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# Annual and seasonal movements of migrating short-tailed shearwaters reflect environmental variation in sub-Arctic and Arctic waters

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<b>Abstract:</b>	<p>The marine ecosystems of the Bering Sea and adjacent southern Chukchi Sea are experiencing rapid changes due to recent reductions in sea ice. Short-tailed shearwaters <i>Puffinus tenuirostris</i> visit this region in huge numbers between the boreal summer and autumn during non-breeding season, and represent one of the dominant top predators. To understand the implications for this species of ongoing environmental change in the Pacific sub-Arctic and Arctic seas, we tracked the migratory movements of 19 and 24 birds in 2010 and 2011, respectively, using light-level geolocators. In both years, tracked birds occupied the western (Okhotsk Sea and Kuril Islands) and eastern (southeast Bering Sea) North Pacific from May to July. In August-September of 2010, but not 2011, a substantial proportion (68% of the tracked individuals in 2010 compared to 38% in 2011) moved through the Bering Strait to feed in the Chukchi Sea. Based on the correlation with oceanographic variables, the probability of shearwater occurrence was highest in waters with sea surface temperatures (SSTs) of 8-10 °C over shallow depths. Furthermore, shearwaters spent more time flying when SST was warmer than 9 °C, suggesting increased search effort for prey. We hypothesized that the northward shift in the distribution of shearwaters may have been related to temperature-driven changes in the abundance of their dominant prey, krill (Euphausiacea), as the timing of krill spawning coincides with the seasonal increase in water temperature. Our results indicate a flexible response of foraging birds to ongoing changes in the sub-Arctic and Arctic ecosystems.</p>

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4 environmental variation in sub-Arctic and Arctic waters

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23 **Abstract** The marine ecosystems of the Bering Sea and adjacent southern Chukchi Sea  
24 are experiencing rapid changes due to recent reductions in sea ice. Short-tailed  
25 shearwaters *Puffinus tenuirostris* visit this region in huge numbers between the boreal  
26 summer and autumn during non-breeding season, and represent one of the dominant top  
27 predators. To understand the implications for this species of ongoing environmental  
28 change in the Pacific sub-Arctic and Arctic seas, we tracked the migratory movements  
29 of 19 and 24 birds in 2010 and 2011, respectively, using light-level geolocators. In both  
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31 (southeast Bering Sea) North Pacific from May to July. In August–September of 2010,  
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37 9 °C, suggesting increased search effort for prey. We hypothesized that the northward  
38 shift in the distribution of shearwaters may have been related to temperature-driven  
39 changes in the abundance of their dominant prey, krill (Euphausiacea), as the timing of  
40 krill spawning coincides with the seasonal increase in water temperature. Our results  
41 indicate a flexible response of foraging birds to ongoing changes in the sub-Arctic and  
42 Arctic ecosystems.

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45 Introduction

46 The Bering and southern Chukchi seas are among the most productive marine  
47 ecosystems in the world (Highsmith and Coyle 1990; Grebmeier 2012; Hunt et al.  
48 2013). Reductions in sea ice have been particularly extensive in parts of this region  
49 (Shimada et al. 2006; Serreze et al. 2007; Steele et al. 2008; Grebmeier 2012; Post et al.  
50 2013), with changes in water temperature and ice cover affecting the seasonality and  
51 biomass of primary production, and hence the distribution and abundance of consumers  
52 (Hunt et al. 2002a; Grebmeier et al. 2006; Mueter and Litzow 2008; Hunt et al. 2011;  
53 Wassmann 2011; Wassmann et al. 2011; Grebmeier 2012). Among the latter, the top  
54 predators (homeothermic marine mammals and seabirds) are mobile and can potentially  
55 respond to a varying environment (e.g. a shift in distribution of prey) by switching  
56 foraging areas or diet; hence, different aspects of their behaviour can serve as useful  
57 indicators of fluctuations in the wider ecosystem (Iverson et al. 2007; Piatt et al. 2007).

58         The short-tailed shearwater *Puffinus tenuirostris* is a trans-equatorial migrant  
59 which breeds in southern Australia from October to March, and spends the  
60 non-breeding period from May to September in the northern North Pacific (Serventy  
61 1967; Carey et al. 2014). Up to 16 million birds are thought to migrate to the southern  
62 Bering Sea annually, and they represent one of the most abundant seabird species in the  
63 Pacific sub-Arctic and Arctic seas in summer and autumn (Schneider and Shuntov  
64 1993; Gall et al. 2013). During this time, they feed mainly on krill (Euphausiacea) (Ogi  
65 et al. 1980; Hunt et al. 2002b; Baduini et al. 2006; Toge et al. 2011), principally  
66 *Thysanoessa raschii* and to a lesser extent *T. inermis* (mid-water of 100–200 m) and *T.*

67 *longipes*, which are found in waters <100 m deep over the continental shelf, at  
68 100–200m, or >200 m, respectively; in addition, *T. raschii* and *T. inermis* are mainly  
69 found at high latitudes, including the Chukchi Sea, and *T. longipes* in waters off Japan,  
70 Okhotsk Sea, and Bering Sea (Nemoto 1962; Lindley 1980; Vidal and Smith 1986;  
71 Smith 1991).

72           As krill are important prey for many species in the northern North Pacific  
73 besides seabirds (e.g. walleye pollock *Theragra chalcogramma*), they play a key role in  
74 the food web, as major links in the energy transfer pathway from primary production to  
75 higher trophic levels (Aydin and Mueter 2007). Knowledge of the relationship between  
76 shearwater distribution and water mass may provide insights into the dynamics of krill  
77 abundance and distribution in this region. Previously, ship-based surveys showed that  
78 short-tailed shearwaters spend the non-breeding period foraging in waters north of  
79 Japan, the Okhotsk Sea, around the Kurile Islands, the northern North Pacific and  
80 southeastern Bering Sea; in addition, in August-September, birds are recorded in high  
81 densities in the Bering Strait and to as far north as Barrow, at the boundary between the  
82 Chukchi and the Beaufort Seas (e.g. Ogi et al. 1980; Piatt et al. 1991; Hunt et al. 1996;  
83 Piatt and Springer 2003; Kurasawa et al. 2011; Sigler et al. 2011; Gall et al. 2013).

84 However, as ship surveys are patchy in terms of spatial and temporal coverage, there is  
85 little detail on the seasonality of shearwater movements or on the environmental drivers.

