in both years. It is well known that the stratification of the water column affects the vertical distribution of prey fish (Schneider et al. 1990; Decker & Hunt 1996; Russell et al. 1999). In frontal areas around southern Hokkaido, acoustically determined biomasses of anchovy were higher in the warm upper layer than that in the cold bottom layer (Murase et al. 2007). Anchovy also distribute within the upper layer of the thermocline (25–40 m; Yatsu et al. 2005). Rhinoceros Auklets chase prey fish while ascending as well as at the bottom of their dives (Kuroki et al. 2003). Thus, birds might catch anchovy concentrated around the depths of the thermocline.

In conclusion, our technique can be applied to wide-ranging alcids and provides valuable information on the interaction between the marine environment and seabird foraging behaviour. Our analysis of Rhinoceros Auklet data indicates that foraging areas and dive depths are influenced by SSTs and thermocline depth, which presumably limit horizontal and vertical distribution of their prey.

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