

1 Manuscript revised for Marine Ecology Progress Series

2
3 Running page head: Auklet migration in northwestern Pacific

4
5 **Connecting the seasonal productivities: migratory movements of**
6 **rhinoceros auklets in the northwestern Pacific**

7
8 Akinori Takahashi^{1,2*}, Motohiro Ito¹, Yuuya Suzuki³, Yutaka Watanuki³, Jean-Baptiste
9 Thiebot¹, Takashi Yamamoto^{1,3}, Takahiro Iida^{1,2}, Phil Trathan⁴, Yasuaki Niizuma⁵,
10 Tomohiro Kuwae⁶

11
12 ¹National Institute of Polar Research, Tachikawa, Tokyo 190-8518, Japan

13 ²Department of Polar Science, The Graduate University for Advanced Studies
14 (SOKENDAI), Tachikawa, Tokyo 190-8518, Japan

15 ³Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho,
16 Hakodate 041-8611, Japan

17 ⁴British Antarctic Survey, Natural Environment Research Council, High Cross,
18 Madingley Road, Cambridge CB3 0ET, UK

19 ⁵Faculty of Agriculture, Meijo University, 1-501, Shiogamaguchi, Tempaku-ku,
20 Nagoya 468-8502, Japan.

21 ⁶Port and Airport Research Institute, 3-1-1, Nagase, Yokosuka 239-0826, Japan

22 *E-mail: atak@nipr.ac.jp

23
24 **ABSTRACT:** Spatial and temporal variability in marine biological productivity may
25 drive heterogeneity in seasonal resources available for marine animals in temperate
26 waters. Migratory seabirds are expected to adjust the annual cycle of breeding activities
27 and migratory movements to exploit seasonally available resources efficiently. We
28 studied the movement and trophic position of rhinoceros auklets *Cerorhinca*
29 *monocerata* breeding at Teuri Island, Japan Sea, during the nonbreeding and early
30 breeding periods over two years. After breeding, the auklets moved northward from the
31 colony to the Sea of Okhotsk, where phytoplankton blooms enhanced biological
32 productivity in autumn. The birds then moved southward to the southwestern Japan Sea

33 (~1470 km from the colony), where major epipelagic fish and squid concentrations have
34 been reported in winter. Stable isotope analyses suggest that the auklets fed on
35 higher-trophic level prey, including fish and/or squid during the autumn and winter
36 nonbreeding periods. The auklets moved northward and returned to the colony in
37 mid-March. During the early breeding period, the birds foraged close to the colony
38 (~380 km) on lower-trophic level prey, including fish and/or krill, which were available
39 during the spring phytoplankton bloom. The timing of the return migration does not
40 match with the northward migration of warm-water anchovy, a profitable prey during
41 summer, but may be related to the adjustment of the chick-rearing period to anchovy
42 arrival. We suggest that rhinoceros auklets follow spatial and seasonal changes in prey
43 availability by a distinctive ‘three-step’ migration (first northward, second southward,
44 third northward) in a temperate marine system of northwestern Pacific.

45

46 **KEY WORDS:** Seabird foraging, Light-based geolocation, Productivity, Seasonal
47 movements, Stable isotope analysis, Japan Sea

48

49

50 **INTRODUCTION**

51

52 Seabirds are faced with challenges in finding their prey in the spatially and
53 temporally variable marine environment (Weimerskirch 2007), under the different
54 foraging constraints that exist during the breeding and nonbreeding periods. During the
55 breeding period, parent seabirds are central place foragers that have to commute
56 between their colony and feeding grounds at sea. Their foraging ranges are relatively
57 limited especially during early chick-rearing period to provision their offspring (e.g.,
58 Charrassin & Bost 2001, Rayner et al. 2012). Despite the constraints on their foraging
59 range, parent seabirds have to feed intensively in order to meet the high energetic
60 demands associated with breeding (Hamer et al. 2001). During the nonbreeding period,
61 seabirds can move over larger distances without the constraints of central-place foraging
62 (e.g., Thiebot et al. 2011), but may experience reduced prey availability due to
63 decreased marine productivity outside the summer breeding season and/or possible
64 changes in the accessibility of prey in the water column (e.g., Charrassin & Bost 2001).

65 An increasing number of studies have shown that seabirds, especially proficient-flying
66 procellariiform seabirds, adjust the annual cycle of breeding activities and migratory
67 movements to seasonally available resources (Shaffer et al. 2006, González-Solís et al.
68 2007, Guilford et al. 2009, Rayner et al. 2011, Carey et al. 2014); though, such
69 adjustments may vary among species of different migration abilities and among
70 different marine regions.

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

91 Rhinoceros auklets *Cerorhinca monocerata* are medium-sized alcids (500 - 600 g)
92 that breed in the North Pacific. The largest breeding colony is located at Teuri Island in
93 the northern Japan Sea, where approximately 0.3 million pairs breed annually
94 (Watanuki & Ito 2012). The auklets feed intensively on Japanese anchovy *Engraulis*
95 *japonicus* close to the breeding colony (~130 km) during chick-rearing period (Kato et
96 al. 2003, Watanuki & Ito 2012), but their movement and diet have been largely

97 unknown outside the breeding period. The objective of this study is therefore to
98 characterize the migratory movements and trophic position of rhinoceros auklets during
99 nonbreeding and early breeding periods, by combining information from light-based
100 geolocation and stable isotope analyses. It is hypothesized that the migratory
101 movements of the auklets follow seasonal changes in regional prey availability, given
102 the heterogeneity of seasonal productivity patterns in Japan Sea and the adjacent Sea of
103 Okhotsk (Lee et al. 2009, Radchenko et al. 2010). We expect that rhinoceros auklets
104 maintain their fish diet by moving among different marine regions during the
105 nonbreeding period, but they may be confined to feed close to the colony on different
106 prey items during the early breeding period.

107

108

109 **MATERIALS AND METHODS**

110

111 • **Geolocator deployments.** The study was conducted at Teuri Island (44°24' N,
112 141°17' E), located in the northern Japan Sea (Fig. 1). Rhinoceros auklets first return
113 to Teuri Island from March to April and lay a single egg in April and May. The single
114 chick hatches between May and June, and fledges in July (Watanuki & Ito 2012). In
115 July 2010, we captured 10 chick-rearing birds from nest burrows, and attached a
116 geolocator (Mk15, 16 x 18 x 6mm, British Antarctic Survey, Cambridge, UK) on the
117 tarsus of each bird using a plastic leg ring. The total mass of geolocators including the
118 ring was 3.5 g (0.62 % of the mean body mass of tracked birds). We retrieved
119 geolocators from 8 out of 10 birds and in May 2011. Upon recapture, the 10th primary
120 feather and 2-3 breast feathers were taken as samples for stable isotope analysis. One
121 additional instrumented bird was recaptured in the breeding season of 2013. We also
122 attached geolocators on 20 birds in July 2011. We retrieved geolocators from 16 out
123 of 20 birds and in May-June 2012. Three individuals were tracked during the
124 nonbreeding and early breeding periods of both 2010-11 and 2011-12. All the
125 geolocators that were recovered recorded data successfully, but 5 geolocators from
126 the 2011-12 deployments stopped recordings prematurely after 1-3 months. We
127 therefore analyzed 20 complete tracks recorded from 17 birds (10 males and 7
128 females). The sex of the birds was determined on the basis of bill and head

129 measurements (Niizuma et al. 1999). The study birds maintained their body mass
130 between device attachment and retrieval on average (average mass change: +12.5 g,
131 range: +75 g to -45 g), although we do not have comparable data from control birds to
132 examine any device effects.

133 • **Geolocation data analysis.** The geolocators record time, light intensity, immersion
134 in seawater and water temperature. The geolocators were programmed to measure
135 light levels at 1 min intervals, and to record the maximum value after each 10 min
136 period. Immersion in seawater was checked every 3 s and the data were compiled as a
137 proportion over each 10 min period. Water temperature was recorded only after
138 continuous immersion for 20 min as the temperature sensors require 10 min to
139 stabilize. Accuracy of the temperature recordings was 0.5 °C as indicated by the
140 manufacturer. Light and water temperature data were used to estimate the daily bird
141 locations (Yamamoto et al. 2011). Times of sunset and sunrise were estimated from
142 the thresholds in the light curves. Latitude was derived from day length and longitude
143 from time of local midday with respect to Greenwich Mean Time and Julian day,
144 using TransEdit and Locator software (British Antarctic Survey). To improve the
145 location estimates from light levels, the daily median of the water temperature records
146 from the geolocators were compared with remotely sensed sea surface temperature
147 (SST) data (8-day composite, 9-km resolution, measured by Aqua-MODIS,
148 downloaded from the ocean color web <http://oceancolor.gsfc.nasa.gov>). We retained
149 the longitude estimates obtained from light-based geolocation, and searched the
150 latitude where SST matches with median water temperature records from geolocators.
151 Since SST varies with latitude (cooler towards higher latitude), this procedure
152 enabled us to refine the latitude estimates during the entire period of at-sea trips,
153 including during the equinoxes. Finally, these daily positions were smoothed using a
154 theoretical movement model in a Bayesian framework (Thiebot & Pinaud 2010). This
155 movement model calculates the most probable location estimates along the tracks
156 (without deleting any locations) that meet with the following three conditions: 1) no
157 locations occur on land, 2) the start and end locations of the tracks are the breeding
158 colony, and 3) mean movement speed is 10 km/h (based on flying speeds measured
159 from GPS tracking, Watanuki et al., unpublished data, corrected by the average time
160 spent flying per day over the nonbreeding period, ~4.5 h, this study), with 5 km /h

161 allowed for variance of the mean (see Thiebot & Pinaud 2010 and references therein
162 for details).