86           An alternative approach for studying timing of migration, routes taken, and  
87 locations of stop-over and wintering areas etc. involves the tracking of individuals using  
88 light-based geolocation, which has been applied in recent years to numerous terrestrial

89 and marine taxa (e.g. Phillips et al. 2005; Shaffer et al. 2006; Stutchbury et al. 2009;  
90 Egevang et al. 2010). These studies can help elucidate habitat use during the  
91 non-breeding period, as well as identify key areas at sea that are species-specific, or  
92 represent ecologically or biologically important regions for multiple species or trophic  
93 levels (BirdLife International 2004; Le Corre et al. 2012). However, few previous  
94 studies have examined changes in non-breeding distribution in relation to seasonal and  
95 annual variation in the environment (Pinet et al. 2011; Jessopp et al. 2013). As  
96 migrating seabirds are mobile and not subject to central-place reproductive constraints  
97 during the non-breeding period, their distributions may better reflect the dynamic aspect  
98 of ecosystems than those of breeding birds, providing insights into changes in habitat  
99 suitability and possible responses at the population level to ongoing environmental  
100 change. Although Carey et al. (2014) used geolocators to provide the first data on the  
101 migratory behaviour of individual short-tailed shearwaters in 2008, birds were tracked  
102 for a single year and hence their movement patterns in response to annual changes in the  
103 marine environment were not measured, and as such, remain unknown.

104           In this study, we tracked individual movements of short-tailed shearwaters  
105 during the non-breeding period (from boreal summer to autumn) in the north Pacific for  
106 two years using geolocators. Seasonal and annual differences in their distribution and  
107 habitat use were analysed in the context of changes in the dynamic marine environment  
108 in the Pacific sub-Arctic and Arctic seas.

109

110 **Materials and methods**

111 Bird tracking

112 Fieldwork was carried out on Great Dog Island (40°15'S, 148°15'E; Tasmania,  
113 Australia). We captured 50 and 46 incubating short-tailed shearwaters (all different  
114 individuals) in early December 2009 and 2010, respectively, and fitted Mk15  
115 geolocation-immersion loggers (British Antarctic Survey, Cambridge, UK; hereafter  
116 loggers or geolocators), weighing 2.4 g, to the tarsus of each bird using an aluminium  
117 band modified according to Carey et al. (2009). The total mass of the geolocator with  
118 the leg band was 6.1g, which represented about 1% of the mean body mass of the birds  
119 ( $X \pm SD$ : 591  $\pm$  52 g,  $n = 96$ ). All birds were handled for less than 10 min, and then  
120 returned to their burrows. We recaptured 16 and 24 equipped birds from their nest  
121 burrows or nearby (burrows within 5 m of the original nest were searched) in early  
122 December 2010 and 2011, respectively. One geolocator was recovered from a bird  
123 equipped in 2009 that was found dead (cause unknown) on the coast of Australia. In  
124 addition, three birds equipped in 2009 were recaptured in 2011, providing data for two  
125 years. Data from three loggers recovered in 2011 were corrupted; consequently, usable  
126 data were available from the non-breeding period (May–September) for 19 birds in  
127 2010, and 24 birds in 2011, including 3 birds tracked for two seasons.

128

129 Data analysis

130 The geolocator measures light levels at 60 s intervals, and records the maximum value  
131 during each 10 min period. Immersion in seawater was tested every 3 s, and data  
132 integrated within each 10 min period, thereby providing a value from 0 to 200 that

133 represents the proportion of time spent wet. Water temperature was recorded every 10  
134 min after continuous immersion for 20 min. Light data were processed following the  
135 procedure in Yamamoto et al. (2010). Sunset and sunrise times were estimated from the  
136 thresholds in the light curves. Then, day length was used to estimate latitude and the  
137 relative timings of local noon and midnight were used to estimate longitude, providing  
138 two positions per day. Simultaneous deployment of geolocators with  
139 satellite-transmitters in polar regions has shown a mean location error of 186 km  
140 (Phillips et al. 2004). Locations were not available from light data around the equinoxes  
141 because of the inability to estimate latitude from day length at these times of year (Hill  
142 1994). During this period, latitude was therefore estimated by matching water  
143 temperature records from the loggers with remotely-sensed sea surface temperature  
144 (SST) data (8-day composite, 9 km resolution, measured by Aqua-MODIS, downloaded  
145 from the Ocean Color Web, <http://oceancolor.gsfc.nasa.gov>) at the median daily  
146 longitude. Daily positions were filtered according to a threshold speed of 50 km h<sup>-1</sup>  
147 (Spear and Ainley 1997), and missing locations were replaced using linear interpolation.

148           Due to the relative inaccuracy of geolocation (Phillips et al. 2004), we  
149 established utilization distributions of the tracked shearwaters for each month  
150 (May–September 2010 and 2011) by generating kernel density maps using the ESRI®  
151 ArcGIS Spatial Analyst tool, with a cell size of 50 km and a search radius of 200 km  
152 (Phillips et al. 2005). Although tracking data consist of presence locations only, this  
153 provides the utilization distribution as a probability gradient. Annual changes in  
154 foraging areas were compared by calculating the overlap of the core area (50% kernel



155 polygon) used in the same month between the two study years. To standardize the  
156 comparison, we calculated the relative density within a given month as a value from 0  
157 (minimum) to 1 (maximum), so that data from different months could be pooled for  
158 habitat modeling (see below).

159           Six environmental variables were included in models as potentially correlates  
160 or drivers of shearwater distribution: bathymetry (ETOPO1), monthly composite sea  
161 surface temperatures (SST: Pathfinder AVHRR), monthly composite chlorophyll *a*  
162 concentration (CHL: Aqua MODIS), monthly composite sea surface height anomalies  
163 (SSHA: AVISO), bathymetric gradient (shelf slope), and SST gradient (an index of  
164 frontal activity; hereafter "front"). Oceanographic data were obtained from satellite  
165 imagery via <http://coastwatch.pfel.noaa.gov/coastwatch/CWBrowserWW360.jsp>. Given  
166 the inherent error in geolocation, the mean value for each environmental covariate  
167 within 50 km grid cells was calculated to obtain a broadly similar spatial resolution to  
168 the geolocator positions. The mean and standard deviation of water depth and SST  
169 within each 50 km cell were used to calculate the coefficient of variation, used as the  
170 value for shelf slope and front, respectively. Analyses excluded all records with a  
171 missing value for any of the remotely-sensed environmental variables, which was  
172 usually the consequence of cloud cover during the relevant period. Collinearity was  
173 examined by calculating the correlation coefficient of paired explanatory variables  
174 using a Spearman's rank correlation matrix; as all correlation coefficients were <0.64,  
175 all variables were included as candidates in models.

176           Habitat use of short-tailed shearwaters during the non-breeding period was  
177 investigated using generalized additive models (GAMs) (Guisan et al. 2002). Values for  
178 the kernel density (ranging from 0 to 1) and oceanographic variables at each cell within  
179 the potential non-breeding habitat in the North Pacific (30°N–75°N by 130°E–125°W;  
180 Fig. 1) on the same month were determined. The data for each month (May–September  
181 2010 and 2011) were pooled into a single dataset (kernel density as the response, and  
182 the environmental variables as predictors), and a smoothed spline fit with all predictors  
183 was applied in GAMs, assuming a binomial distribution with the logit-link function.  
184 This analysis compared the characteristics of habitat where birds were present, relative  
185 to the possible locations during that time period. Models were ranked based on Akaike's  
186 Information Criterion (AIC). To test the importance of parameters, the change in  
187  $\chi^2$ -value between models (Žydelis et al. 2011) was measured with the full dataset  
188 (including data from both 2010 and 2011) and reduced datasets (data from either 2010  
189 or 2011) (Table 1).

