

Migratory movements of rhinoceros auklets in the northwestern Pacific: connecting seasonal productivities

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ABSTRACT: Spatial and temporal variability in marine biological productivity may drive heterogeneity in seasonal resources available for marine animals in temperate waters. Migratory seabirds are expected to adjust their annual cycle of breeding activities and migratory movements to exploit seasonally available resources efficiently. We studied the movement and trophic position of rhinoceros auklets *Cerorhinca monocerata* breeding at Teuri Island, Japan Sea, during the nonbreeding and early breeding periods over 2 yr. After breeding, the auklets moved northward from the colony to the Sea of Okhotsk, where phytoplankton blooms enhanced biological productivity in autumn. The birds then moved southward to the southwestern Japan Sea (~1470 km from the colony), where major epipelagic fish and squid concentrations have been reported in winter. Stable isotope analyses suggest that the auklets fed on higher-trophic level prey, including fish and/or squid during the autumn and winter nonbreeding periods. The auklets moved northward and returned to the colony in mid-March. During the early breeding period, the birds foraged close to the colony (~380 km) on lower-trophic level prey including fish and/or krill, which were available during the spring phytoplankton bloom. The timing of the return migration does not match with the northward migration of warm-water anchovy, a profitable prey during summer, but may be related to timing the chick-rearing period to correspond with anchovy arrival. We suggest that rhinoceros auklets follow spatial and seasonal changes in prey availability by a distinctive '3-step' migration (first northward, second southward, third northward) in the temperate marine system of the northwestern Pacific.

KEY WORDS: Seabird foraging · Light-based geolocation · Productivity · Seasonal movements · Stable isotope analysis · Japan Sea

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INTRODUCTION

Seabirds are faced with challenges in finding their prey in the spatially and temporally variable marine environment (Weimerskirch 2007), under the different foraging constraints that exist during the breed-

ing and nonbreeding periods. During the breeding period, parent seabirds are central place foragers that commute between their colony and the feeding grounds at sea. Their foraging ranges are relatively limited, especially during the early chick-rearing period when they are provisioning their offspring

(e.g. Charrassin & Bost 2001, Rayner et al. 2012). Despite the constraints on their foraging range, parent seabirds have to feed intensively in order to meet the high energetic demands associated with breeding (Hamer et al. 2001). During the nonbreeding period, seabirds can move over larger distances without the constraints of central-place foraging (e.g. Thiebot et al. 2011), but may experience reduced prey availability due to decreased marine productivity outside the summer breeding season and/or possible changes in the accessibility of prey in the water column (e.g. Charrassin & Bost 2001). An increasing number of studies have shown that seabirds, especially proficient-flying procellariiforms, adjust their annual cycle of breeding activities and migratory movements to conform with seasonally available resources (Shaffer et al. 2006, González-Solís et al. 2007, Guilford et al. 2009, Rayner et al. 2011, Carey et al. 2014), although such adjustments may vary among species of different migration abilities and among different marine regions.

Recent advances in bio-logging technologies, such as light-based geolocators, have allowed researchers to examine the year-round movements of individual seabirds over extensive periods (Burger & Shaffer 2008, Wakefield et al. 2009). In addition, stable isotope analysis of animal tissues can be used to examine the trophic position of seabirds during these annual movements (Hobson & Bond 2012). Based on these techniques, long-distance trans-equatorial migrations have been documented for proficient-flying medium-sized petrels, which presumably allow them to exploit the summer peaks in biological productivities in both northern and southern hemispheres successively (Shaffer et al. 2006, González-Solís et al. 2007, Rayner et al. 2011). However, less is known about the movements of seabirds with higher energetic costs of flying, such as auks (Elliott et al. 2013), in relation to seasonal changes in regional marine productivities and breeding constraints. So far, previous studies on the migratory movements of alcids have all been conducted in the North Atlantic, highlighting the area off Newfoundland as an important foraging area during autumn and winter (Mosbech et al. 2012, Jessopp et al. 2013, Linnebjerg et al. 2013, McFarlane Tranquilla et al. 2013). In contrast, no such information is yet available for any alcid species breeding in the North Pacific. Information on migratory patterns will also be valuable for understanding population trends with respect to marine environmental changes and for assessing any potential conservation issues (Harris et al. 2013, McFarlane Tranquilla et al. 2013).

Rhinoceros auklets *Cerorhinca monocerata* are medium-sized alcids (500 to 600 g) that breed in the North Pacific. The largest breeding colony is located at Teuri Island in the northern Japan Sea, where approximately 0.3 million pairs breed annually (Watanuki & Ito 2012). The auklets feed intensively on Japanese anchovy *Engraulis japonicus* close to the breeding colony (~130 km) during the chick-rearing period (Kato et al. 2003, Watanuki & Ito 2012), but their movements and diet are largely unknown outside the breeding period. Therefore, the objective of this study was to characterize the migratory movements and trophic position of rhinoceros auklets during the nonbreeding and early breeding periods, by combining information from light-based geolocation and stable isotope analyses. We hypothesized that the migratory movements of the auklets would follow seasonal changes in regional prey availability, given the heterogeneity of seasonal productivity patterns in the Japan Sea and the adjacent Sea of Okhotsk (Lee et al. 2009, Radchenko et al. 2010). We expected that rhinoceros auklets would maintain their fish diet by moving among different marine regions during the nonbreeding period, but that they may be confined to feeding close to the colony on different prey items during the early breeding period.

MATERIALS AND METHODS

Geocator deployments

The study was conducted at Teuri Island (44° 24' N, 141° 17' E), located in the northern Japan Sea (Fig. 1). Rhinoceros auklets first return to Teuri Island in March or April and lay a single egg in April or May. The chicks hatch in May and June, and fledge in July (Watanuki & Ito 2012). In July 2010, we captured 10 chick-rearing birds from their nest burrows and attached a geocator (Mk15; 16 × 18 × 6 mm, British Antarctic Survey) onto the tarsus of each bird with a plastic leg ring. The total mass of geolocators including the ring was 3.5 g (0.62% of the mean body mass of tracked birds). We retrieved geolocators from 8 out of 10 birds in May 2011. Upon recapture, the 10th primary feather and 2 or 3 breast feathers were taken as samples for stable isotope analysis. One additional instrumented bird was recaptured in the 2013 breeding season. We also attached geolocators to 20 birds in July 2011. We retrieved geolocators from 16 out of 20 birds in May and June 2012. Three individuals were tracked during the nonbreeding and early