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

173 • **Stable isotope analysis of feathers.** We analyzed stable isotopes of feathers grown
174 during the nonbreeding period. Although accurate molt cycles are not known for
175 rhinoceros auklets, the 10th primary and breast feathers presumably grow during the
176 pre-basic molt (August - October) and pre-alternate molt (February – March),
177 respectively (Pyle 2009, Sorensen et al. 2010). Feathers were stored in a freezer
178 (-20°C) until laboratory analyses. Nitrogen and carbon stable isotope ratios ($\delta^{15}\text{N}$ and
179 $\delta^{13}\text{C}$) were measured at Meijo University (Nagoya, Japan) for 2010-11 samples and at
180 Port and Airport Research Institute (Yokosuka, Japan) for 2011-12 samples. At Meijo
181 University, feathers were washed using 0.25 mol/L sodium hydroxide aqueous
182 solution and distilled water, dried in a oven (60°C) for 24 hours, placed in liquid
183 nitrogen for 1 minute, then homogenized using a sample crusher (TK-AM5, TITEC).
184 At Port and Airport Research Institute, feathers were washed using 0.25 mol/L
185 sodium hydroxide aqueous solution and distilled water, freeze-dried for 36-48 hours,
186 cut as small as possible, then homogenized using a mortar. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were
187 measured using a SerCon ANCA-GSL, Hydra 20-20MASS spectrometer (SerCon
188 Ltd.) (Meijo University) or a Delta Plus Advantage mass spectrometer (Thermo
189 Electron) coupled with an elemental analyzer (Flash EA 1112, Thermo Electron)
190 (Port and Airport Research Institute). Stable isotope ratios are expressed in δ notation
191 as the deviation from standard (air) in parts per thousand (‰) according to the
192 following equation: $\delta^{15}\text{N}$ or $\delta^{13}\text{C} = [R_{\text{sample}} / R_{\text{standard}} - 1] \times 1000$, where $R = {}^{15}\text{N}/{}^{14}\text{N}$

193 or $^{13}\text{C}/^{12}\text{C}$. Replicate measurements of internal laboratory standards indicated that the
194 measurement precision was ± 0.16 ‰ and ± 0.12 ‰ for $\delta^{15}\text{N}$ (SD) and ± 0.16 ‰
195 and ± 0.11 ‰ for $\delta^{13}\text{C}$ (SD) in the laboratories at Meijo University and Port and
196 Airport Research Institute, respectively.

197 We need to take into account the tissue-specific discrimination factors of
198 isotopic values, to compare isotopic values of different tissues of consumers with that
199 of prey. We used the discrimination factors as follows, based on a study of common
200 murre *Uria aalge* (Becker et al. 2007): 3.7 ‰ and 3.6 ‰ for $\delta^{15}\text{N}$ and 1.9 ‰ and
201 1.0 ‰ for $\delta^{13}\text{C}$, for primary and breast feathers. We compared the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$
202 values of feathers with those of egg yolk and blood plasma obtained during breeding
203 season as well as potential prey species (Euphausiids: *Thysanoessa inermis*; 0+ and
204 >1+ sandlance *Ammodytes personatus*; Japan sea greenling *Pleurogrammus azonus*;
205 Japanese anchovy; Squid Coleoides; juvenile chum salmon *Oncorhynchus keta*),
206 reported in Ito et al. (2009, 2012). Ito et al. (2012) used the following discrimination
207 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
208 and blood plasma, respectively, based on other avian studies (egg yolk) and their own
209 measurements from rhinoceros auklet chicks (blood plasma).

210 • **Primary productivity.** To characterize the seasonal patterns in primary
211 productivity, monthly average values of sea surface chlorophyll a concentrations were
212 calculated from January 2003 to December 2012 for an area in the Sea of Okhotsk
213 (area A) and two areas in the Japan Sea (areas B and C; Fig. S1). The areas were
214 chosen on the basis of 50 % kernel density boundaries of bird locations during the
215 nonbreeding (areas A and C) and early breeding (area B) periods. We used the Aqua
216 MODIS level 3 monthly standard mapped image 9-km resolution chlorophyll a data
217 that were downloaded from the ocean color web.

218 • **Statistics.** Maximum distance reached from the colony by the birds was compared
219 between years or sexes with one-way ANOVA. Two males and one female had
220 repeated measurements (i.e. tracked during both 2010-11 and 2011-12). We show
221 here the statistics that include the six tracks from these three birds as independent.
222 Statistical results were similar, even if we included only one (the track of either
223 2010-11 or 2011-12) of the two tracks for these three birds in the analyses. Minitab
224 software (Minitab Inc., Pennsylvania, USA) was used for statistical analyses. Kernel

225 densities for geolocation data were calculated using the ArcGIS Spatial Analyst
226 Density tool (ESRI, California, USA) with a cell size of 0.2 degree and a search
227 radius of 2 degrees. Means (\pm SE) are shown.

228

229

230 **RESULTS**

231

232 **Seasonal movement patterns**

233 After the breeding season, tracked birds departed the colony on 23rd July in both
234 years (\pm 0.7 and \pm 1.4 days for 2010-11 and 2011-12, respectively), indicated by the
235 immersion records of geolocators. In the first phase of migration, the birds moved
236 northward from the colony to the Sea of Okhotsk, which was consistent during both
237 years (Fig. 2, Fig. 3). The birds were distributed mainly at the east or south of Sakhalin
238 Island until September, and then moved southward to the northeastern or southeastern
239 shore of Hokkaido Island in October (Fig. 4). In the second phase, the birds moved
240 southward across the Japan Sea, during November - January. Most birds (7 of 9 birds
241 and 8 of 11 birds in 2010-11 and 2011-12, respectively) reached the sea around the
242 Korean Peninsula and Tsushima Strait (Fig. 3, Fig. 4). The remaining four birds (5
243 tracks) appeared to spend winter farther east in Japan Sea, with a mean westernmost
244 longitude of 135.6 °E. From February, the birds undertook their third movement phase
245 by migrating northward again along the coast of Japan, and returned to the colony on
246 11th and 18th March (\pm 2.3 and \pm 1.1 days) in the 2010-11 and 2011-12 seasons,
247 respectively (Fig. 3). Overall, kernel density of locations identified the Sea of Okhotsk
248 and the sea around the Korean Peninsula and Tsushima Strait as key areas during the
249 nonbreeding period in both 2010-11 and 2011-12 (Fig. 4).

250 The average maximum distance reached from the colony by the auklets during the
251 nonbreeding period did not differ between the two years (1549 ± 77 km vs. 1403 ± 91
252 km for 9 and 11 tracks in 2010-11 and 2011-12, respectively; $F_{1,18} = 1.43$, $p = 0.25$) nor
253 between sexes (1481 ± 96 km vs. 1460 ± 83 km for 8 and 12 tracks from females and
254 males, respectively; $F_{1,18} = 0.03$, $p = 0.87$).

255 After the initial arrival to the colony, the birds made foraging trips during
256 pre-laying and the early incubation periods, until the end of the geolocator records.

257 During this early breeding period, the birds stayed relatively close to the colony (Fig.4);
258 half of the daily at-sea locations were within 157 ± 10 km and 237 ± 21 km from the
259 colony, for 2010-11 and 2011-12, respectively. The average maximum distance reached
260 from the colony by the auklets during the early breeding period did not differ between
261 the two years (376 ± 24 km vs. 386 ± 19 km for 9 and 11 tracks in 2010-11 and 2011-12,
262 respectively; $F_{1,18} = 0.1$, $p = 0.75$) nor between sexes (407 ± 29 km vs. 365 ± 14 km for
263 8 and 12 tracks from females and males; $F_{1,18} = 2.12$, $p = 0.16$).

264

265 **Activity and water temperature records**

266 During the nonbreeding period, the leg-mounted geolocators remained dry for
267 4.42 ± 0.42 h per day ($n = 20$ tracks). There were no apparent seasonal patterns in the
268 time spent dry, and no clear evidence of flightless periods (Fig. 2). During the early
269 breeding period, the daily time spent dry increased as the birds attended the colony at
270 night or throughout a day for incubation (Fig. 2).

271 Water temperature recorded by the geolocators showed large seasonal changes in
272 both years (Fig. 5). Water temperature experienced by the birds remained around 11 -
273 14 °C from October to late February, but dropped to 4 - 6 °C in early March associated
274 with a northward migration of auklets to the breeding colony.

275

276 **Isotopic value of feathers**

277 Mean measured isotopic values (without adjustment for discrimination factors)
278 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 ‰
279 for $\delta^{13}\text{C}$ in primary feathers, versus 13.5 ± 0.2 ‰ and 14.1 ± 0.1 ‰ for $\delta^{15}\text{N}$ and
280 -19.5 ± 0.2 ‰ and -18.1 ± 0.2 ‰ for $\delta^{13}\text{C}$ in breast feathers, in 2010-11 ($n = 8$) and
281 2011-12 ($n = 16$) respectively (Fig. 6). The $\delta^{15}\text{N}$ values of primary and breast feathers
282 adjusted for discrimination factors (3.7 ‰ and 3.6 ‰ for primary and breast feathers)
283 were higher than those of egg yolk and blood plasma (adjusted for discrimination
284 factors) during the prelaying, incubation and chick-rearing periods (Fig. 6). The $\delta^{13}\text{C}$
285 values of primary feathers were lower than those of breast feathers, egg yolk and blood
286 plasma (all values adjusted for discrimination factors) (Fig. 6).

287

288 **Marine primary productivity**

289 Chlorophyll a concentration was highest in April over the annual cycle in each
290 area of A-C, and the peak values were higher in areas A and B (Sea of Okhotsk and
291 northern Japan Sea) compared to area C (southwestern Japan Sea) (Fig. 7). A second,
292 clear peak in chlorophyll a concentration was observed in autumn (September –
293 November) in area A only.

