ORIGINAL PAPER

Hierarchical foraging strategies of migratory short-tailed shearwaters during the non-breeding stage

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Abstract

Foraging specialisations are common in animal populations, because they increase the rate at which individuals acquire food from a known and reliable source. Foraging plasticity, however, may also be important in variable or changing environments. To better understand how seabirds might respond to changing environmental conditions, we assessed how plastic the foraging behaviours of short-tailed shearwaters (*Ardenna tenuirostris*) were during their non-breeding season. To do this, we tracked 60 birds using global location sensing loggers (GLS) over a single year between 2012 and 2016 with the exception of 8 individuals that were tracked over 2 consecutive years. Birds predominantly foraged in either the Sea of Okhotsk/North Pacific Ocean (Western strategy) or the southeast Bering Sea/North Pacific (Eastern strategy). The eight birds tracked for 2 consecutive years all returned to the same core areas, indicating that these birds were faithful to foraging areas between years, although the time spent there varied, probably in response to local changes in food availability. Overall, 50% of the birds we tracked left their core area towards the end of the non-breeding period, moving into the Chukchi Sea, suggesting that the birds have flexible intra-seasonal foraging strategies whereby they follow prey aggregations. We hypothesise that seasonal declines in chlorophyll *a* concentrations in their primary core foraging areas coincide with changes in the availability of large-bodied krill, an important food source for short-tailed shearwaters. Decreasing prey abundance likely prompts the movement of birds out of their core foraging areas in search of food elsewhere. This strategy, through which individuals initially return to familiar areas but disperse if food is limited, provides a mechanism that allows the birds to respond to the effects of climate variability.

Keywords Seabirds · Climate change · Foraging · Plasticity · Bering Sea · Migratory

Introduction

Knowing where individuals find their food and how they adapt their foraging strategies in response to changes in prey distribution and abundance is an important component of animal ecological studies. Physical features such as fronts, continental shelves and slope areas, and sites of up-welling are important to marine predators as they can provide predictable, dense aggregations of prey for marine predators in otherwise ephemeral environments (Lea et al. 2006; Weimerskirch 2007; Bost et al. 2009; Lee et al. 2017). Accordingly, marine predators tend to show fidelity to these features (Nel et al. 2001; Queiroz et al. 2012; Patrick and Weimerskirch 2014). When individuals repeatedly return to the same foraging sites, they gain experience in how to find prey in that habitat, increasing foraging efficiency (Piper 2011; Phillips et al. 2017). Consequently, foraging site fidelity can be maintained over a number of days to months and these sites may be revisited over many years (Bradshaw et al. 2004; Auge et al. 2014; Arthur et al. 2015; Samarra et al. 2017).

The sites to which individuals show fidelity during the non-breeding stage are important, because the amount of energy accrued can influence short-term survival and subsequent reproductive output (Harrison et al. 2011; Shoji et al.

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2015; Fayet et al. 2016b; Abrahms et al. 2018). For marine predators that migrate after breeding to exploit remote, seasonally available resources, the costs of migration must be outweighed by energy gained in the non-breeding habitat (Cox 1985; Ramenofsky and Wingfield 2007; Lea et al. 2015). Therefore, returning to familiar sites (Irons 1998) could reduce searching time and increase the rate at which prey is encountered. However, if environmental conditions change unidirectionally, then high levels of site fidelity could be disadvantageous (Irons 1998; Bolnick et al. 2003; Forcada et al. 2008; Travis et al. 2013). Under such conditions, a strategy where animals are initially faithful to known areas, *i.e.* sites where they have previously found food, and then disperse to new areas if resources are poor or limited, may increase prey encounters within a season (Switzer 1993). Nonetheless, determining foraging site fidelity in wild animals is not straightforward because it is difficult to follow individuals over multiple years and the degree of individual site fidelity is likely to differ greatly within populations. Some of this variation in site fidelity could be explained under the win-stay–lose-shift (WSLS) strategy framework, where an individual returns to its most recent foraging area only if the previous visit was profitable (Bonnet-Lebrun et al. 2021), much like the hierarchical strategy outlined above.

The migratory short-tailed shearwater (*Ardenna tenuirostris*) is a long-lived seabird that breeds in colonies in southern Australia and spends the non-breeding stage, May to October, in the North Pacific Ocean (Skira 1991). During this time, short-tailed shearwaters go to the Sea of Japan, the Bering Sea, the Gulf of Alaska and the Chukchi Sea (Carey et al. 2014; Yamamoto et al. 2015). The existence of a number of foraging areas within the population may allow short-tailed shearwaters to maximise foraging success both during and amongst years. The environmental conditions in the regions in the Northern Hemisphere that are used by short-tailed shearwaters have undergone considerable environmental change in recent decades (Grebmeier et al. 2006; Overland et al. 2008; Brown et al. 2011; Ogi et al. 2015), causing shifts in sea ice dynamics, the location and timing of spring phytoplankton blooms, water column temperature and stratification (Brown et al. 2011; Hunt et al. 2011; Duffy-Anderson et al. 2017). These all influence the distribution and abundance of prey upon which shearwaters and other meso-predators such as seabirds and marine mammals rely (Trites and Donnelly 2003; Grebmeier et al. 2006; Bluhm and Gradinger 2008; Gall et al. 2017).