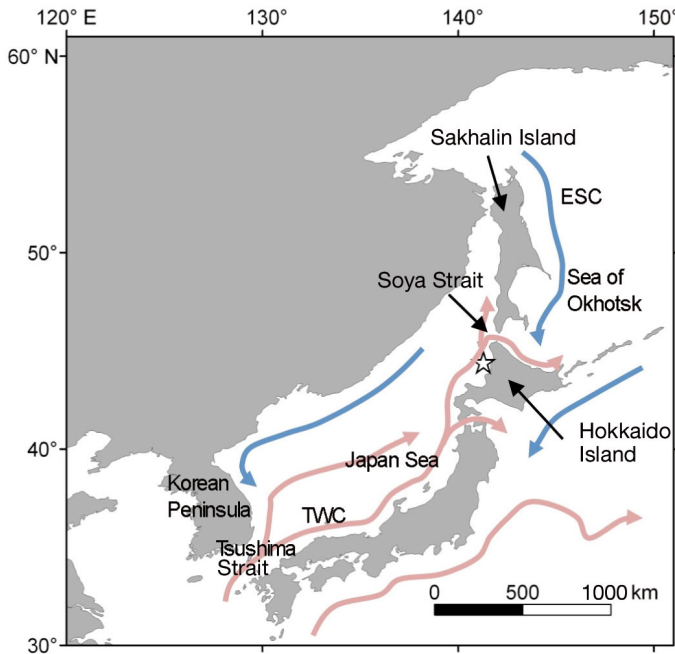


Fig. 1. Oceanographic features of study area; warm and cold currents are displayed in pink and blue, respectively. TWC: Tsushima Warm Current; ESC: East Sakhalin Current. Teuri Island (rhinoceros auklet *Cerorhinca monocerata* breeding colony) is marked with a star

breeding periods of both 2010/2011 and 2011/2012. All geolocators that were recovered had recorded data successfully, but 5 geolocators from the 2011/2012 deployments stopped recordings prematurely after 1 to 3 mo. We therefore analyzed 20 complete tracks recorded from 17 birds (10 males, 7 females). The sex of the birds was determined on the basis of bill and head measurements (Niizuma et al. 1999). On average, the study birds maintained their body mass between device attachment and retrieval (average mass change: +12.5 g, range: +75 to -45 g), although we do not have comparable data from control birds to examine any potential device effects.

Geolocation data analysis

The geolocators recorded time, light intensity, immersion in seawater and water temperature. They were programmed to measure light levels at 1 min intervals, and to record the maximum value after each 10 min period. Immersion in seawater was checked every 3 s and the data were compiled as a proportion over each 10 min period. Water temperature was recorded only after continuous immersion for 20 min as the temperature sensors require 10 min to stabilize. Accuracy of the temperature recordings

was 0.5°C as indicated by the manufacturer. Light and water temperature data were used to estimate the birds' daily locations (Yamamoto et al. 2011). Sunset and sunrise times were estimated from the thresholds in the light curves. Latitude was derived from day length, and longitude from time of local midday with respect to Greenwich Mean Time and day of the year, using TransEdit and Locator software (British Antarctic Survey). To improve location estimates from light levels, the daily median of the water temperature records from the geolocators were compared with remotely sensed sea surface temperature (SST) data (8 d composite, 9 km resolution, measured by Aqua-MODIS, downloaded from the ocean color web <http://oceancolor.gsfc.nasa.gov>). We retained the longitude estimates obtained from light-based geolocation, and searched the latitude where SST matched with median water temperature records from the geolocators. Since SST varies with latitude (cooler towards higher latitude), this procedure enabled us to refine the latitude estimates during the entire period of at-sea trips, including during the equinoxes. Finally, these daily positions were smoothed using a theoretical movement model in a Bayesian framework (Thiebot & Pinaud 2010). This movement model calculates the most probable location estimates along the tracks (without deleting any locations) that meet with 3 conditions: (1) no locations occur on land, (2) the start and end locations of the tracks are the breeding colony, and (3) mean movement speed is 10 km h⁻¹ (based on flying speeds measured from GPS tracking; Y. Watanuki & K. Hoshina unpubl. data, corrected by the average time spent flying per day during the nonbreeding period, ~4.5 h; this study), with 5 km h⁻¹ allowed for variance of the mean (for details see Thiebot & Pinaud 2010 and references therein).

Attendance at the colony was assessed from the geolocators' immersion records. We defined colony attendance as periods in the data when the geocator was continuously dry for >5 h through midnight, because most birds that are not at the colony rest on the sea surface during the night (Kato et al. 2003). The nonbreeding period was defined as the period from the last attendance at the colony (defined using activity data) after breeding (late July) until the first attendance at the colony in the following year (mid-March). Similarly, the early breeding period was defined as the period from the first attendance at the colony to the end of April, as most geolocators were retrieved from birds in early May, when birds were normally in the incubation period (Watanuki & Ito 2012).

Stable isotope analysis of feathers

We analyzed stable isotopes of feathers grown during the nonbreeding period. Although accurate molt cycles are not known for rhinoceros auklets, the 10th primary and breast feathers presumably grow during the pre-basic molt (August to October) and pre-alternate molt (February to March), respectively (Pyle 2009, Sorensen et al. 2010). Feathers were stored in a freezer (-20°C) until laboratory analyses. Nitrogen and carbon stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) were measured at Meijo University (Nagoya, Japan) for 2010/2011 samples, and at Port and Airport Research Institute (Yokosuka, Japan) for 2011/2012 samples. At Meijo University, feathers were washed using 0.25 mol l^{-1} sodium hydroxide aqueous solution and distilled water, dried in an oven at 60°C for 24 h, placed in liquid nitrogen for 1 min, then homogenized using a sample crusher (TK-AM5, TITEC). At Port and Airport Research Institute, feathers were washed using 0.25 mol l^{-1} sodium hydroxide aqueous solution and distilled water, freeze-dried for 36 to 48 h, cut as small as possible, then homogenized using a mortar. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were measured using a ANCA-GSL elemental analyzer connected to a Hydra 20–20 mass spectrometer (SerCon) (Meijo University) or a Delta Plus Advantage mass spectrometer (Thermo Electron) coupled with an elemental analyzer (Flash EA 1112, Thermo Electron) (Port and Airport Research Institute). Stable isotope ratios are expressed in δ notation as the deviation from standard (air for N and Pee Dee Belemnite for C) in parts per thousand (‰) according to the following equation: $\delta^{15}\text{N}$ or $\delta^{13}\text{C} = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1000$, where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$. Replicate measurements of internal laboratory standards indicated that the measurement precision was ± 0.16 and $\pm 0.12\%$ for $\delta^{15}\text{N}$ (SD) and ± 0.16 and $\pm 0.11\%$ for $\delta^{13}\text{C}$ (SD) in the laboratories at Meijo University and Port and Airport Research Institute, respectively.

The tissue-specific discrimination factors of isotopic values must be taken into account when comparing isotopic values of consumers' tissues with that of their prey. We used the discrimination factors as follows, based on a study of common murre *Uria aalge* (Becker et al. 2007): 3.7 and 3.6‰ for $\delta^{15}\text{N}$ and 1.9 and 1.0‰ for $\delta^{13}\text{C}$, for primary and breast feathers, respectively. We compared the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of feathers with those of egg yolk and blood plasma obtained during the breeding season as well as potential prey species (euphausiids: *Thysanoessa inermis*; 0+ and >1+ sandlance *Ammodytes personatus*; Japan sea greenling *Pleurogrammus azonus*; Japanese

anchovy; squid Coleoides; juvenile chum salmon *Oncorhynchus keta*), reported in Ito et al. (2009, 2012). Ito et al. (2012) used the following discrimination factors: 3.4 and 2.8‰ for $\delta^{15}\text{N}$ and 0.1 and -1.3% for $\delta^{13}\text{C}$ for egg yolk and blood plasma, respectively, based on other avian studies (egg yolk) and their own measurements from rhinoceros auklet chicks (blood plasma).