294

295

296 **DISCUSSION**

297

298 Our results, together with previous results from the chick-rearing period (Kato et
299 al. 2003), suggest that, interannually, rhinoceros auklets from the largest colony in the
300 northwestern Pacific mainly use three marine regions year-round: the Sea of Okhotsk in
301 autumn, the southwestern Japan Sea in winter, and the northern Japan Sea during the
302 breeding season in spring and summer. The auklets consistently used these areas over
303 two successive years. The Sea of Okhotsk, northern Japan Sea and southwestern Japan
304 Sea are highly productive areas (Lee et al. 2009, Radchenko et al. 2010) among which
305 the seasonal patterns of biological productivity differ considerably (Fig. 7). We
306 hypothesize that the auklets are able to connect such seasonal peaks in productivity by a
307 distinctive ‘three-step’ migration pattern.

308

309 **Migratory movements and regional prey availability**

310 Rhinoceros auklets feed mainly on warm-water Japanese anchovy during the
311 chick-rearing period (Watanuki & Ito 2012), and change their foraging locations from
312 south to north of the colony during May - July, presumably following the northward
313 migration of anchovy (Deguchi et al. 2010). Our results showed that the auklets
314 continued to move northward into the Sea of Okhotsk after the breeding season, which
315 is in accordance with previous ship-based surveys that reported the concentrations of
316 auklets along Soya Strait and in the Sea of Okhotsk in late July – late August (Shuntov
317 2000, Deguchi et al. 2010). The auklets moved within the Sea of Okhotsk until October
318 (Fig. 3). The Sea of Okhotsk is one of the southernmost seasonal sea ice zones in the
319 northern hemisphere, and supports high biological productivity associated with spring
320 ice-edge blooms as well as autumn blooms (Mustapha et al. 2009, Radchenko et al.

2010). High summer as well as 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 – 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 mostly feeding on fish (Rayner et al. 2011) and 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 crassirostris* that breed in a colony in the northern Japan Sea move into the Sea of Okhotsk in August (Kazama et al. 2013). Such 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 mackerels (*Scomber japonicus* and *Trachurus japonicus*) (Kim et al. 2008). In particular, Japanese anchovy are found distributed around the Korean Peninsula in winter, and are available at shallow depths (5 – 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 winter (Kidokoro et al. 2010).

The three-step migration, or three-phased migratory pattern (first northward, second southward, third northward) will increase the total distance travelled during the nonbreeding period, compared with the direct migration from the colony to the southern wintering area. The costs of travelling by flight are expected to be high in alcids that have high wing loading such as rhinoceros auklets (Elliott et al. 2013). The auklets

353 presumably gain sufficient energy in autumn in the Sea of Okhotsk, which outweighs
354 the energy costs of moving any extra distances to southern wintering areas. The birds
355 appeared to experience a similar temperature range (12 – 14 °C) between October and
356 late February (Fig. 5) due to southward seasonal movement, and relatively constant sea
357 temperature may be favorable for thermoregulation.

358 The three-step migration is also observed in little auks *Alle alle* breeding in East
359 Greenland (Mosbech et al. 2012). The little auk used an autumn staging area in the
360 Greenland Sea at the northeast of the colony, and then performed a long southerly
361 migration (~2000 km) to winter off Newfoundland. Other alcids show diverse migratory
362 patterns even within a species. For example, common murrelets in a colony at Svalbard
363 migrate southward (~1000 km from the colony) to the Barents Sea and adjacent areas
364 (Fort et al. 2013), but the same species from a colony in central Norway migrate
365 northward to the Barents Sea (Lorentsen et al. 2012). Atlantic puffins *Fratercula*
366 *arctica* from the Isle of May off east Scotland stay within the North Sea or move north
367 to the northeast Atlantic (Harris et al. 2013), but the same species from southwest
368 Ireland make long-distance east-west movements to Newfoundland in
369 August-September (2537 km on average; Jessopp et al. 2013). Thick-billed murrelets *Uria*
370 *lomvia* from 5 colonies spanning eastern Canadian Coast from the high Arctic to
371 Newfoundland show variable degrees of southward movement (700 – 3500 km) to
372 common wintering areas in the Labrador Sea and the seas off Newfoundland
373 (McFarlane Tranquilla et al. 2013). We suggest that the migratory patterns of alcids are
374 highly flexible depending upon the spatial and seasonal patterns of prey availability
375 relative to their breeding location and timing. However, the maximum migration
376 distances of alcids from the colony (~3500 km) are relatively limited, compared to the
377 distances traveled by proficient-flying procellariiform seabirds (~12000 km from the
378 colony; Guilford et al. 2009, Yamamoto et al. 2010), suggesting that the high energetic
379 costs of flight would constrain the ability of alcids to exploit seasonally available
380 resources through migration.

381

382 **Trophic position during the nonbreeding period**

383 The nitrogen and carbon isotope signatures of the 10th primary feathers and breast
384 feathers of auklets presumably reflect the diet during autumn and winter, respectively

385 (see ‘Stable isotope analysis of feathers’ in Materials and Methods). The relatively high
386 $\delta^{15}\text{N}$ values of both primary and breast feathers (adjusted for discrimination factors),
387 compared with $\delta^{15}\text{N}$ values of auklet blood samples during the breeding period, suggest
388 that the auklets fed on higher trophic level prey, including fish and/or squid, rather than
389 zooplankton (Fig. 6). This contrasts with isotopic studies of other alcids such as Atlantic
390 puffins or thick-billed murrelets, which showed seasonal shifts to low $\delta^{15}\text{N}$ values,
391 suggesting the dependence on lower trophic level zooplankton during the nonbreeding
392 period (Hedd et al. 2010, Hobson & Bond 2012).

393 We have to note that the relatively low $\delta^{13}\text{C}$ values in both primary and breast
394 feathers (adjusted for discrimination factors) may reflect the carbon source for primary
395 producers, varying with habitat (nearshore/benthic vs. offshore/pelagic) and/or season
396 (summer vs. autumn and winter). Information on regional differences in measured $\delta^{15}\text{N}$
397 and $\delta^{13}\text{C}$ values of particulate organic matter (POM) are not available in Japan Sea or
398 the Sea of Okhotsk. Nearshore/benthic marine habitat is known to show higher $\delta^{13}\text{C}$
399 values than offshore/pelagic habitat in general (Graham et al. 2011). However,
400 rhinoceros auklets fed on pelagic fishes and yet showed higher $\delta^{13}\text{C}$ values (adjusted for
401 discrimination factors) during the breeding period than during the nonbreeding period
402 (Fig. 6). In northern Japan Sea, the $\delta^{13}\text{C}$ values of sinking particles were higher in early
403 summer bloom period than the rest of the year (range: -25 - -23 ‰; Nakanishi &
404 Minagawa 2003), which may partly explain the lower adjusted $\delta^{13}\text{C}$ values observed
405 during the nonbreeding period.

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

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

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

428

429 **Adjustment of breeding timing and location**

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

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

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

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

473

474 **Conservation implications**

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

481 shifts, and 2) oil spill threats, which have been observed in both the Sea of Okhotsk and
482 southwestern Japan Sea.

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

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

502

503 **CONCLUSION**

504 Our results suggest that rhinoceros auklets followed spatial and seasonal changes
505 in prey availability by a distinctive ‘three-step’ migration after breeding; moving
506 northward to the Sea of Okhotsk in autumn, southward to the southwestern Japan Sea in
507 winter, and then returning northward to the breeding colony in the northern Japan Sea in
508 early spring. The auklets appeared to continue feeding on higher trophic level prey
509 including fish and/or squid during the autumn and winter nonbreeding periods, but
510 switched to lower trophic level prey in early spring when they were confined to forage
511 close to the colony. The accessibility of foraging habitats with different seasonal
512 productivity patterns would be important for nonbreeding seabirds that have high

513 energetic constraints on migratory movements.

514

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

521

522 **LITERATURE CITED**

523

524 Becker BH, Newman SH, Inglis S, Beissinger SR (2007) Diet-feather stable isotope
525 (¹⁵N and ¹³C) fractionation in common murrelets and other seabirds. *Condor*
526 109:451-456

527 Burger AE, Shaffer SA (2008) Application of tracking and data-logging technology in
528 research and conservation of seabirds. *Auk* 125: 253-264

529 Carey MJ, Phillips RA, Silk JRD, Shaffer SA (2014) Trans-equatorial migration of
530 Short-tailed shearwaters revealed by geolocators. *Emu* 114: 352-359.

531 Charrassin JB, Bost CA (2001) Utilization of the oceanic habitat by king penguins over
532 the annual cycle. *Mar Ecol Prog Ser* 221:285-297

533 Deguchi T, Wada A, Watanuki Y, Osa Y (2010) Seasonal changes of the at-sea
534 distribution and food provisioning in rhinoceros auklets. *Ecol Res* 25:123-137

535 Elliott KH, Ricklefs RE, Gaston AJ, Hatch SA, Speakman JR, Davoren GK (2013)
536 High flight costs, but low dive costs, in auks support the biomechanical hypothesis
537 for flightlessness in penguins. *Proc Natl Acad Sci USA* 110:9380-9384

538 Fort J, Steen H, Strøm H, Tremblay Y, Grønningsæter E, Pettex E, Porter WP,
539 Grémillet D (2013) Energetic consequences of contrasting winter migratory
540 strategies in a sympatric Arctic seabird duet. *J Avian Biol* 44: 255-262

541 Fries J, Uematsu K, Takaki J, Tobai S (1998) Oil spills and the protection of wildlife:
542 What have we learned since the Nakhodka Spill? The Nippon Foundation, Tokyo.
543 (In Japanese)

544 Gaston AJ, Jones IL (1998) *The Auks*. Oxford University Press, New York.

545 Guilford T, Meade J, Willis J, Phillips RA, Boyle D, Roberts S, Collett M, Freeman R,
546 Perrins CM (2009) Migration and stopover in a small pelagic seabird, the Manx
547 shearwater *Puffinus puffinus*: insights from machine learning. *Proc Biol Sci*
548 276:1215-1223.