190           The time spent in continuous flight was calculated from the logger immersion  
191 data. As these data can be used to determine whether a bird was flying, or on or under  
192 the water, we summed the number of consecutive complete dry events (i.e. records of  
193 0), representing the total length of each flight bout. GAMs with a Poisson error  
194 distribution were then used to predict changes in the time spent in continuous flight, as  
195 an index of the search effort (i.e. distances between prey patches), in relation to mean  
196 water temperature recorded by the logger on the same day, considering the flight time as  
197 a response variable and the temperature as an explanatory variable. This analysis, which

198 examines the activity of shearwaters in relation to water temperature, provides a  
199 potential indication of the responses to changes in krill availability. Statistical analyses  
200 were carried out in R software (version 2.15.3, R Development Core Team 2008).  
201 Habitat modeling and model evaluation were conducted using the R packages mgcv  
202 (Wood 2006) and MuMIn (Bartoń 2013).

203

## 204 Results

### 205 At-sea distribution: seasonal and annual differences

206 Most short-tailed shearwaters departed the breeding latitude (40 °S) in April, spent the  
207 main non-breeding period (May–September) in the northern North Pacific (north of  
208 40°N), and began their return migration to colonies from late September to early  
209 October (Fig. 1). During the non-breeding period, the tracked short-tailed shearwaters  
210 used waters from the northwestern Pacific to southern Okhotsk Sea, and from the  
211 Aleutian Islands to southern Chukchi Sea (Fig. 2). The core area of their distribution  
212 (within the 50% kernel density contour) was in the southern Okhotsk Sea and around  
213 the Kuril Islands from May to August, and also the eastern Bering Sea from June to  
214 August (Fig. 2). In September, their distribution was concentrated over the southwest  
215 Chukchi Sea in 2010 (Fig. 2e), but in the same month in 2011 was further south around  
216 the northern Bering Sea and Bering Strait, extending over a wider region from the North  
217 Pacific to northern Chukchi Sea, and from the Okhotsk Sea to off Barrow (Fig. 2j).  
218 Relatively high densities were also apparent around the Aleutian Islands in September  
219 (Fig. 2e, j). Comparing the two years, core areas overlapped to a higher degree from

220 May to July (42–95%), than in August and September (9–31%). At the individual level,  
221 shearwaters showed two different movement patterns; using waters either towards the  
222 east coast of Japan, or in the south-central Bering Sea around the Aleutian Islands (ESM  
223 1). Some birds that migrated initially to waters off Japan or the eastern Bering Sea later  
224 moved to the Aleutian Islands or into the Chukchi Sea, whereas birds never moved to  
225 waters off Japan after spending time in the Bering Sea or Aleutian Islands. In  
226 August–September, 13 of 19 birds (68%) moved into the Chukchi Sea in 2010, but only  
227 nine of 24 birds (38%) in 2011. Individuals tracked for two years showed broadly the  
228 same migratory patterns in terms of space and time between the years (ESM 2).  
229 However, the core area of their distribution in August–September appeared to differ  
230 between two years, as their distributions were more concentrated in northern areas in  
231 2010 than in 2011.

232

### 233 Environmental characteristics

234 Overall, short-tailed shearwaters appeared to utilize a wide range of habitats throughout  
235 the non-breeding period in the North Pacific (Fig. 3). The tracked birds were distributed  
236 over areas with SSTs of 0–25 °C in both years, and showed a seasonal pattern in habitat  
237 use, tending to be associated with increasingly warm waters until August, and then with  
238 cooler waters in September. In the North Pacific, they were distributed primarily over  
239 shallow depths (>200 m), but also occupied relatively deep waters of <5,000 m in May  
240 and August (Fig. 3), probably during the post-breeding migration to the North Pacific,  
241 and while in the eastern North Pacific (Aleutian Islands, southeastern Bering Sea, and

242 Chukchi Sea) (Fig. 2, ESM 1). Primary productivity in the areas used by the  
243 shearwaters increased from May to July, but then decreased towards September. There  
244 were no clear seasonal trends in the other environmental variables, and shearwater  
245 densities were not related to SSHA, front, or shelf slope (Fig. 3).

246           The best-fitting model predicting the oceanographic habitat of short-tailed  
247 shearwaters during the non-breeding period included water depth, productivity, SST,  
248 front, and SSHA. Based on the comparison of  $\chi^2$  values, the probability of shearwater  
249 occurrence varied mainly with changes in SST and water depth, and to a lesser extent,  
250 primary productivity and front (Table 1, Fig. 4). According to model response curves,  
251 the probability of occurrence was highest at SSTs of 8–10 °C at shallow (>200 m) and  
252 mid-range depths (1,000–2,000 m) (Fig. 4). Although the model also suggested that  
253 shearwater occurrence increases again over very deep water (<6,000 m), this is not  
254 reliable given the wide confidence interval. The model response curves did not show  
255 clear relationships between shearwater occurrence and the other variables.

256           In the North Pacific, SST -the dynamic environmental variable that was most  
257 closely related to the distribution of tracked birds- increased seasonally from summer to  
258 autumn. Based on the maps of SST distribution in July–September 2010 and 2011 (Fig.  
259 5), the surface temperatures over the shelf region of the Bering Sea (>200 m depth)  
260 were relatively cool in 2011 than in 2010. In particular, SSTs along the Alaskan coast,  
261 including waters off Barrow, were warmer in September 2010 than in 2011 (Fig. 5c, f),  
262 when shearwater distribution was more concentrated in the northern Bering Sea and  
263 Chukchi Sea (Fig. 2e, j). The duration of bouts of continuous flight changed in relation

264 to water temperature, with more time flying in areas of water temperatures warmer than  
265 9 °C (Fig. 6).

266

## 267 Discussion

268 The overall patterns of migratory movements by the short-tailed shearwaters in our  
269 study was broadly similar to that reported by Carey et al. (2014); birds started the  
270 northward migration in the mid–late April, spent May–mid September in areas that  
271 ranged from waters off Japan to the northern Bering Sea and the Chukchi Sea, and  
272 began their return migration in late September–early October. Although the accuracy of  
273 geolocation is relatively low regardless of whether latitudes are light-based or estimated  
274 using water temperatures (Phillips et al. 2004, Teo et al. 2004) and our data were  
275 limited to a single breeding colony, our analyses nevertheless show convincingly that  
276 the shifts in at-sea distribution of the tracked birds were related to seasonal and annual  
277 changes in the marine environment of the Pacific sub-Arctic and Arctic seas. Ship-based  
278 surveys may provide valuable quantitative data on at-sea distribution of seabirds at finer  
279 spatial scales (Gall et al. 2013; Wong et al. 2014), but do not allow individuals to be  
280 followed for long periods, or reveal the dynamics of seabird movements beyond the  
281 areas surveyed.