Primary productivity

To characterize seasonal patterns in primary productivity, monthly average values of sea surface chlorophyll *a* (chl *a*) concentrations were calculated from January 2003 to December 2012 for an area in the Sea of Okhotsk (Area A) and 2 areas in the Japan Sea (Areas B and C; Fig. A1 in the Appendix). The areas were chosen on the basis of 50% kernel density boundaries of bird locations during the nonbreeding (Areas A and C) and early breeding (Area B) periods. We used the Aqua MODIS level 3 monthly standard mapped image 9 km resolution chl *a* data downloaded from the ocean color web.

Statistical analysis

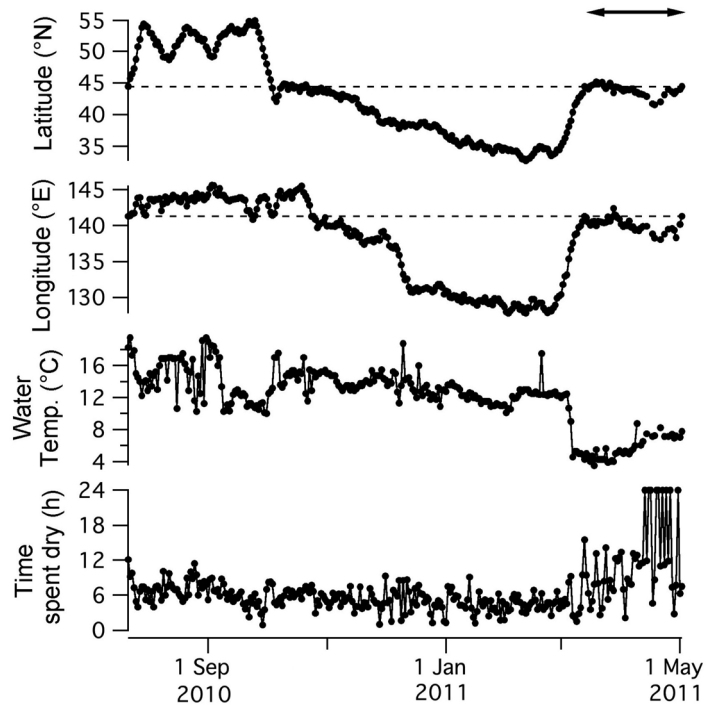
Maximum distance traveled from the colony by the birds was compared between years and sexes with 1-way ANOVA. Repeated measurements were made on 2 males and 1 female (i.e. were tracked during both 2010/2011 and 2011/2012). Here, we show the statistics that include the 6 tracks from these 3 birds as independent. Statistical results were similar, even if we included only 1 (the track of either 2010/2011 or 2011/2012) of the 2 tracks for these 3 birds in the analyses. Minitab software (Minitab) was used for statistical analyses. Kernel densities for geolocation data were calculated using the ArcGIS Spatial Analyst Density tool (ESRI) with a cell size of 0.2° and a search radius of 2° . Means (\pm SE) are shown.

RESULTS

Seasonal movement patterns

After the breeding season, tracked birds departed the colony on 23 July in both years (± 0.7 and ± 1.4 d for 2010/2011 and 2011/2012, respectively), indicated by the immersion records of geolocators. In the first phase of migration, the birds moved northward from the colony to the Sea of Okhotsk, a

Fig. 2. Example of time-series data obtained by geolocators for one rhinoceros auklet *Cerorhinca monocerata*. Latitude and longitude were estimated using light levels and water temperature, and were smoothed using a movement model (see 'Materials and methods' for details). Dotted lines represent the location of the breeding colony. Water temperature recorded by the geocator and time spent dry per day are also shown. Horizontal double-headed arrows indicate the early breeding period (after the first return to the breeding colony)



pattern that was consistent in both years (Figs. 2 & 3). The birds were distributed mainly along the east or south coast of Sakhalin Island until September, and then moved southward to the northeastern or southeastern shore of Hokkaido Island in October (Fig. 4). During the second phase, the birds moved southward across the Japan Sea from November to January. Most birds (7 of 9 birds in 2010/2011 and 8 of 11 birds in 2011/2012) reached the sea around the Korean Peninsula and Tsushima Strait (Figs. 3 & 4). The remaining 4 birds (5 tracks) appeared to spend winter farther east in the Japan Sea, with a mean westernmost longitude of 135.6° E. In February, the birds undertook their third movement phase, migrating northward again along the coast of Japan, and returned to the colony on 11 and 18 March (± 2.3 and ± 1.1 d) in the 2010/2011 and 2011/2012 seasons, respectively (Fig. 3). Overall, the kernel density of locations identified the Sea of Okhotsk and the sea around the Korean Peninsula and Tsushima Strait as key areas during the nonbreeding period in both 2010/2011 and 2011/2012 (Fig. 4).

The average maximum distance traveled from the colony by the auklets during the nonbreeding period did not differ between years (1549 ± 77 vs. 1403 ± 91 km for 9 and 11 tracks in 2010/2011 and 2011/2012, respectively; $F_{1,18} = 1.43$, $p = 0.25$) or between sexes (1481 ± 96 vs. 1460 ± 83 km for 8 and 12 tracks

from females and males, respectively; $F_{1,18} = 0.03$, $p = 0.87$).

After the initial arrival at the colony, the birds made foraging trips during the pre-laying and early incubation periods, until the end of the geocator records. During this early breeding period, the birds stayed relatively close to the colony (Fig. 4); half of the daily at-sea locations were within 157 ± 10 and 237 ± 21 km from the colony, for 2010/2011 and 2011/2012, respectively. The average maximum distance reached from the colony by the auklets during the early breeding period did not differ between years (376 ± 24 vs. 386 ± 19 km for 9 and 11 tracks in 2010/2011 and 2011/2012, respectively; $F_{1,18} = 0.1$, $p = 0.75$) or between sexes (407 ± 29 vs. 365 ± 14 km for 8 and 12 tracks from females and males; $F_{1,18} = 2.12$, $p = 0.16$).

Activity and water temperature records

During the nonbreeding period, the leg-mounted geolocators remained dry for 4.42 ± 0.42 h d^{-1} ($n = 20$ tracks). There were no apparent seasonal patterns in the time spent dry, and no clear evidence of flightless periods (Fig. 2). During the early breeding period, the daily time spent dry increased as the birds attended the colony at night or throughout the day for incubation (Fig. 2).