549 González-Solís J, Croxall JP, Oro D, Ruiz X (2007) Trans-equatorial migration and
550 mixing in the wintering areas of a pelagic seabird. *Front Ecol Environ* 5:297-301.

551 Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using
552 isoscapes to trace the movements and foraging behavior of top predators in oceanic
553 ecosystems. In: West JB, Brown GJ, Dawson TE, Tu KP (eds) *Isoscapes: understanding movement, pattern and processes on Earth through isotope mapping*. Springer, New York. p. 299-318.

556 Harris MP, Daunt F, Bogdanova MI, Lahoz-Monfort JJ, Newell MA, Phillips RA,
557 Wanless S (2013) Inter-year differences in survival of Atlantic puffins *Fratercula*
558 *arctica* are not associated with winter distribution. *Mar Biol* 160:2877-2889.

559 Hamer KC, Schreiber EA, Burger J (2001) Breeding biology, life histories, and life
560 history-environment interactions in seabirds. In: Schreiber EA, Burger J (eds)
561 *Biology of marine birds*. CRC Press, Florida. p. 217-261

562 Hanamura Y, Kotori M, Hamaoka S (1989) Daytime surface swarms of the euphausiid
563 *Thysanoessa inermis* off west coast of Hokkaido, northern Japan. *Mar Biol* 102:
564 369-376.

565 Hedd A, Fifield DA, Burke CM, Montevecchi WA, McFarlane Tranquilla LA, Regular
566 PM, Buren AD, Robertson GJ (2010) Seasonal shift in the foraging niche of Atlantic
567 puffins *Fratercula arctica* revealed by stable isotope (δ^{15} N and δ^{13} C) analyses.
568 *Aquat Biol* 9:13-22

569 Hobson KA, Bond AL (2012) Extending an indicator: year-round information on

570 seabird trophic ecology from multiple-tissue stable-isotope analyses. *Mar Ecol Prog*
571 *Ser* 461:233-243

572 Ito M, Minami H, Tanaka Y, Watanuki Y (2009) Seasonal and inter-annual
573 oceanographic changes induce diet switching in a piscivorous seabird. *Mar Ecol Prog*
574 *Ser* 393:273-284

575 Ito M, Kazama K, Niizuma Y, Minami H, Tanaka Y, Watanuki Y (2012) Prey resources
576 used for producing egg yolks in four species of seabirds: insight from stable-isotope
577 ratios. *Ornithol Sci* 11:1-7

578 Iversen SA, Zhu D, Johannessen A, Toresen R (1993) Stock size, distribution and
579 biology of anchovy in the Yellow Sea and East China Sea. *Fish Res* 16:147-163

580 Jessopp MJ, Cronin M, Doyle TK, Wilson M, McQuatters-Gollop A, Newton S,
581 Phillips RA (2013) Transatlantic migration by post-breeding puffins: a strategy to
582 exploit a temporarily abundant food resource? *Mar Biol* 160:2755-2762

583 Kato A, Watanuki Y, Naito Y (2003) Foraging behaviour of chick-rearing rhinoceros
584 auklets *Cerorhinca monocerata* at Teuri Island, Japan, determined by
585 acceleration-depth recording micro data loggers. *J Avian Biol* 34: 282-287

586 Kazama K, Hirata K, Yamamoto T, Hashimoto H, Takahashi A, Niizuma Y, Trathan P,
587 Watanuki Y (2013) Movements and activities of male black-tailed gulls in breeding
588 and sabbatical years. *J Avian Biol* 44: 603-608

589 Kitaysky AS, Golubova EG (2000) Climate change causes contrasting trends in
590 reproductive performance of planktivorous and piscivorous alcids. *J Anim Ecol* 69:
591 248-262.

592 Kidokoro H, Goto T, Nagasawa T, Nishida H, Akamine T, Sakurai Y (2010) Impact of
593 a climate regime shift on the migration of Japanese common squid (*Todarodes*
594 *pacificus*) in the Sea of Japan. *ICES J Mar Sci* 67:1314-1322

595 Kim S, Zhang CI, Kim JY, Kang S, Lee JB (2008) Republic of Korea. In: Beamish RJ
596 (ed) Impacts of climate and climate change on the key species in the fisheries in the
597 North Pacific. PICES Scientific Reports No. 35, p 101-134.

598 Lee JY, Kang DJ, Kim IN, Rho T, Lee T, Kang CK, Kim KR (2009) Spatial and
599 temporal variability in the pelagic ecosystem of the East Sea (Sea of Japan): a review.
600 *J Mar Syst* 78:288-300

601 Linnebjerg JF, Fort J, Guilford T, Reuleaux A, Mosbech A, Frederiksen M (2013)
602 Sympatric breeding auks shift between dietary and spatial resource partitioning
603 across the annual cycle. *PloS one*, 8(8), e72987.

604 Lorentsen SH, May R (2012) Inter-breeding movements of common guillemots (*Uria*
605 *aalge*) suggest the Barents Sea is an important autumn staging and wintering area.
606 *Polar Biol* 35: 1713-1719

607 McFarlane Tranquilla LA, Montevecchi WA, Hedd A, Fifield DA, Burke CM, Smith
608 PA, Regular PM, Robertson GJ, Gaston AJ, Phillips RA (2013) Multiple-colony
609 winter habitat use by murre *Uria* spp. in the northwest Atlantic Ocean: implications
610 for marine risk assessment. *Mar Ecol Prog Ser* 472: 287-303

611 Mosbech A, Johansen KL, Bech NI, Lyngs P, Harding AM, Egevang C, Phillips RA,
612 Fort J (2012) Inter-breeding movements of little auks *Alle alle* reveal a key
613 post-breeding staging area in the Greenland Sea. *Polar Biol* 35:305-311

614 Mustapha MA, Saitoh S, Lihan T (2009) Satellite-measured seasonal variations in
615 primary production in the scallop-farming region of the Okhotsk Sea. *ICES J Mar*
616 *Sci* 66:1557-1569

617 Nagasawa K (1998) Fish and seabird predation on juvenile chum salmon

618 (*Oncorhynchus keta*) in Japanese coastal waters, and an evaluation of the impact. N
619 Pac Anadr Fish Comm Bull 1:480-495

620 Nagasawa K, Ueno Y, Sakai J, Mori J (1998) Autumn distribution of epipelagic fishes
621 and squids in the Okhotsk Sea and western North Pacific Ocean off the Kuril Islands
622 and southeast Hokkaido. Bull Nat Res Inst Far Seas Fish 35: 113-130

623 Nakanishi T, Minagawa M (2003) Stable carbon and nitrogen isotopic compositions of
624 sinking particles in the northeast Japan Sea. Geochemical Journal 37: 261-276.

625 Niizuma Y, Takahashi A, Kuroki M, Watanuki Y (1999) Sexing by external
626 measurements of adult rhinoceros auklets breeding in Teuri Island. Jpn J Ornithol
627 48:145-150

628 Ogi H (1980) The pelagic feeding ecology of thick-billed murrelets in the North Pacific,
629 March-June. Bull Facul Fisheries Hokkaido Univ 31:50-72

630 Pyle P (2009) Age determination and molt strategies in North American alcids. Mar
631 Ornithol 37:219-225

632 Radchenko VI, Dulepova EP, Figurkin AL, Katugin ON, Ohshima K, Nishioka J,
633 McKinnell SM, Tsoy AT (2010) Status and trends of the Sea of Okhotsk region,
634 2003-2008. In: McKinnell SM, Dagg MJ (eds) Marine ecosystems of the North
635 Pacific Ocean, 2003-2008. PICES Special Publication 4, Sidney, B.C, Canada. p
636 268-299

637 Rayner MJ, Taylor GA, Thompson DR, Torres LG, Sagar PM, Shaffer SA (2011)
638 Migration and diving activity in three non-breeding flesh-footed shearwaters
639 *Puffinus carneipes*. J Avian Biol 42:266-270.

640 Rayner MJ, Taylor GA, Gummer HD, Phillips RA, Sagar PM, Shaffer SA, Thompson
641 DR (2012) The breeding cycle, year-round distribution and activity patterns of the
642 endangered Chatham Petrel (*Pterodroma axillaris*). Emu 112: 107-116.

643 Sakurai Y, Ohshima KI, Ohtaishi N (2013) Ecosystem and its conservation in the Sea of
644 Okhotsk. Hokkaido University Press, Sapporo. (In Japanese with English abstract)

645 Sato H (1999) Seabirds affected by the oil pollution in the Japan Sea in January 1986. J
646 Yamashina Inst Ornithol 31:134-141 (In Japanese with English abstract)

647 Shaffer SA, Tremblay Y, Weimerskirch H, Scott D, Thompson DR, Sagar PM, Moller
648 H, Taylor GA, Foley DG, Block BA, Costa DP (2006) Migratory shearwaters
649 integrate oceanic resources across the Pacific Ocean in an endless summer. Proc Natl
650 Acad Sci USA 103: 12799-12802

651 Shirai M, Ito M, Yoda K, Niizuma Y (2013) Basal metabolic rate of the rhinoceros
652 auklet *Cerorhinca monocerata*, as measured using respirometry. Mar Ornithol 41:
653 151-153

654 Shuntov VP (2000) Seabird distribution in the marine domain. In: Kondratyev AY,
655 Litvinenko NM, Kaiser GW (eds) Seabirds of the Russian Far East. Canadian
656 Wildlife Service Special Publication. p 83-104.