282           At the end of the breeding season, the short-tailed shearwaters tracked from  
283 the Great Dog colony in Tasmania migrated north to spend May–July in waters of the  
284 western (Okhotsk Sea and around the Kuril Islands) and eastern (southeast Bering Sea)  
285 North Pacific, predominantly over the shelf. This distribution was broadly similar to

286 that suggested in previous analyses of at-sea survey data (Schneider et al. 1986;  
287 Schneider 1997; Schneider and Shuntov 1993; Kurasawa et al. 2011). In the Northern  
288 Hemisphere, short-tailed shearwaters feed predominantly on krill, particularly *T. raschii*  
289 and *T. inermis*, and to a lesser extent, *T. longipes* (Ogi et al. 1980; Hunt et al. 2002b;  
290 Baduini et al. 2006). *T. raschii* is generally found in waters <100 m deep over the  
291 continental shelf, *T. inermis* in mid-water (~150-200 m deep), and *T. longipes* in pelagic  
292 regions (>200 m bottom depth) (Nemoto 1962; Lindley 1980; Vidal and Smith 1986;  
293 Smith 1991). Krill are usually abundant and widespread in shelf regions, especially in  
294 the southeast Bering Sea (Sigler et al. 2012).

295           From August to September, the tracked shearwaters moved into the southern  
296 Chukchi Sea. This seasonal change in their distribution appeared to coincide with the  
297 change in availability of their main prey. Krill forms surface mating swarms usually at  
298 depths of 30–45 m (Smith and Adams 1988; Hanamura et al. 1989; Hunt et al. 1996;  
299 Vlietstra et al. 2005), which are accessible to short-tailed shearwaters that can dive up to  
300 70 m (Weimerskirch and Cherel 1998). Spawning of high-latitude krill species is  
301 coupled with the onset of the phytoplankton bloom, usually in April–May in the  
302 Okhotsk and Bering seas (Ponomareva 1966; Smith 1991). Although the density of  
303 shearwaters was not related to remotely-sensed values for primary productivity, this is  
304 probably because of the lag between the timing of plankton blooms and increased prey  
305 abundance at higher trophic levels (Stafford et al. 2010). Because the timing of krill  
306 spawning progresses across the shelf, coincident with the seasonal increase in water  
307 temperature (Smith 1991), krill biomass increases and peaks relatively late in the

308 northern Bering Sea (Berline et al. 2008). Krill are likely to cease swarming when SSTs  
309 become warm ( $>7-10$  °C for *T. inermis*), and they descend to deep and cool water  
310 (Hanamura et al. 1989; Kotori 1994; Iguchi and Ikeda 2004). Thus, if warm SST  
311 reduces the availability of krill for short-tailed shearwaters, this would explain the  
312 overall northward shift in their distribution from summer to autumn. This hypothesis  
313 was also supported, in part, by the analysis of foraging behaviour, as the tracked  
314 shearwaters increased the duration of bouts of continuous flight in areas with water  
315 temperatures  $>9$  °C. Activity patterns of seabirds (e.g. time spent in flight, and landings  
316 on the water surface) appear to reflect resource availability (i.e. prey abundance and  
317 distances between patches) and hence foraging effort (Weimerskirch et al. 2005; Phalan  
318 et al. 2007; Mackley et al. 2010). The changes in activity of short-tailed shearwaters  
319 suggested that availability of krill within the birds' diving range decreases with  
320 increasing water temperatures, and, consequently, that their search effort probably has  
321 to increase because foraging is efficient only where krill occur in high density swarms  
322 (Lovvorn et al. 2001).

323           Although *Thysanoessa* spp. are endemic to the Bering and Okhotsk seas  
324 (Brinton 1962; Ponomareva 1966; Dalpadado and Skjoldal 1991), large zooplankton  
325 including krill (mainly *T. raschii* and *T. inermis*) are transported into the southern  
326 Chukchi Sea through the Bering Strait during summer at the confluence of the Alaskan  
327 Coastal, Anadyr and Bering Shelf water masses (Springer et al. 1989; Piatt and Springer  
328 2003; Grebmeier et al. 2006; Berline et al. 2008). Transport rates are assumed to peak in  
329 late July or early August (Hunt et al. 2013). Although direct observations of seasonal



330 abundance of krill in the southern Chukchi Sea are limited, several previous studies  
331 confirm the presence of krill in autumn (Bluhm et al. 2007; Hopcroft et al. 2010; Eisner  
332 et al. 2013), and aggregations or movements of other krill-eating predators (including  
333 fish, seabirds, and whales) into the region at this time of year (Moore et al. 1995; Lowry  
334 et al. 2004; Bluhm et al. 2007; Moss et al. 2009; Gall et al. 2013; Hunt et al. 2013).

335         The distribution of short-tailed shearwaters in September was concentrated in  
336 more northwesterly waters, between the Bering Strait and western Chukchi Sea, in 2010,  
337 whereas birds were more widely distributed in the Chukchi Sea, including waters off the  
338 Barrow in 2011. Annual variation in the abundance of short-tailed shearwaters in the  
339 northeastern Chukchi Sea has also been reported by Gall et al. (2013). In our study, the  
340 surface temperatures over the shelf region (<200 m depth) which were the core areas  
341 used by short-tailed shearwaters in the Bering and Chukchi seas were warmer in 2010  
342 than in 2011, particularly along the Alaskan coast, including waters off the Barrow (Fig.  
343 5c, f). As such, differences in SST might explain the annual variation in shearwater  
344 distribution in the Chukchi Sea, as short-tailed shearwaters movements appear to follow  
345 the temperature-driven changes in the abundance or availability of krill (see above). The  
346 volume of Pacific water transported north through the Bering Strait appears to have a  
347 major influence not only on water temperature in the southern Chukchi Sea (Woodgate  
348 et al. 2010), but also on the biomass of zooplankton that enters this region (Berline et al.  
349 2008; Matsuno et al. 2012). The mean transport rate was actually higher in 2011,  
350 leading to increased warming of mid to deep, but not surface waters (Woodgate et al.  
351 2012). The inverse relationship between temperatures in the lower layer and the surface

352 might reflect increased vertical mixing that resulted in cooler SST in 2011 (Woodgate et  
353 al. 2012). Both planktivorous and piscivorous seabirds appear to prefer foraging in  
354 well-stratified water where prey are likely to be concentrated (Piatt and Springer 2003).  
355 In addition, low seabird abundance in the Chukchi Sea has in the past been associated  
356 with cooler water temperatures and weak stratification (Gall et al. 2013). Presumably  
357 the tracked short-tailed shearwaters moved north in order to utilize the relatively high  
358 food concentrations available after the main bloom in the south had passed. Shearwaters  
359 must have sufficient energy reserves prior to the southward migration to complete the  
360 long journey (ca. 18 days) (Carey et al. 2014), because, as in the sooty shearwater  
361 *Puffinus griseus*, tracked birds do not appear to stop for intensive refueling en route  
362 (Shaffer et al. 2006).