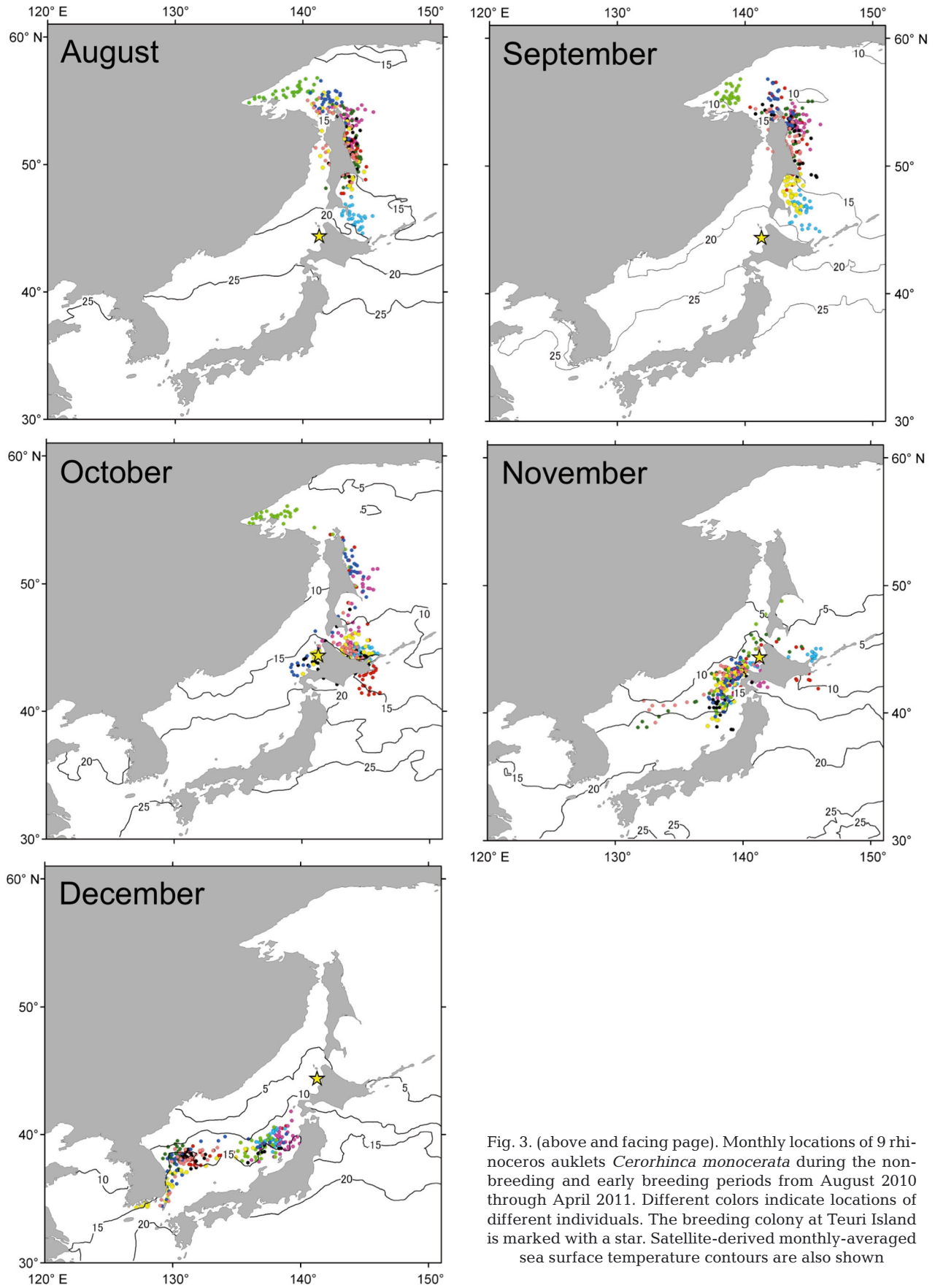


Fig. 3. (above and facing page). Monthly locations of 9 rhinoceros auklets *Cerorhinca monocerata* during the non-breeding and early breeding periods from August 2010 through April 2011. Different colors indicate locations of different individuals. The breeding colony at Teuri Island is marked with a star. Satellite-derived monthly-averaged sea surface temperature contours are also shown

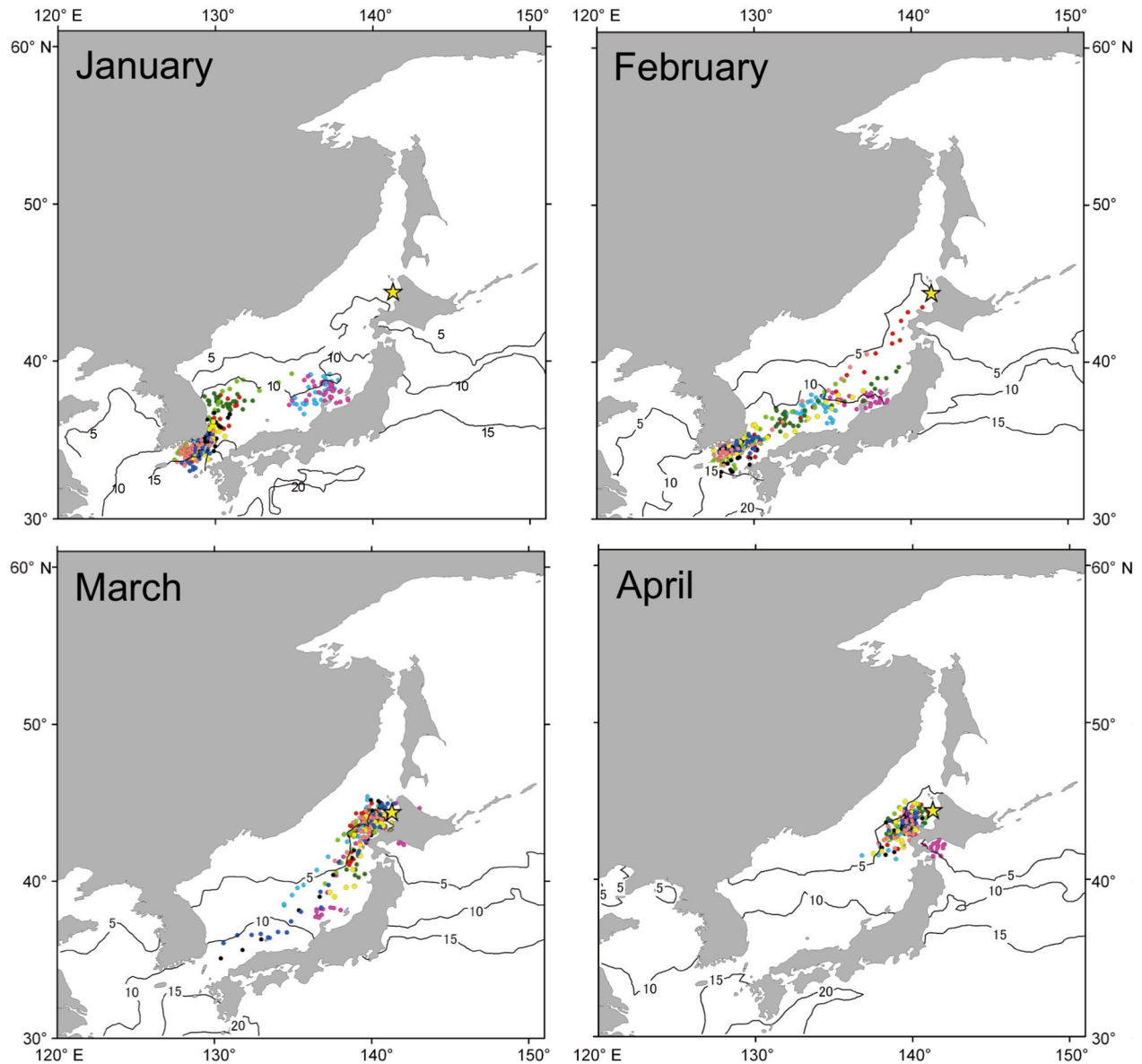


Fig. 3. (continued)

Water temperatures recorded by the geolocators showed large seasonal changes in both years (Fig. 5). Water temperatures experienced by the birds remained between 11 and 14°C from October to late February, but dropped to between 4 and 6°C in early March, associated with the northward migration of auklets to the breeding colony.