657 Sorensen MC, Hipfner JM, Kyser TK, Norris DR (2010) Pre-breeding diet influences
658 ornament size in the Rhinoceros Auklet *Cerorhinca monocerata*. Ibis 152:29-37

659 Tanaka H, Takasuka A, Aoki I, Ohshimo S (2008) Geographical variations in the
660 trophic ecology of Japanese anchovy, *Engraulis japonicus*, inferred from carbon and
661 nitrogen stable isotope ratios. Mar Biol 154: 557-568

662 Thiebot JB, Lescroël A, Pinaud D, Trathan PN, Bost CA (2011) Larger foraging range
663 but similar habitat selection in non-breeding versus breeding sub-Antarctic penguins.
664 Antarct Sci 23: 117-126

665 Thiebot JB, Pinaud D (2010) Quantitative method to estimate species habitat use from

666 light-based geolocation data. *Endang Species Res* 10: 341-353
667 Wakefield ED, Phillips RA, Matthiopoulos J (2009) Quantifying habitat use and
668 preferences of pelagic seabirds using individual movement data: a review. *Mar Ecol*
669 *Prog Ser* 391:165-182
670 Watanuki Y, Ito M (2012) Climate effects on breeding seabirds of the northern Japan
671 Sea. *Mar Ecol Prog Ser* 454:183-196
672 Watanuki Y, Ito M, Deguchi T, Minobe S (2009) Climate-forced seasonal mismatch
673 between hatching of rhinoceros auklets and the availability of anchovy. *Mar Ecol*
674 *Prog Ser* 393:259-271
675 Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep-Sea*
676 *Res II* 54:211-223
677 Yamamoto T, Takahashi A, Katsumata N, Sato K, Trathan PN (2010) At-sea
678 distribution and behavior of streaked shearwaters (*Calonectris leucomelas*) during
679 the nonbreeding period. *Auk* 127: 871-881.
680 Yamamoto T, Takahashi A, Oka N, Iida T, Katsumata N, Sato K, Trathan PN (2011)
681 Foraging areas of streaked shearwaters in relation to seasonal changes in the marine
682 environment of the Northwestern Pacific: inter-colony and sex-related differences.
683 *Mar Ecol Prog Ser* 424: 191-204
684

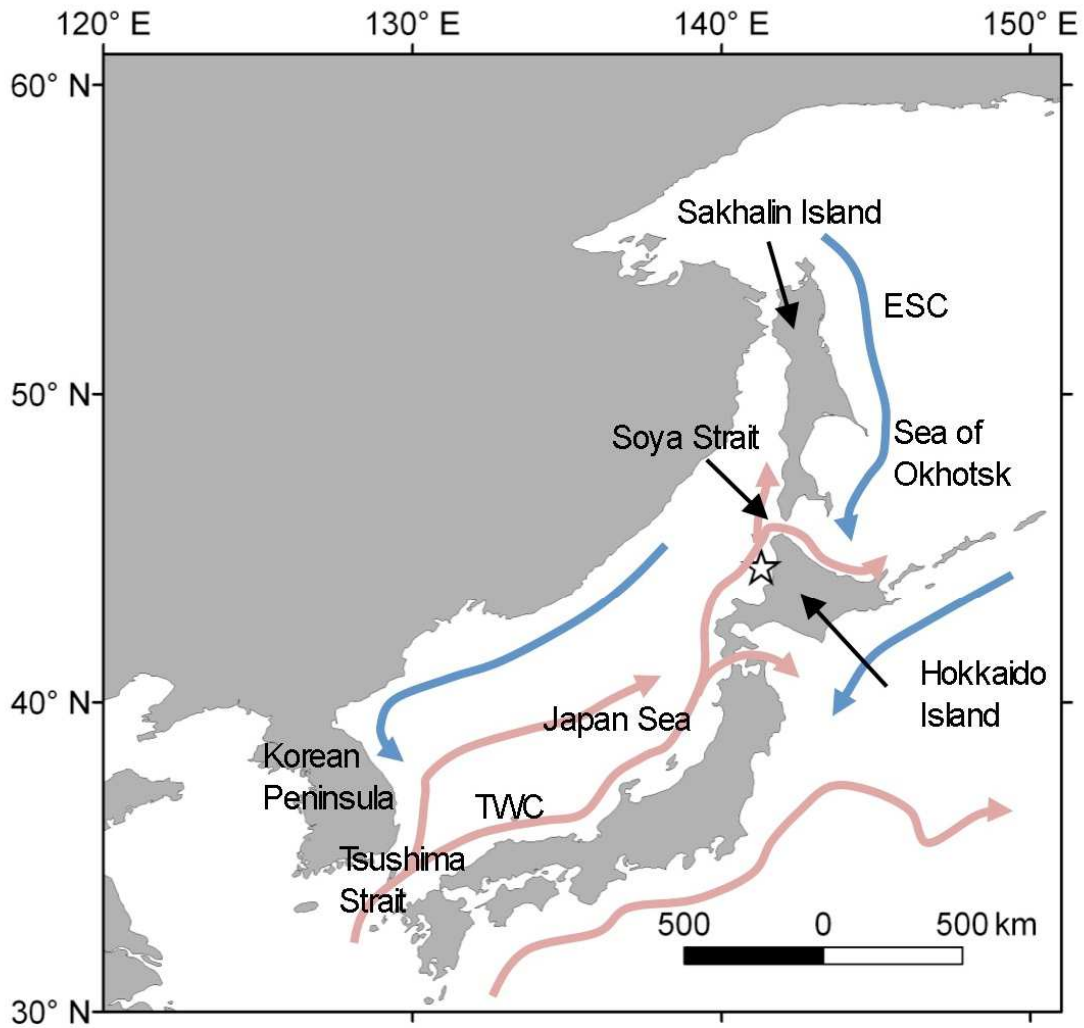


Figure 1

687
688
689 Fig. 1. *Cerorhinca monocerata*. Oceanographic features of study area. Warm and cold
690 currents displayed in pink and blue, respectively. TWC and ESC indicate the Tsushima
691 Warm Current and the East Sakhalin Current, mentioned in the text. Teuri Island
692 (breeding colony) is marked with a star.

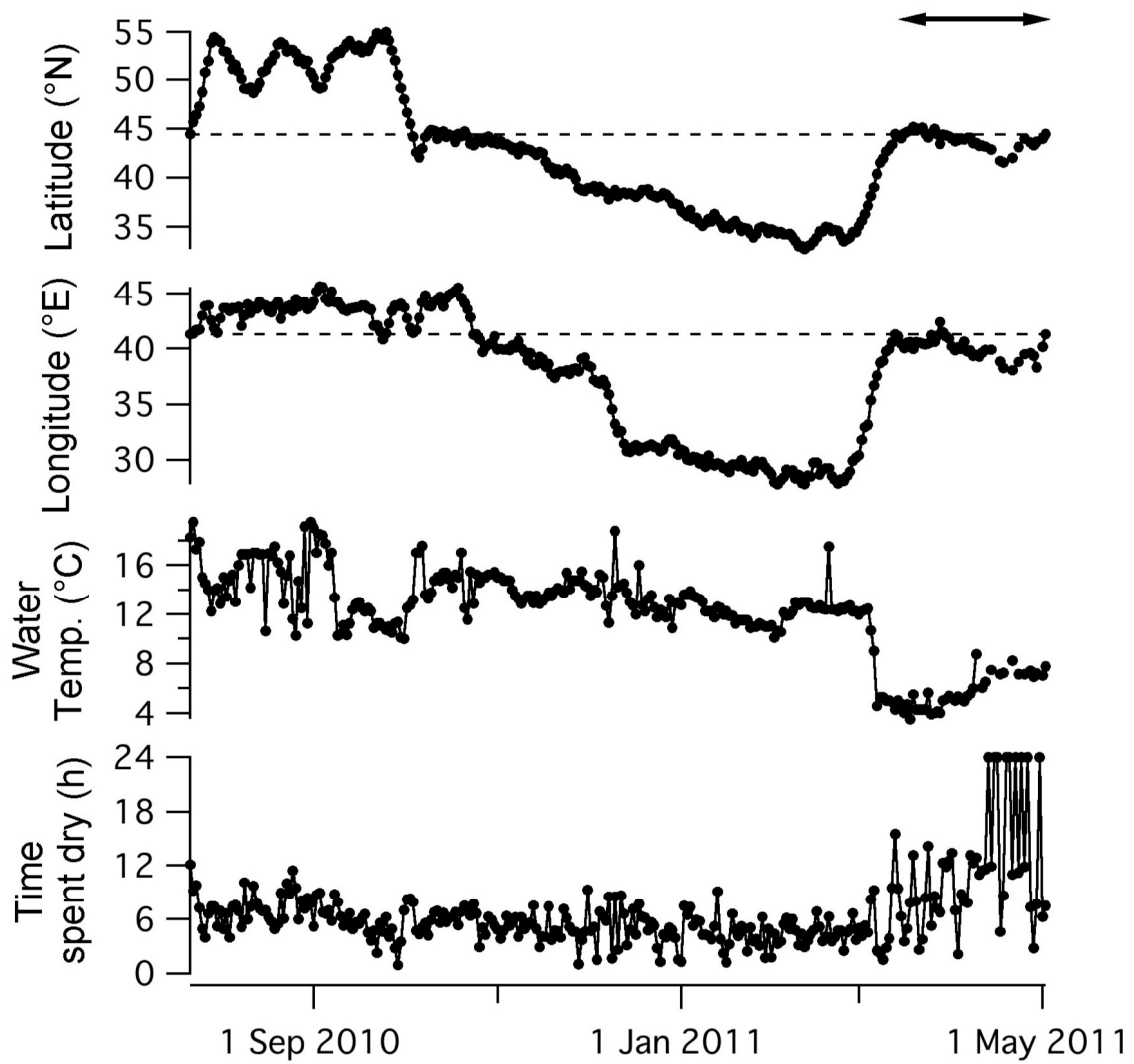


Figure 2

693
694
695
696
697
698
699
700
701

Fig. 2. *Cerorhinca monocerata*. An example of time-series data obtained by geolocators for one bird. Latitude and longitude were estimated using light level and water temperature, and were smoothed using a movement model (see Materials and Methods for details). Water temperature recorded by the geolocator and time spent dry per day are also shown. Horizontal arrows indicate the early breeding period (after the first return to the breeding colony).