363           Although the general pattern was of a northerly movement, nevertheless, a  
364 proportion of the tracked short-tailed shearwaters also used waters in the Okhotsk Sea  
365 and around the Aleutian Islands until September. The shallow channels of the Aleutian  
366 Islands are known to generate localized physical features such as eddies and fronts  
367 (Coyle 2005; Vlietstra et al. 2005). Frontal regions generally enhance phytoplankton  
368 production which supports the food necessary to sustain mating swarms of krill long  
369 after near-surface phytoplankton concentrations elsewhere have decreased, and thus  
370 may ensure high availability of zooplankton for prolonged periods for planktivorous  
371 predators including short-tailed shearwaters (Coyle and Cooney 1993; Schneider and  
372 Shuntov 1993; Hunt et al. 1996; Jahncke et al. 2005; Vlietstra et al. 2005). Also, frontal  
373 systems appear to entrain krill in shallow water through physical processes that make

374 them accessible for shearwaters (Hunt et al. 1996, 1998; Ladd et al. 2005; Vlietstra et al.  
375 2005). However, we were not able to detect a clear effect of frontal strength on  
376 shearwater distribution, possibly due to the relatively low spatial resolution of  
377 geolocation (mean error of ca. 100–150 km: Phillips et al. 2004; Teo et al. 2004)  
378 compared with the scale of frontal features (often <10s of kilometers: Ladd et al. 2005;  
379 Vlietstra et al. 2005).

380           Another factor for which we could not account that might explain shearwater  
381 distribution relates to their diet diversity and capacity for prey switching. Previous  
382 studies reported that, in addition to krill, short-tailed shearwaters also feed on a wide  
383 range of alternative prey (sandlance *Ammodytes hexapterus*, age-0 walleye pollock,  
384 copepods, and amphipods *Parathemisto libellula*) (Ogi et al. 1980; Hunt et al. 1996,  
385 2002b; Baduini et al. 2006). In the southeast Bering Sea, the importance of these other  
386 prey may increase when the availability of krill is low during a warm year (Baduini et al.  
387 2001; Coyle and Pinchuk 2002; Hunt et al. 2002b). In addition, the main prey species  
388 varies among regions, and for example is fish in waters around the Kuril Islands (Ogi et  
389 al. 1980). Therefore, the response of the shearwaters to seasonal changes in physical  
390 and biological conditions is likely to depend on the region, due to differences in the  
391 annual cycle and environmental association of their particular prey.

392           In this study, the seasonal distribution of short-tailed shearwaters did not  
393 appear to relate to distance from the sea ice edge in the Pacific sub-Arctic and Arctic  
394 seas (Fig. 2), though we did not consider the distance to sea ice as an explanatory  
395 variable in the habitat analysis because birds arrived in the southeastern Bering Sea long

396 after the retreat of sea ice through the Bering Strait, and left the northern Bering Sea and  
397 southern Chukchi Sea during the period of minimum sea ice extent in these regions  
398 (September: Grebmeier et al. 2006) (Figs. 1, 2). Nevertheless, our study indicated that  
399 short-tailed shearwaters might follow seasonal availability of krill that is driven to some  
400 extent by changes in sea ice timing and extent, which affects water temperatures and  
401 primary productivity (Smith 1991; Deibel and Daly 2007). Our results indicate a  
402 flexible response of foraging birds to ongoing changes in the sub-Arctic and Arctic  
403 ecosystems. This is also implied, in part, from the limited samples of individuals that  
404 were tracked for two non-breeding season; they showed a broadly similar  
405 spatio-temporal movement patterns in both years, but utilized more northern areas in  
406 2010 (ESM 2) when SSTs were relatively warmer over the shelf (Fig. 5). Hence, the  
407 expected future reduction in sea ice will possibly shift the distribution of shearwaters  
408 northwards. The movements of this species may therefore provide a useful indicator of  
409 wider ecosystem changes, especially in krill availability, in this region, unless other  
410 environmental changes associated with reduced sea ice result in a shift in diet of  
411 short-tailed shearwaters from krill to other types of prey (Hunt et al. 2002b). Given the  
412 huge numbers of shearwaters that migrate to this region, changes in the size or species  
413 composition of their diet, as well as in their foraging locations, may have a top-down  
414 influence on the abundance or distribution of their prey (Ressler et al. 2012), with  
415 potentially major effects on energy transfer pathways in local marine ecosystems, and  
416 on food web structure in general (Schneider et al. 1986; Aydin and Mueter 2007).  
417

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427

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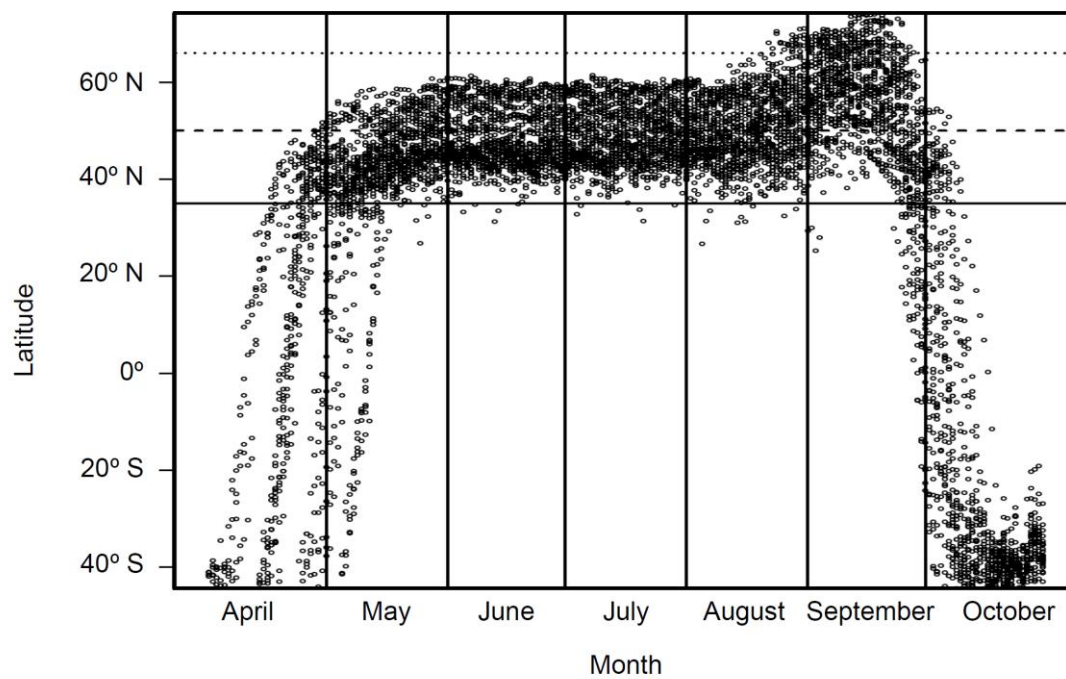


Fig. 1 Latitudinal movements of short-tailed shearwaters between the breeding colony (40°15'S) and the North Pacific during the non-breeding period (April to October).