Isotopic value of feathers

Mean measured isotopic values (without adjustment for discrimination factors) were 15.6 ± 0.3 and 15.1 ± 0.1 ‰ for $\delta^{15}\text{N}$, and -19.8 ± 0.2 and

-18.8 ± 0.1 ‰ for $\delta^{13}\text{C}$ in primary feathers, versus 13.5 ± 0.2 and 14.1 ± 0.1 ‰ for $\delta^{15}\text{N}$, and -19.5 ± 0.2 and -18.1 ± 0.2 ‰ for $\delta^{13}\text{C}$ in breast feathers in 2010/2011 ($n = 8$) and 2011/2012 ($n = 16$), respectively (Fig. 6). The $\delta^{15}\text{N}$ values of primary and breast feathers adjusted for discrimination factors (3.7 and 3.6‰ for primary and breast feathers) were higher than those of egg yolk and blood plasma (adjusted for discrimination factors) during the pre-laying, incubation and chick-rearing periods (Fig. 6). The $\delta^{13}\text{C}$ values of primary feathers were lower than those of breast feathers, egg yolk and blood plasma (all values adjusted for discrimination factors) (Fig. 6).

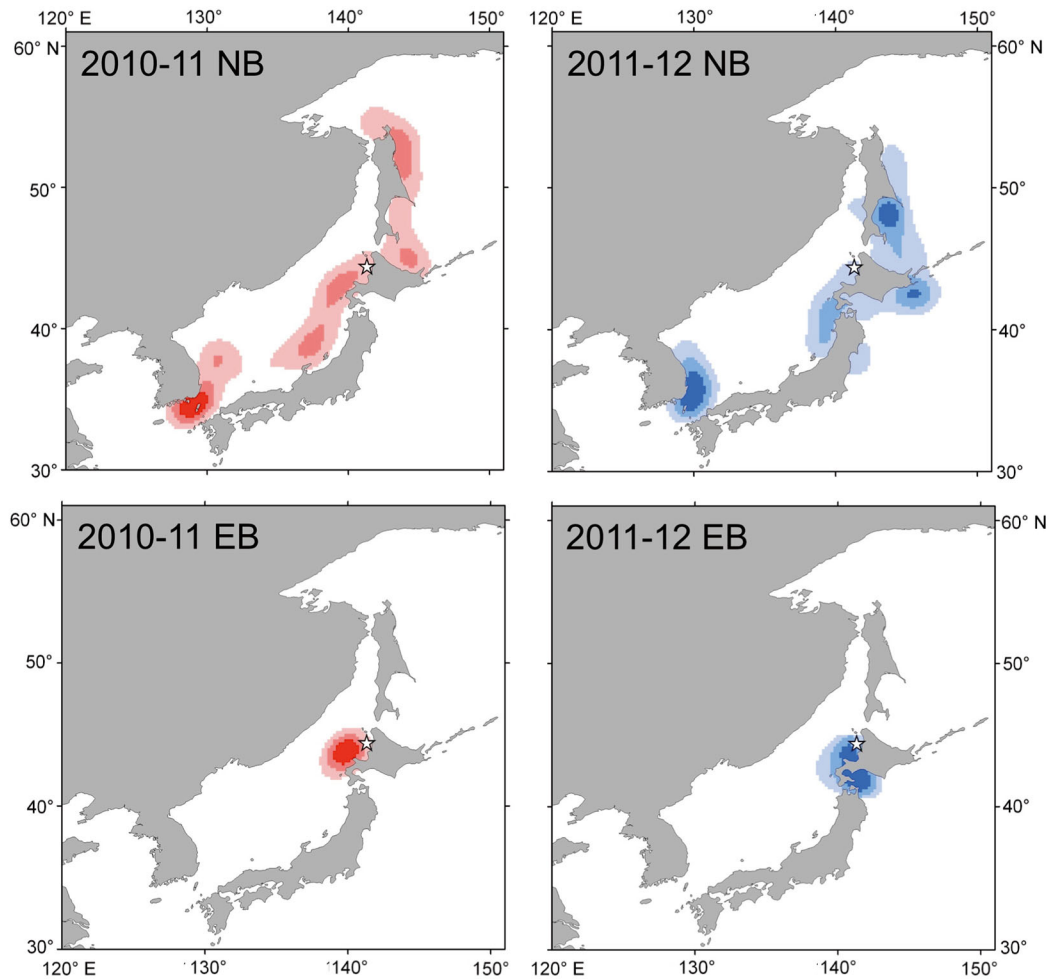


Fig. 4. Kernel density distribution of rhinoceros auklet *Cerorhinca monocerata* locations during the nonbreeding (NB) and early breeding (EB) periods of first and second study year (2010/2011 and 2011/2012; red and blue, respectively). Kernel densities indicate 25, 50 and 75 %, from darker to lighter colors. The breeding colony at Teuri Island is marked with a star

Marine primary productivity

Chl *a* concentration was highest in April over the annual cycle in Areas A–C, with higher peak values in Areas A and B (Sea of Okhotsk and northern Japan Sea) compared to Area C (southwestern Japan Sea) (Fig. 7). A second, clear peak in chl *a* concentration was observed in autumn (September to November) in Area A only.

DISCUSSION

Our results, together with previous results from the chick-rearing period (Kato et al. 2003), suggest that inter-annually, rhinoceros auklets from the largest colony in the northwestern Pacific predominantly use 3 marine regions year-round: the Sea of Okhotsk in

autumn, the southwestern Japan Sea in winter, and the northern Japan Sea during the breeding season in spring and summer. The auklets consistently used these areas over 2 successive years. These are highly productive areas (Lee et al. 2009, Radchenko et al. 2010), among which the seasonal patterns of biological productivity differ considerably (Fig. 7). We hypothesize that the auklets are able to connect such seasonal peaks in productivity by a distinctive ‘3-step’ migration pattern.

Migratory movements and regional prey availability

Rhinoceros auklets feed mainly on warm-water Japanese anchovy during the chick-rearing period (Watanuki & Ito 2012), and change their foraging locations from south to north of the colony between

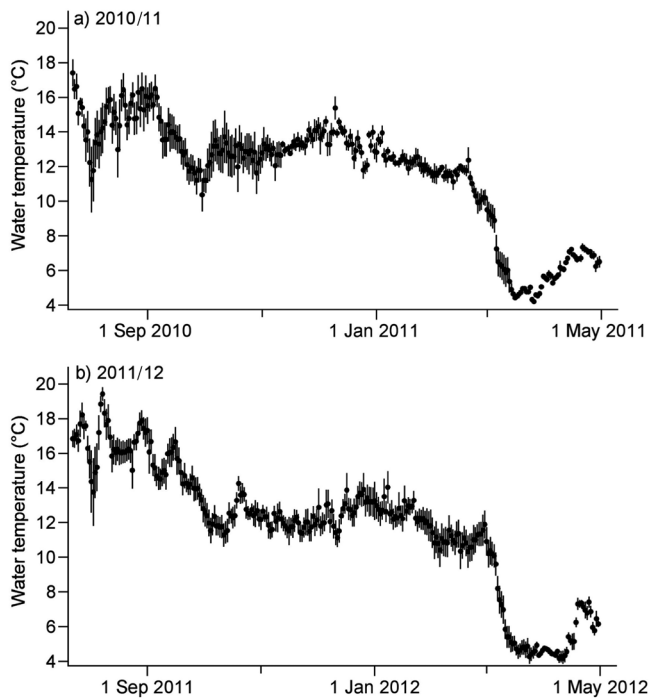


Fig. 5. Seasonal patterns in water temperature (mean \pm SE) recorded by the geolocators attached to rhinoceros auklets *Cerorhinca monocerata* during (a) August 2010 to April 2011, and (b) August 2011 to April 2012 ($n = 9$ and 11 birds, respectively)