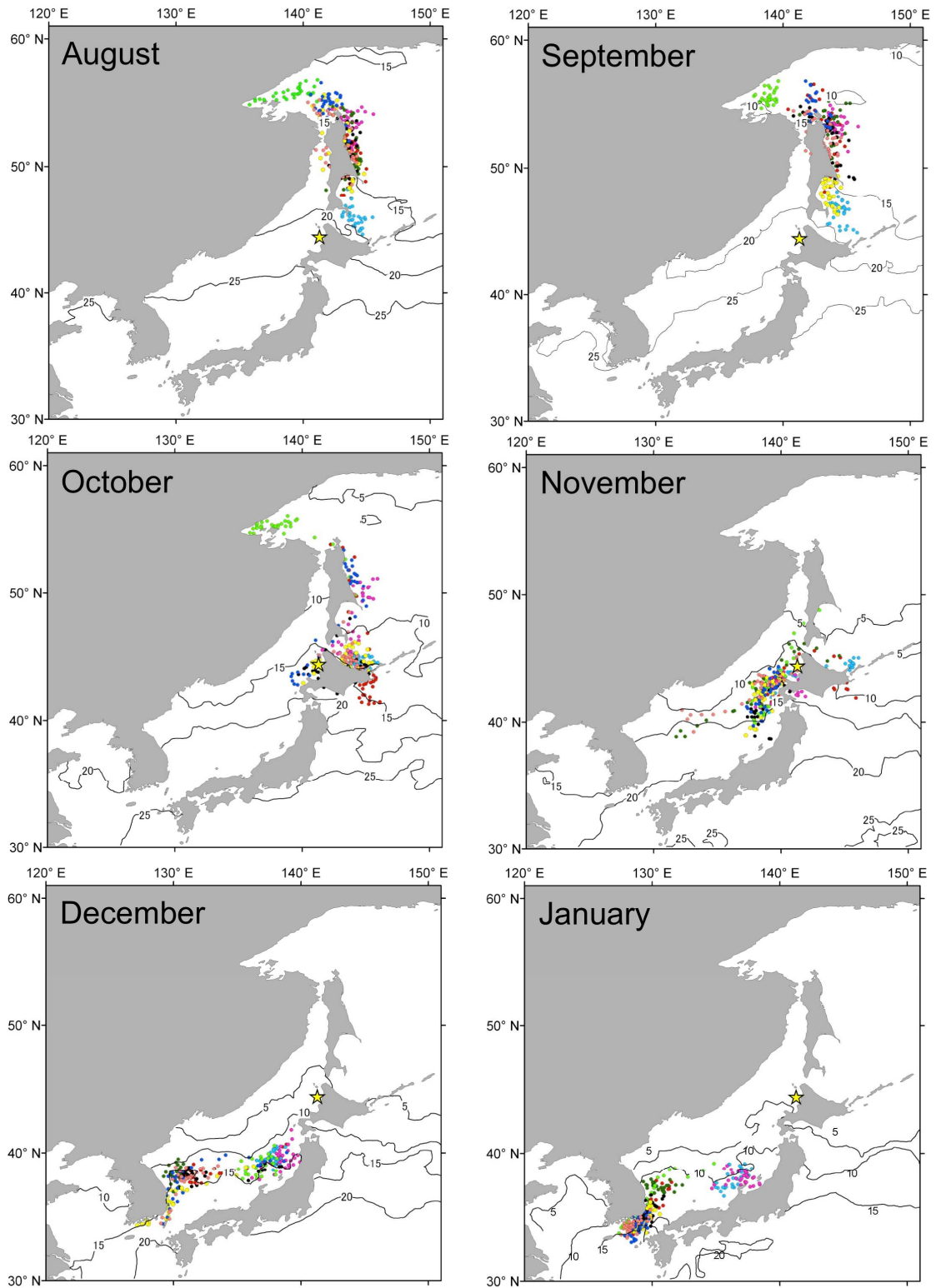


Figure 3

702
703

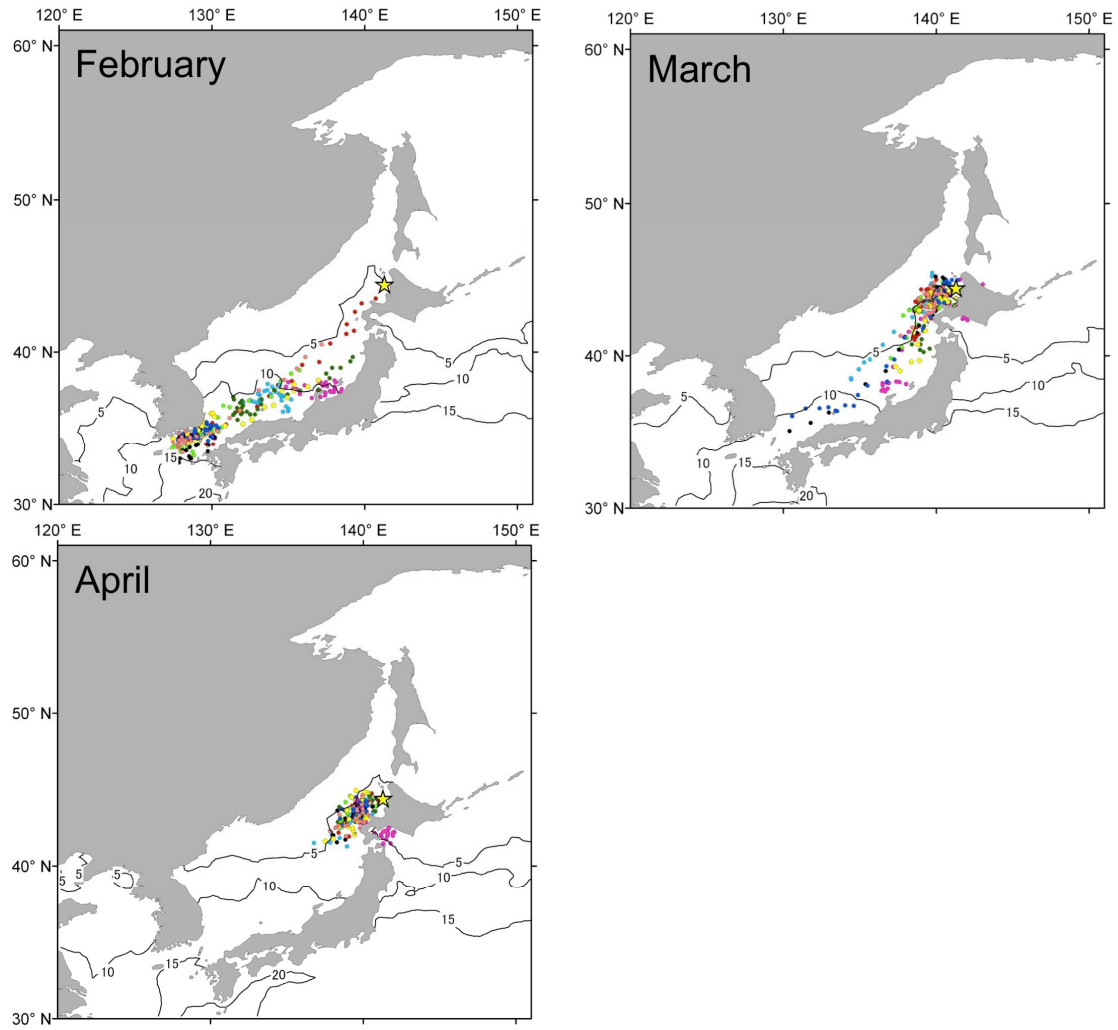


Figure 3 (continued)

704
705
706
707
708
709
710

Fig. 3. *Cerorhinca monocerata*. Monthly locations of nine rhinoceros auklets during the nonbreeding and early breeding periods in August 2010 – April 2011. Each colour shows locations from different individuals. Teuri Island is marked with a star. Satellite-derived monthly-averaged sea surface temperature contours are also shown.