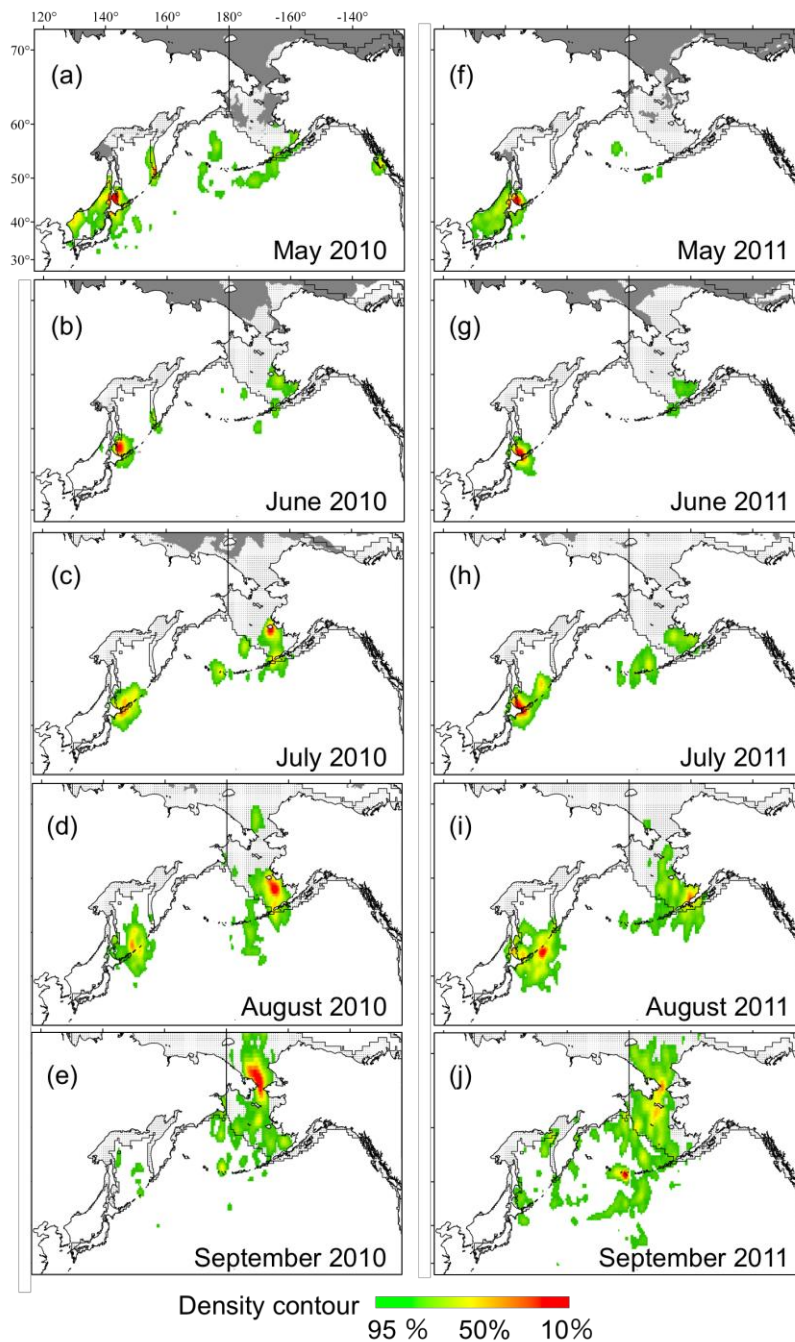


Fig. 2 Seasonal changes in at-sea distribution of tracked short-tailed shearwaters during the non-breeding period in (a) May 2010, (b) June 2010, (c) July 2010, (d) August 2010, (e) September 2010, (f) May 2011, (g) June 2011, (h) July 2011, (i) August 2011, and (j) September 2011. Density distribution of the tracked shearwaters are shown in relation to the extent of water of <200 m depth contour (dotted area bordered by thin lines) and >10% sea ice concentration (AMSER-E).