May and July, presumably following the northward migration of anchovy (Deguchi et al. 2010). Our results showed that the auklets continued to move northward into the Sea of Okhotsk after the breeding season, which is in accordance with previous ship-based surveys that reported concentrations of auklets along Soya Strait and in the Sea of Okhotsk in late July through late August (Shuntov 2000, Deguchi et al. 2010). The auklets remained within the Sea of Okhotsk until October (Fig. 3). The Sea of Okhotsk is one of the southernmost seasonal sea-ice zones in the northern hemisphere, and supports high biological

Fig. 7. Mean monthly-average chl *a* concentrations of 3 different foraging areas (defined by 50% kernel boundary of rhinoceros auklet *Cerorhinca monocerata* locations) in the Sea of Okhotsk (Area A) and the northern and southwestern Japan Sea (Areas B and C, respectively) over 10 yr (2003 to 2012). Mean values are shown with a thick line, and values of mean \pm 1 SD are shown with dotted lines, to show inter-annual variability. The double-headed arrows below each graph show the approximate period when the auklets stayed in each of Areas A, B, and C (see Fig. A1 in the Appendix for area locations). Note the occurrence of the autumn bloom in Area A

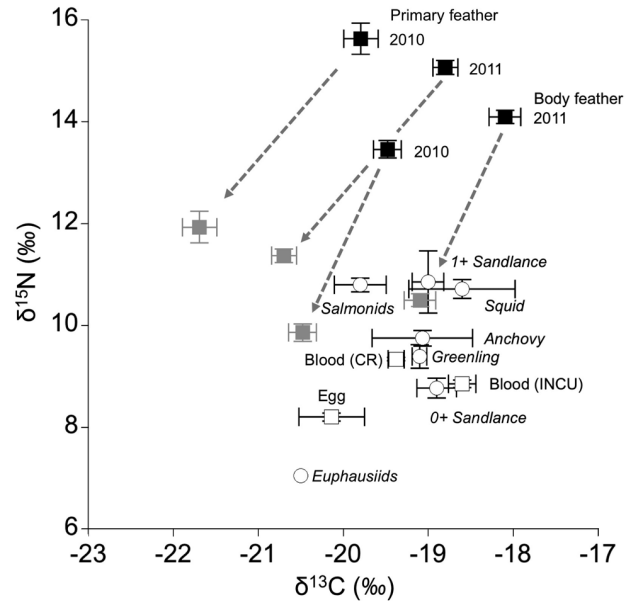
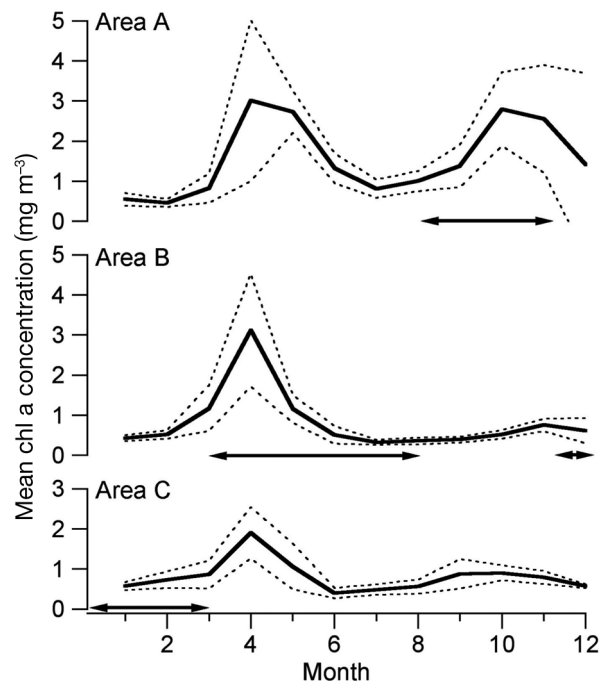


Fig. 6. Mean (\pm SE) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of primary and body feathers of rhinoceros auklets *Cerorhinca monocerata* collected in 2010/2011 and 2011/2012, before (black closed squares) and after (grey closed squares) applying the adjustment for discrimination factors (indicated by grey arrows). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of auklet egg yolks and blood plasma collected during the incubation (INCU) and chick-rearing (CR) periods (open squares; adjusted for discrimination factors), and those of prey species (open circles, with names in italics) are also shown. Prey samples were obtained at the colony during the chick-rearing periods in 2004 and 2005 (Ito et al. 2009). Isotopic values of prey, and egg and blood plasma of auklets (open symbols) are based on Ito et al. (2009, 2012)



productivity associated with spring ice-edge blooms as well as autumn blooms (Mustapha et al. 2009, Radchenko et al. 2010). High summer and autumn primary productivity was measured by satellite (Area A in Fig. 7) as well as from ship-based observations in this region, associated with the seasonal intrusion of the Tsushima Warm Current and the East Sakhalin Current along the northern coast of Hokkaido Island (Mustapha et al. 2009). The high biological productivity in summer and autumn attracts forage fish, including Japanese anchovy (at shallow depths 0 to 60 m; Nagasawa et al. 1998) and their predators to the Sea of Okhotsk (Radchenko et al. 2010, Sakurai et al. 2013). For example, nonbreeding flesh-footed shearwaters *Puffinus carneipes* from breeding colonies in New Zealand and Australia move into the Sea of Okhotsk in August and September, presumably feeding mainly on fish (Rayner et al. 2011); other southern hemisphere migrants such as sooty and short-tailed shearwaters *Puffinus griseus* and *P. tenuirostris* have been observed through July and August (Shuntov 2000, Sakurai et al. 2013, Carey et al. 2014). Similarly, black-tailed gulls *Larus crasirostris* that breed in a colony in the northern Japan Sea move into the Sea of Okhotsk in August (Kazama et al. 2013). This enhanced marine food web might also attract rhinoceros auklets in autumn.

From November to December, the auklets moved to the southwest region of the Japan Sea, and 75% of the tracks reached as far as the sea around the Korean Peninsula. They stayed in this region until mid-February before migrating back to their breeding colony in mid-March. The southwest region of the Japan Sea is known to be productive due to coastal upwelling (Lee et al. 2009). The region is a major fishing ground for warm-water pelagic fish such as Japanese anchovy, chub and jack mackerel *Scomber japonicus* and *Trachurus japonicus* (Kim et al. 2008). In particular, Japanese anchovy are found around the Korean Peninsula in winter, and are available at shallow depths (5 to 60 m; Iversen et al. 1993). This region is also known as a major autumn spawning ground for Japanese common squid *Todarodes pacificus*, so juvenile squid would be available for auklets in the water column during the winter (Kidokoro et al. 2010).