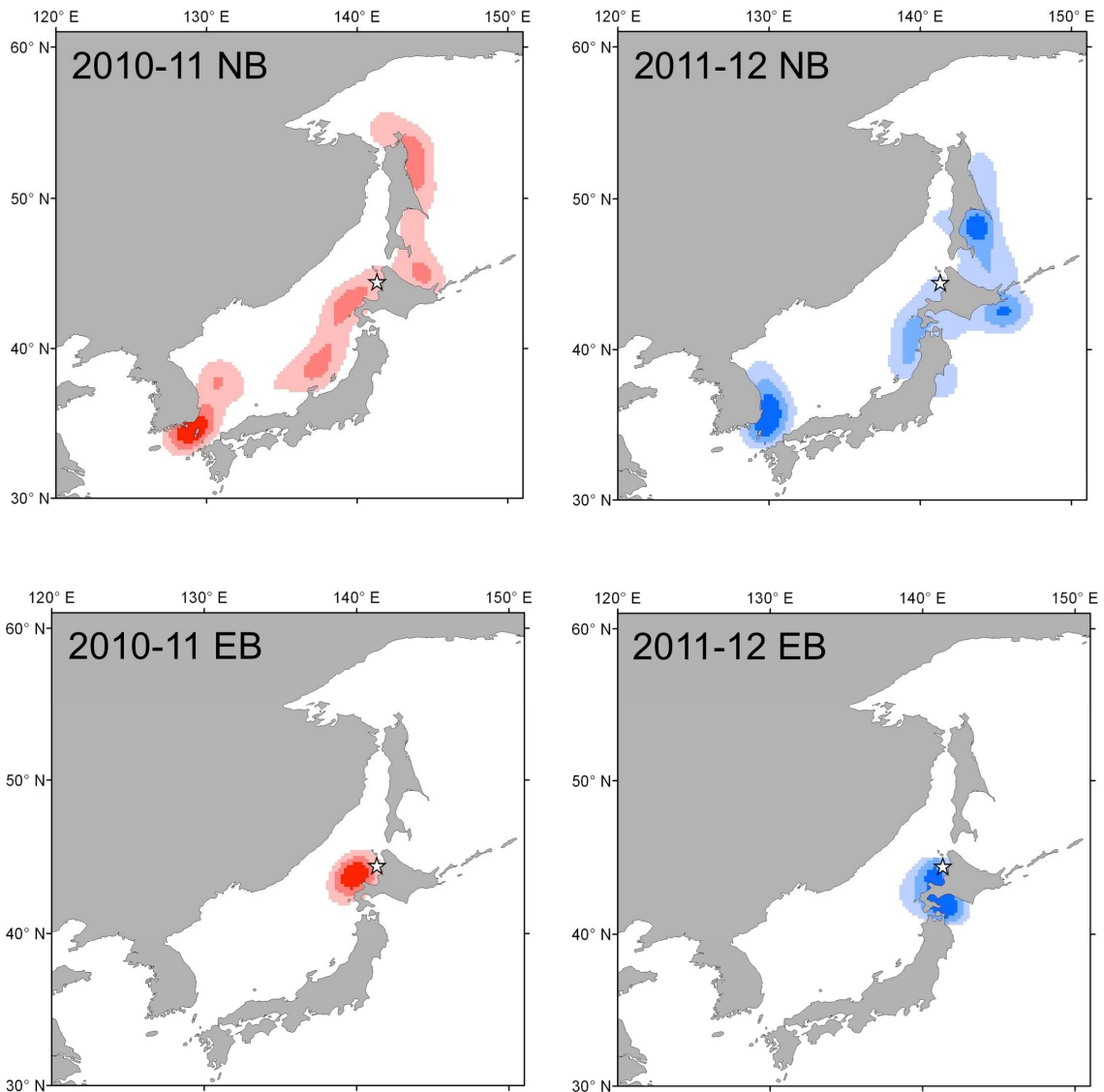


Figure 4

711
712
713
714
715
716
717

Fig. 4. *Cerorhinca monocerata*. Kernel density distribution of auklet locations during the nonbreeding (NB) and early breeding (EB) periods of first and second study year (2010-11 and 2011-12). Kernel densities indicate 25 %, 50 %, and 75 % from darker to lighter colours. Teuri Island is marked with a star.

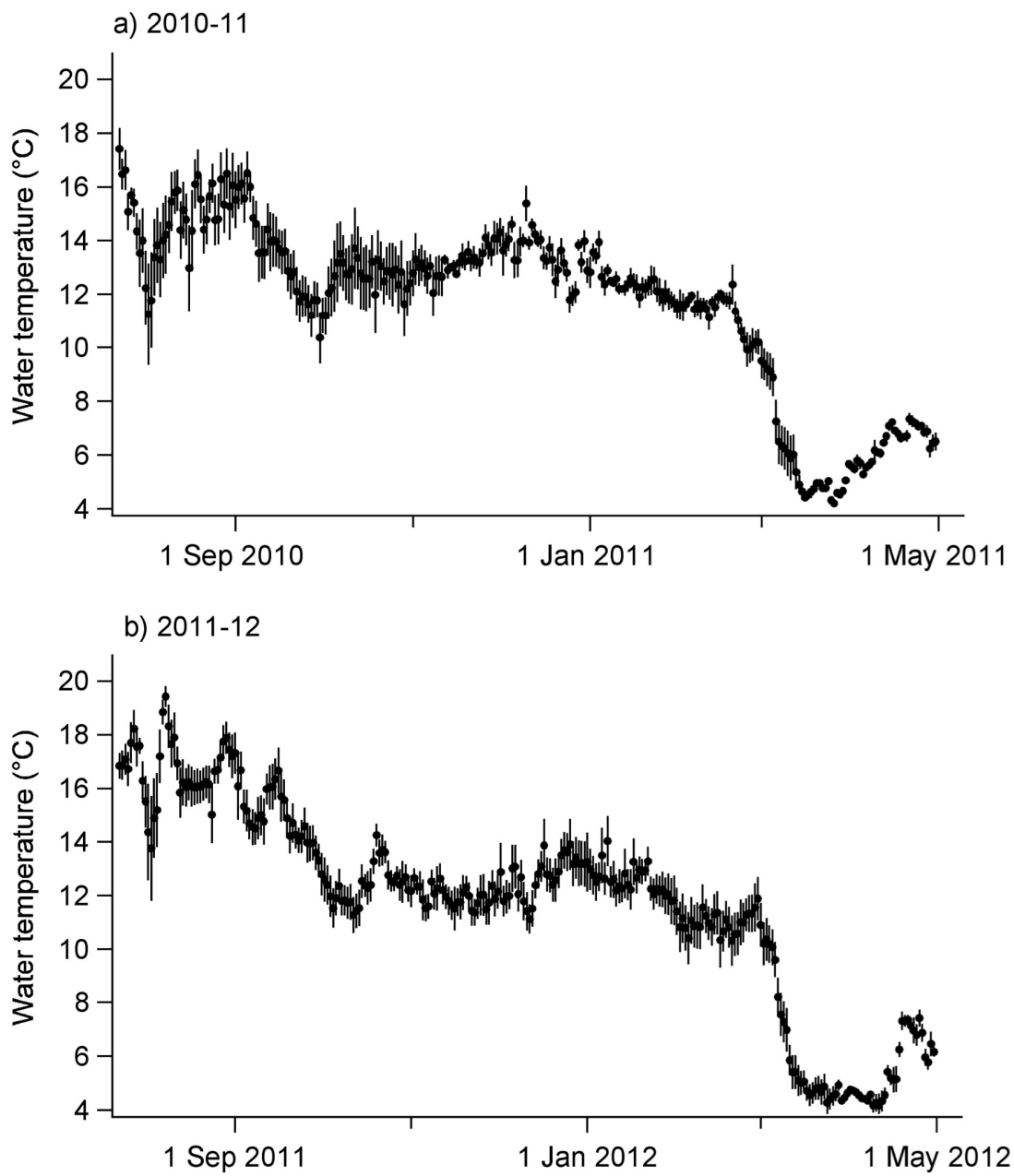


Figure 5

718
719
720
721
722
723

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

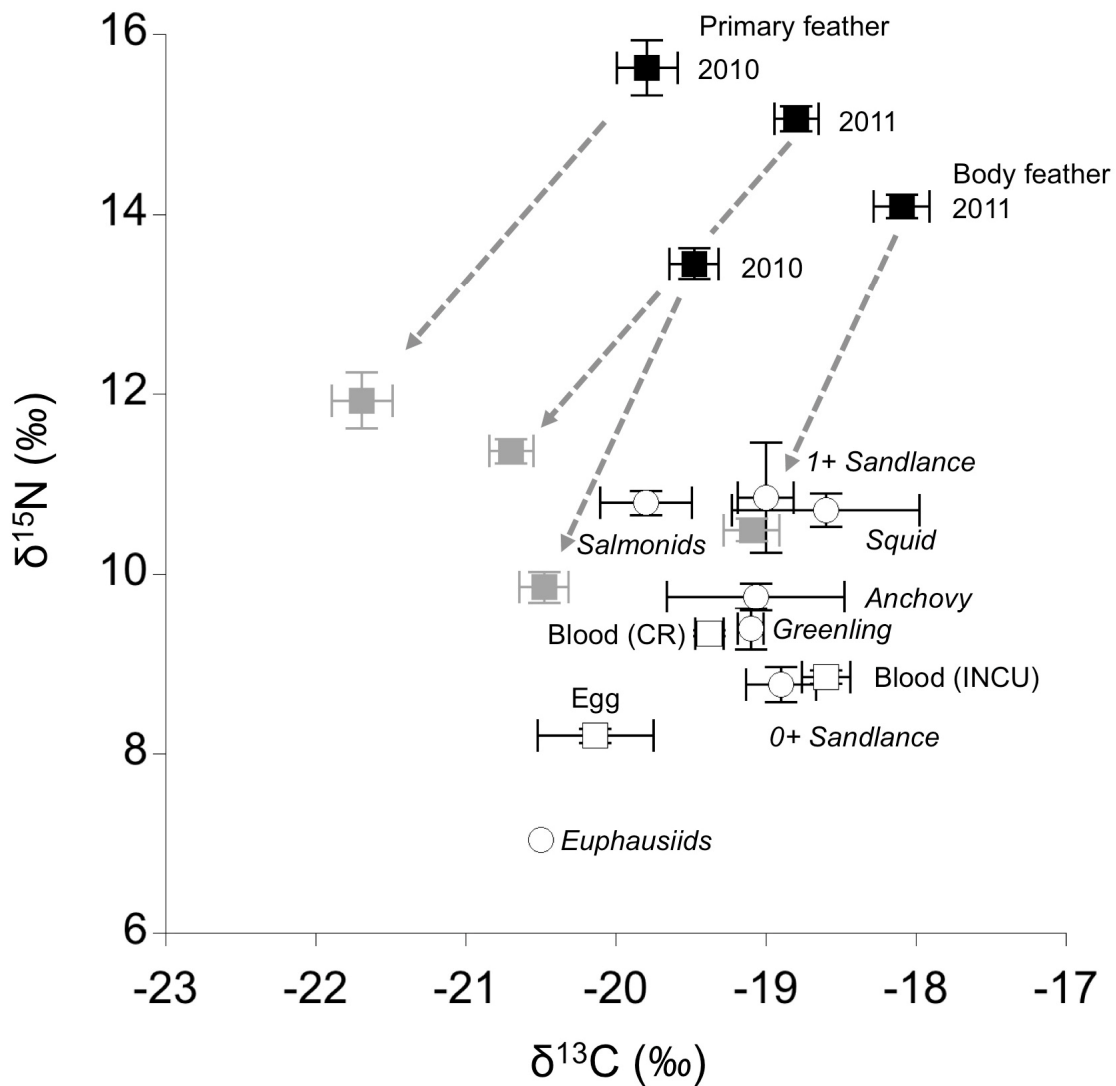


Figure 6

724
725
726
727
728
729
730
731
732
733
734
735
736

Fig. 6. *Cerorhinca monocerata*. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of primary and body feathers of rhinoceros auklets collected in 2010-11 and 2011-12, before (black closed squares) and after (grey closed squares) applying the adjustment of 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. The prey samples were obtained at the colony during the chick-rearing periods in 2004 and 2005 (Ito et al. 2009). Means \pm SE are shown. Isotopic values of prey, the egg and blood plasma of auklets (open symbols) are based on Ito et al. (2009, 2012).