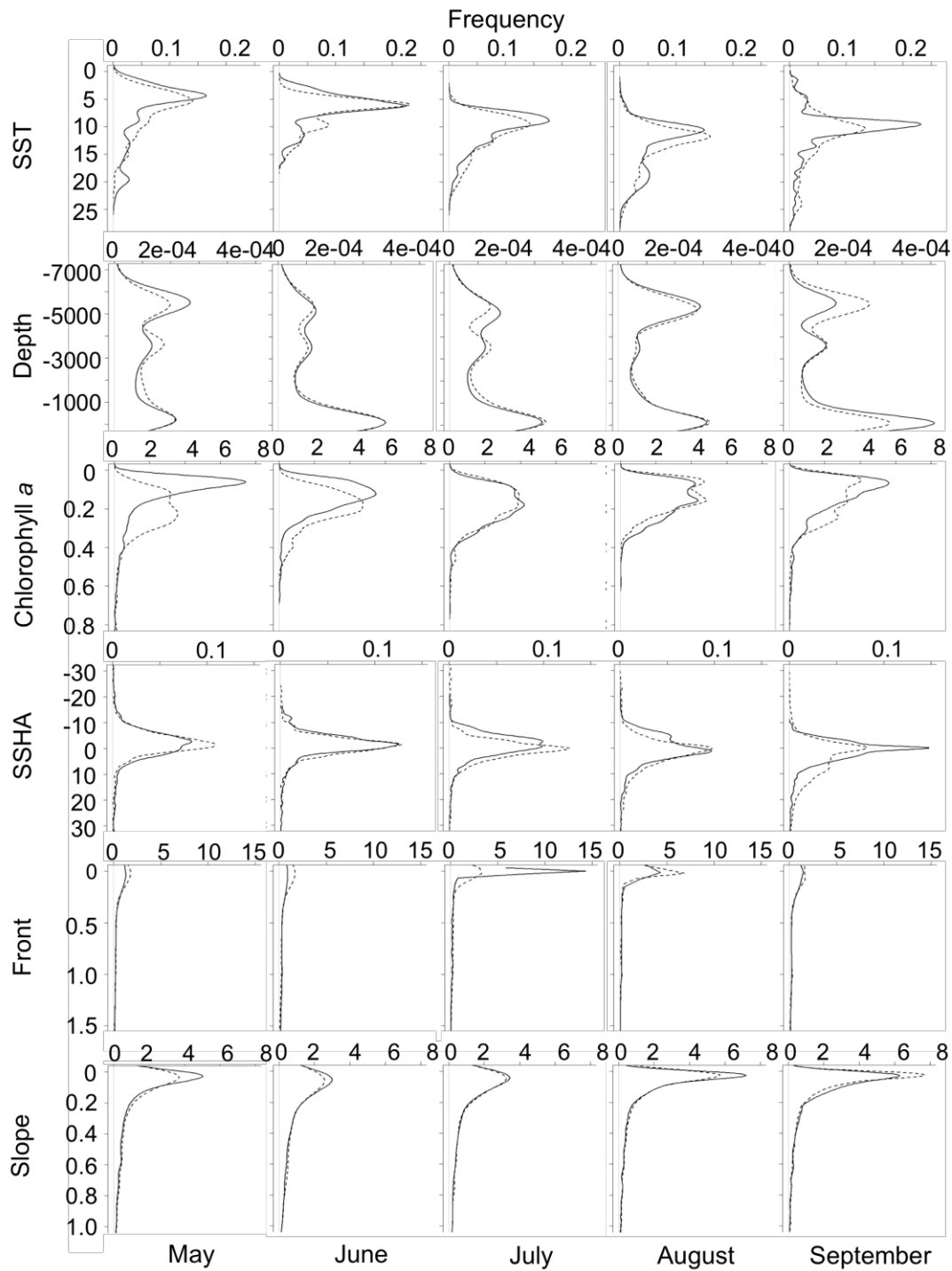


Fig. 3 Smoothed histograms of six environmental variables within 95% kernel density distribution of the tracked short-tailed shearwaters for each month (May-September 2010 (black lines) and 2011 (dashed lines)): sea surface temperature (SST), bathymetry (depth), chlorophyll a concentration (productivity), sea surface height anomalies (SSHA), SST gradient (front), and bathymetry gradient (slope).

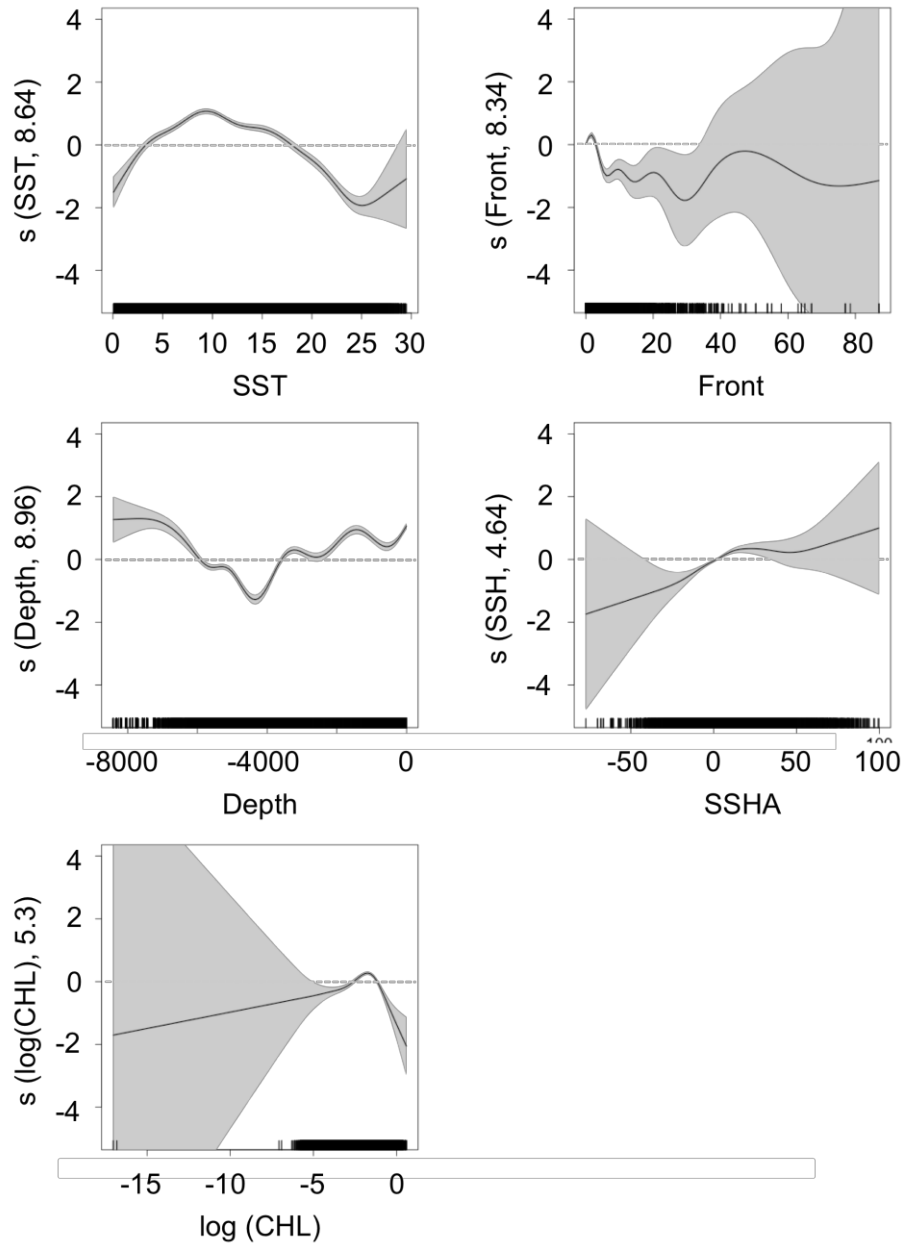


Fig. 4 Response curves of the five influential variables in the oceanographic habitat model (GAM) of short-tailed shearwaters tracked during the non-breeding period.