The 3-step migration, or 3-phased migratory pattern (first northward, second southward, third northward) results in an increase in the total distance travelled during the nonbreeding period compared with a direct migration from the colony to the southern wintering area. The costs of flight are expected to be high in alcids such as rhinoceros auklets which have

high wing loading (Elliott et al. 2013). The auklets presumably gain sufficient energy in autumn in the Sea of Okhotsk, which outweighs the energy costs of moving the extra distance to the southern wintering areas. The birds appeared to experience a similar temperature range (12 to 14°C) between October and late February (Fig. 5) due to their southward seasonal movements, and this relatively constant sea temperature may be favorable for thermoregulation.

The 3-step migration pattern has also been observed in little auks *Alle alle* breeding in East Greenland (Mosbech et al. 2012). The little auk uses an autumn staging area in the Greenland Sea at the northeast of the colony, and then performs a long southerly migration (~2000 km) to winter off Newfoundland. Other alcids show diverse migratory patterns even within a species. For example, common murrelets in a colony at Svalbard migrate southward (~1000 km from the colony) to the Barents Sea and adjacent areas (Fort et al. 2013), but the same species from a colony in central Norway migrate northward to the Barents Sea (Lorentsen & May 2012). Atlantic puffins *Fratercula arctica* from the Isle of May off east Scotland stay within the North Sea or move north to the northeast Atlantic (Harris et al. 2013), but the same species from southwest Ireland make long-distance east–west movements to Newfoundland in August and September (2537 km on average; Jessopp et al. 2013). Thick-billed murrelets *Uria lomvia* from 5 colonies spanning the eastern Canadian coast from the high Arctic to Newfoundland show variable degrees of southward movement (700 to 3500 km) to common wintering areas in the Labrador Sea and the seas off Newfoundland (McFarlane Tranquilla et al. 2013). We suggest that the migratory patterns of alcids are highly flexible, depending upon the spatial and seasonal patterns of prey availability relative to their breeding location and timing. However, the maximum migration distances of alcids from the colony (~3500 km) are relatively limited compared to the distances traveled by proficient-flying procellariiform seabirds (~12 000 km from the colony; Guilford et al. 2009, Yamamoto et al. 2010), suggesting that the high energetic costs of flight would constrain the ability of alcids to exploit seasonally available resources through migration.

Trophic position during the nonbreeding period

The nitrogen and carbon isotope signatures of the 10th primary feathers and breast feathers of auklets presumably reflect the diet during autumn and win-

ter, respectively (see 'Materials and methods: Stable isotope analysis of feathers'). The relatively high $\delta^{15}\text{N}$ values of both primary and breast feathers (adjusted for discrimination factors), compared with $\delta^{15}\text{N}$ values of auklet blood samples during the breeding period, suggest that the auklets feed on higher trophic level prey, including fish and/or squid, rather than zooplankton (Fig. 6). This contrasts with isotopic studies of other alcids such as Atlantic puffins or thick-billed murre, which showed seasonal shifts to low $\delta^{15}\text{N}$ values, suggesting a dependence on lower trophic level zooplankton during the nonbreeding period (Hedd et al. 2010, Hobson & Bond 2012).

We must note that the relatively low $\delta^{13}\text{C}$ values in both primary and breast feathers (adjusted for discrimination factors) may reflect the carbon source for primary producers, varying with habitat (nearshore/benthic vs. offshore/pelagic) and/or season (summer vs. autumn and winter). Information on regional differences in measured $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of particulate organic matter (POM) are not available for the Japan Sea or the Sea of Okhotsk. Nearshore/benthic marine habitat is known to show higher $\delta^{13}\text{C}$ values than offshore/pelagic habitat in general (Graham et al. 2010). However, rhinoceros auklets feed on pelagic fishes, and yet showed higher $\delta^{13}\text{C}$ values (adjusted for discrimination factors) during the breeding period than during the nonbreeding period (Fig. 6). In the northern Japan Sea, the $\delta^{13}\text{C}$ values of sinking particles were higher in the early summer bloom period than the rest of the year (range: -25 to -23‰ ; Nakanishi & Minagawa 2003), which may partly explain the lower adjusted $\delta^{13}\text{C}$ values observed during the nonbreeding period.

Estimation of prey species based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are difficult without more data on isotopic baseline and potential prey species in both the Sea of Okhotsk and the southwestern Japan Sea. Nagasawa (1998) suggests that rhinoceros auklets would be a major predator of juvenile chum salmon migrating along the coasts of Hokkaido during the summer and autumn season, although the nitrogen isotopic value of juvenile chum salmon (collected during the chick-rearing season at the colony) was not as high as that of the auklets' primary feathers (Fig. 6). Ogi (1980) found juvenile Atka mackerel *Pleurogrammus monopterygius* in the stomach contents of thick-billed murre, horned *Fratercula corniculata* and tufted *F. cirrhata* puffins caught entangled in the Sea of Okhotsk in the summer. Juvenile chum salmon and Atka mackerel would also be potential prey for rhinoceros auklets, but isotopic data are lacking in the

Sea of Okhotsk. Japanese anchovy sampled in the southwestern Japan Sea in summer had $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of 9.73 to 10.16 ‰ and -17.75 to -17.44‰ , respectively (Tanaka et al. 2008). The $\delta^{15}\text{N}$ values of the breast feathers of auklets (adjusted for discrimination factors) were similar to that of anchovy, but the adjusted $\delta^{13}\text{C}$ values were 1.3 to 3.0 ‰ lower than that of anchovy collected in the southwestern Japan Sea.

To compare the isotopic values of feathers with that of the prey, we used the discrimination factors of feathers obtained from a closely-related species (common murre; Becker et al. 2007) but not from rhinoceros auklets. The discrimination factors of feathers can be variable among different seabird species or different studies on the same species, especially for $\delta^{13}\text{C}$ (Becker et al. 2007), and this might have been another confounding factor.

Adjustment of breeding timing and location

Rhinoceros auklets return to their breeding colony in mid-March. Thereafter, they forage around the breeding colony during the pre-laying, incubation (Fig. 4), and chick-rearing periods (Kato et al. 2003, Watanuki et al. 2009). The auklets experienced the lowest sea temperatures (4 to 6°C) during the early breeding period compared with the rest of the year (11 to 18°C), based on the water temperature records from the geolocators (Fig. 5). Therefore, the thermoregulatory energy costs may be highest during the early breeding period, as the lower end of the auklets' thermoneutral zone has been estimated to be 15°C based on body mass (Shirai et al. 2013). The auklets often attended to the nest burrow during the night, and this might improve thermoregulatory efficiency in the early breeding period. However, it remains unclear why auklets choose to return in March to breed in the northern Japan Sea, given the relatively high thermoregulatory costs.