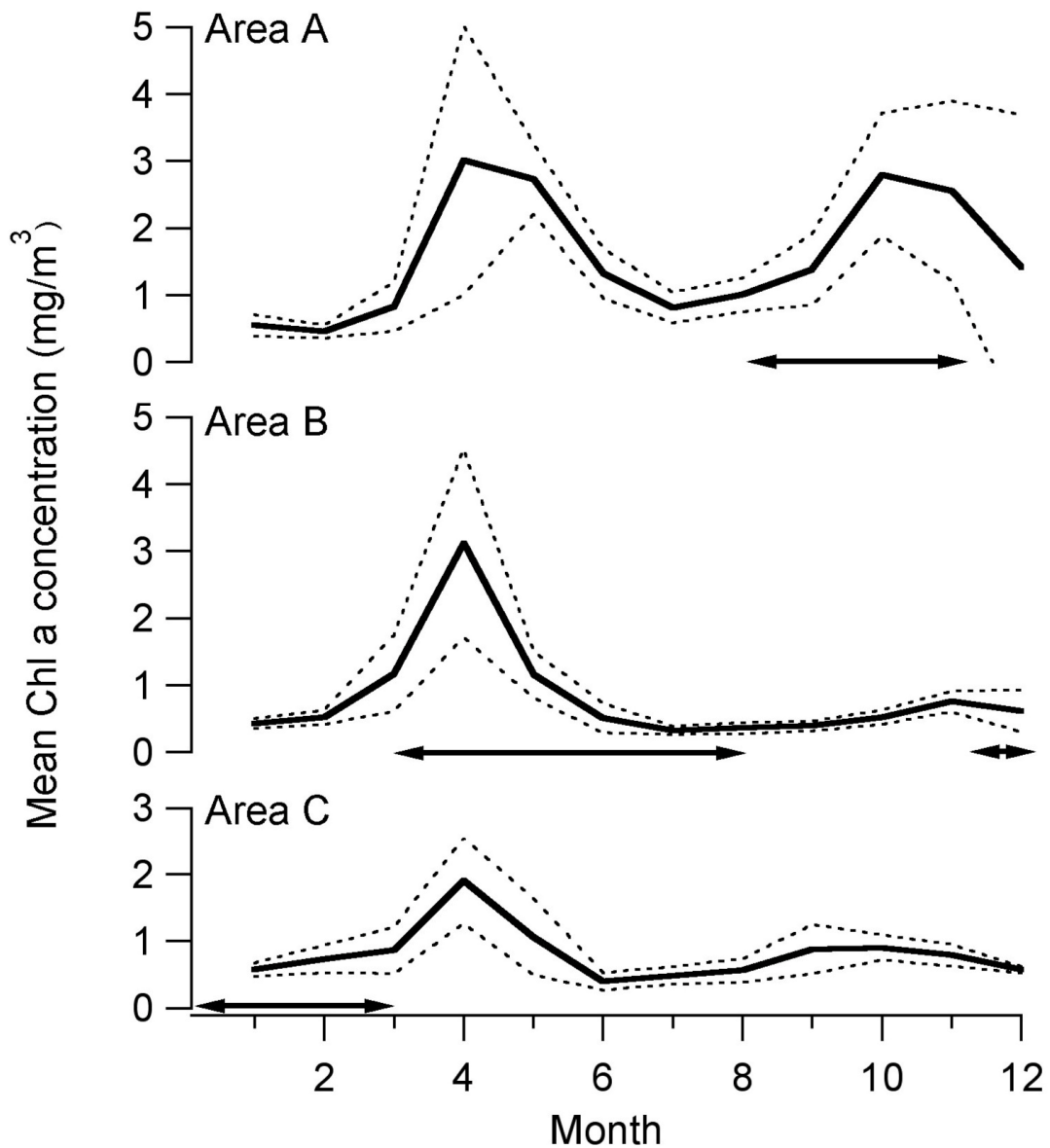


Figure 7

737
738
739
740
741
742
743
744
745
746
747

Fig. 7. *Cerorhinca monocerata*. Mean monthly-average chlorophyll a concentrations of three different foraging areas (defined by 50 % kernel boundary of auklet locations) in the Sea of Okhotsk (Area A) and the northern and southwestern Japan Sea (Areas B and C) over 10 years (2003-2012). 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 arrows below each graph show the approximate period when the auklets stayed in each of Area A, B, and C. Please refer to Fig. S1 for the locations of the Areas A-C. Note the occurrence of autumn bloom in Area A.

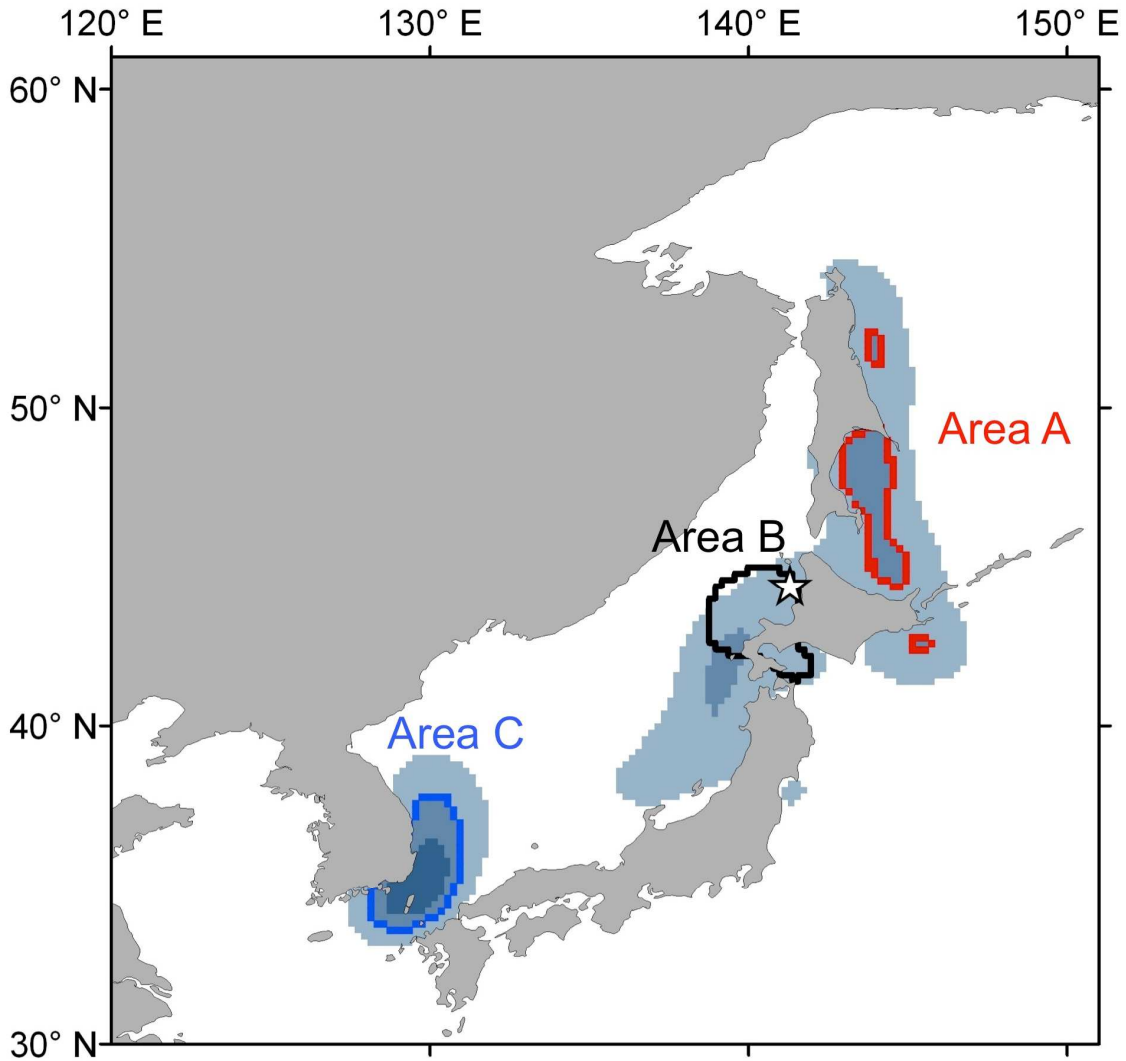


Figure S1

750
751
752
753
754
755
756
757
758

Fig. S1. Kernel density distribution of auklet locations during the nonbreeding period of the first and second study year combined (2010-11 and 2011-12 combined). Kernel densities indicate 25 %, 50 %, and 75 % from darker to lighter colours. Chlorophyll 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.