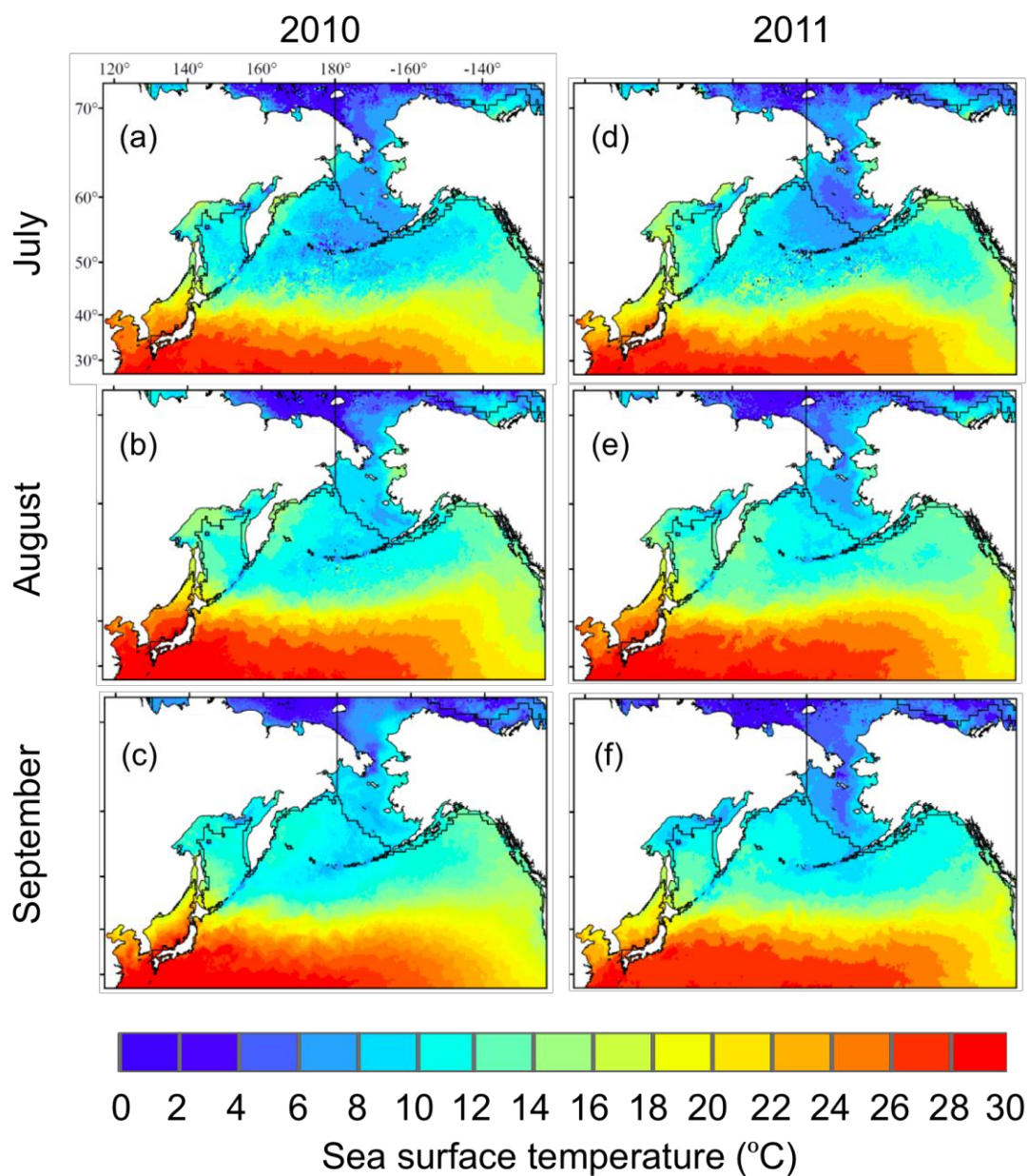


Fig. 5 Seasonal and annual differences in sea surface temperatures (SST: AVHRR) in the non-breeding range of short-tailed shearwaters: (a) July 2010, (b) August 2010, (c) September 2010, (d) July 2011, (e) August 2011, and (f) September 2011. The black color indicates areas where no data was available, or SSTs cooler than 0 °C or warmer than 30 °C.

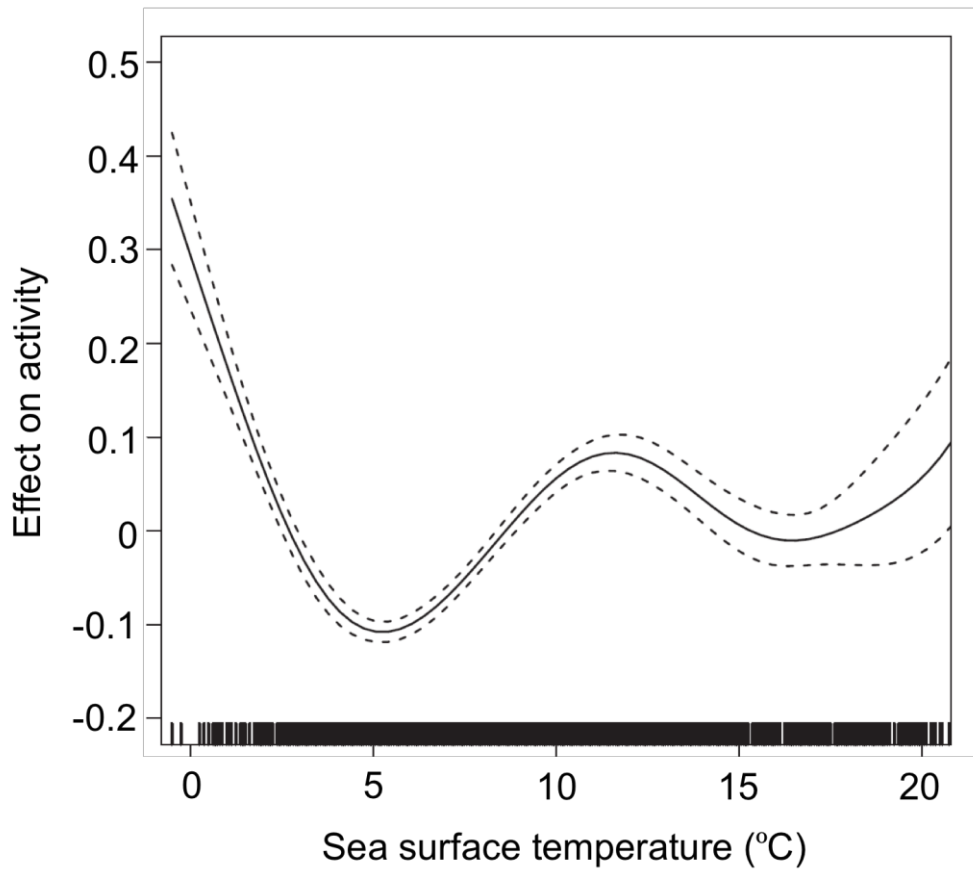


Fig. 6 Fitted relationship between at-sea activity (time spent in continuous flight) and water temperature of short-tailed shearwaters tracked during the non-breeding period.

Table 1 Estimates of parameter Chi-square values and significance of the most plausible habitat models of tracked short-tailed shearwaters using the reduced (either data in 2010 or 2011) and full (data both in 2010 and 2011) datasets. Dashes indicate variables that were eliminated during the process of model selection using AIC.

Variable	2010 dataset		2011 dataset		2010 & 2011 dataset	
	$\chi^2$	$P$	$\chi^2$	$P$	$\chi^2$	$P$
Depth	388.5	<0.01	394.1	<0.01	746.7	<0.01
Slope	-	-	-	-	-	-
Productivity	142.6	<0.01	50.2	<0.01	172.0	<0.01
SST	383.4	<0.01	632.9	<0.01	931.8	<0.01
Front	122.7	<0.01	84.8	<0.01	186.2	<0.01
SSH	30.2	<0.01	160.7	<0.01	88.2	<0.01
AIC	7513		7320		14914	

Electronic Supplementary Material (Tables, Figures, Video, Movie, Audio, etc.)

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