One explanation could be the availability of euphausiids around the breeding colony in early spring. In the northern Japan Sea, euphausiids *Thysanoessa longipes* and *T. inermis* come to the surface to spawn when spring phytoplankton blooms occur (Area B in Fig. 7) and when SSTs are 4 to 8°C (Hanamura et al. 1989). The auklets feed on euphausiids and low trophic level juvenile fish in early spring based on egg yolk isotope values (Fig. 6). The carotenoid-rich euphausiids may be suitable prey for females during egg production (Ito et al. 2009), and could be an important factor determining

the timing of the auklets' migration to the northern Japan Sea. Another, not mutually exclusive, explanation could be that the auklets need to adjust their chick-rearing period to the arrival of migrating warm water forage fish in early summer (Watanuki et al. 2009). Japanese anchovy, a profitable prey during the chick-rearing period, migrates to the sea around Teuri Island when warm waters ($>13^{\circ}\text{C}$) from the Tsushima Warm Current intrude into the foraging area in late May and mid-June (Watanuki et al. 2009). If the auklets are to adjust the timing of chick-rearing to correspond to the warm water arrival, they must be back in the colony and have laid their eggs by mid-April to early May (even though the SSTs are still low at this time), given that incubation takes 45 d on average (Gaston & Jones 1998).

Proficient-flying procellariiform seabirds can move long distances and shift their foraging ranges seasonally, even while attending the colony. For example, streaked shearwaters *Calonectris leucomelas* from the colony on the Pacific coast of Japan shift their foraging area from south to the north of the colony between April and July while attending the colony (Yamamoto et al. 2011). They fly up to a mean distance of 600 km from the colony, presumably following the northward migration of Japanese anchovy (Yamamoto et al. 2011). Rhinoceros auklets shift their foraging area seasonally during the early to late breeding period (Deguchi et al. 2010, this study), but the range of shift is much smaller, reflecting higher flight costs (up to a median distance of 240 km from the colony, see 'Results'). We suggest that the adjustment of breeding timing and location is an important factor affecting the migratory patterns, especially in a species with a short foraging range during the breeding period. In fact, the seasonal mismatch between breeding timing and anchovy migration has important fitness consequences in rhinoceros auklets (Watanuki et al. 2009).

Conservation implications

The breeding population of rhinoceros auklets at Teuri Island is the largest in the northwestern Pacific, comprising more than 90% of the total population in Asia (Gaston & Jones 1998). High concentrations of nonbreeding auklets in the Sea of Okhotsk in autumn and in the southwestern Japan Sea in winter (Fig. 4) indicate that these 2 regions offer critical nonbreeding habitat for the population of Teuri Island. We suggest that the auklets are susceptible to (1) ocean warming and climatic regime shifts, and (2) oil

spill threats, which have been observed in both the Sea of Okhotsk and southwestern Japan Sea.

Significant warming and reductions in winter sea-ice production have been observed in the Sea of Okhotsk, and this may negatively influence the biological productivity of these regions (Radchenko et al. 2010 and references therein). In the northern part of the Sea of Okhotsk, increased SSTs negatively affected the breeding performance of planktivorous alcids, but the opposite was the case for piscivorous alcids (Kitaysky & Golubova 2000). Climatic regime shifts are suggested to have occurred in the Japan Sea, which may have influenced the stock size of epipelagic fish including Japanese anchovy (Kim et al. 2008) and the migration patterns of Japanese common squid (Kidokoro et al. 2010).

Oil platform development is planned for the Sea of Okhotsk, east of Sakhalin Island (Sakurai et al. 2013), where auklets concentrate in autumn. If oil spills were to occur in this region in autumn, it would have severe implications for the global population of auklets. Also, in the southwestern Japan Sea, oil spills from tankers passing through the Tsushima Strait may also affect the population if the spill occurs in the winter. Indeed, 1326 and 482 oiled carcasses of rhinoceros auklets were recovered from the shore of the southwestern Japan Sea, during oil spills from unknown sources in January 1986 (Sato 1999) and from a tanker in January 1997 (Fries et al. 1998), respectively. Therefore, the information presented here is crucial for identifying key areas of global significance for seabird conservation.

CONCLUSIONS

Our results suggest that rhinoceros auklets follow spatial and seasonal changes in prey availability by employing a distinctive '3-step' migration pattern after breeding; moving northward to the Sea of Okhotsk in autumn, southward to the southwestern Japan Sea in winter, and then returning northward to the breeding colony in the northern Japan Sea in early spring. The auklets appear to continue feeding on higher trophic level prey including fish and/or squid during the autumn and winter nonbreeding periods, but switch to lower trophic level prey in early spring when they are confined to foraging close to the colony. The accessibility of foraging habitats with different seasonal productivity patterns is important for nonbreeding seabirds that have high energetic constraints on migratory movements.

Acknowledgements. We thank M. Aotsuka, Y. Kusakabe, M. Shikata, and K. Hoshina for their help during the fieldwork at Teuri Island. Anonymous referees, N. Payne, and A. Burger provided helpful comments about the manuscript. The fieldwork was conducted under the permits of the Ministry of the Environment and the Agency of Cultural Affairs. This study was supported by Grant-in-Aid for Scientific Research (20241001 and 24370016).

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Appendix

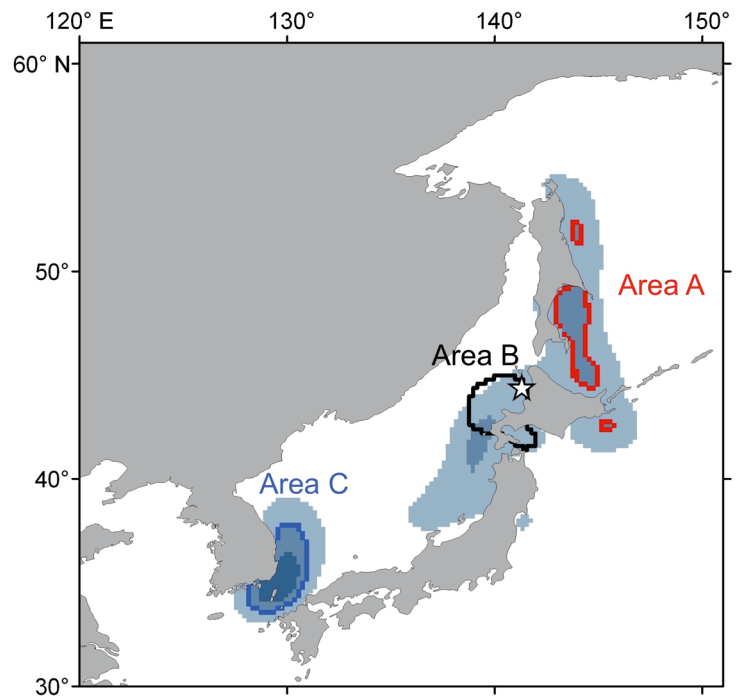


Fig. A1. Kernel density distribution of rhinoceros auklet locations during the nonbreeding period of the first and second study year (i.e. 2010/2011 and 2011/2012) combined. Kernel densities indicate 25, 50, and 75% from darker to lighter colors. Chl *a* concentrations were calculated for Area A (red), Area B (black) and Area C (blue). The areas were chosen on the basis of 50% kernel density boundaries during nonbreeding (Areas A and C) and early breeding (Area B; see Fig. 4) periods. Teuri Island is marked with a star

Editorial responsibility: Jacob González-Solís, Barcelona, Spain

*Submitted: June 19, 2014; Accepted: December 29, 2014
Proofs received from author(s): March 12, 2015*