Using a 5-year tracking dataset on shearwaters in Tasmania, Australia, we described the non-breeding foraging areas in the northern Pacific Ocean of short-tailed shearwaters to determine: (i) the core foraging areas of shearwaters in the North Pacific, (ii) whether individual birds use different foraging sites during their post-breeding foraging trips; (iii) if individual birds maintain fidelity to these areas between years; (iv) if and how foraging areas affect the level of bird activity; (v) the environmental characteristics within the foraging areas; and (vi) whether environmental conditions in these broad foraging sites changed intra-annually and across our 5-year study.

Methods

Global location sensors (GLS)

Shearwater movements and distribution during the non-breeding season were estimated with global location sensing (GLS) devices attached to birds at Wedge Island, southeast Tasmania, Australia (43° 07' S, 147° 40' E) from 2011 to 2015. The GLS devices were deployed on average for 11 months (range 7–52 months) (Table S1). Three types of GLS devices were used over the course of the study, all of which collected ambient light, activity (wet/dry events) and sea surface temperature data (SST; − 0.125 °C resolution), which were used to estimate twice daily locations (Hill 1994). The C250 tags recorded water temperature when the device had been continuously wet for 20 min, and the minimum, maximum and mean measurements were taken every 4 h, allowing the data to be compared to remotely sensed SST. The MK19 and MK3005 tags provided temperature data when the device had been submerged for 25 min. Recording stopped if the sensor was dry for 6 s or longer. The C250 tags sampled every 6 s and recorded the total number of seconds the device was wet/dry on change of state from wet to dry and dry to wet. The MK19 and MK3005 tags recorded activity data on state change (within three seconds), if the state persisted for longer than 6 s. All loggers recorded activity data based on the relative time that they were in seawater (wet), which was used to infer foraging behaviour; either foraging or resting on the water surface, compared to when they were flying (dry).

Tags were attached to the tarsus after Cleeland et al. (2014). The maximum weight of the tag and attachment was 4.5 g, < 1% of the mean mass (597.1 ± 57.3 g, $n = 421$) of the birds. Tags were calibrated at the deployment site by placing them under the open sky for 2 to 7 days prior to deployment to provide light recordings at a known location allowing for accurate estimation of sun elevation (Lisovski et al. 2012). A subset of non-tagged birds ($n = 74$) were weighed using a 1 kg (± 5 g) Salter spring balance (Super Samson models, Salter Australia Pty Ltd, Melbourne, Australia) and compared with those of tagged birds to check for device effects at the end of the return migration. A total of 141 GLS tags were deployed during the breeding season (Table 1) and 93 GLS tags were retrieved during subsequent breeding seasons except for one individual found in South Australia in

Table 1 The year, the model and the number of GLS devices deployed on and retrieved from short-tailed shearwaters at Wedge Island

Year	Model	GLS deployed[a]	GLS recovered	Tracks included in analyses[b,c]	Activity data included in analyses[d]
2012	MK19	15	10	8	0
2013	MK3005	30	13	10*	4
2014	MK3005	32	27	7**	5
2015	MK3005 & C250	64	38	39	38
2016	C250	NA	5	4***	0
Total	**–**	**141**	**93**	**68**	**47**

(a) Excluding birds only tracked for the breeding season

(b) Some tags failed during deployment and consequently did not provide data for the entire non-breeding stage. Data were only included if available for ~80% of the non-breeding stage, resulting in 60 birds being included in analyses

(c) Includes data from eight individuals that were tracked for two consecutive non-breeding stages

(d) The tags used in this study had limited capacity to store activity data (~7 months). In the instances where the logger had been deployed during the breeding season and/or for multiple years, the tag ceased recording activity data prior to the end of the non-breeding stage. Individual activity data were only included if available for ~80% of the non-breeding stage

*Includes data from three devices retrieved in 2013 that were deployed during 2012 (providing consecutive non-breeding stage data)

**Includes data of a device retrieved in 2014 that was deployed during 2013 (providing consecutive non-breeding stage data)

***Data from five devices retrieved in 2016 that were deployed in 2015 (providing consecutive non-breeding stage data)

2013. Tags were recovered from eight birds after 2 years. Overall, a total of 60 devices provided data that were used in analyses.

Location estimation

Daily positions were estimated from the light and SST values in the R package SGAT (https://github.com/SWotherspoon/SGAT) (Sumner et al. 2009; Wotherspoon et al. 2013). Because the tags deployed on these birds were attached to their leg, the sensor was sometimes shaded by the bird, so anomalous data were, therefore, manually adjusted to match the overall trend in the light level prior to twilight. Similarly, anomalously high SST values were removed using the *SST-filter* and *selectData* functions in SGAT.

The package SGAT is based on a Bayesian framework that uses Markov Chain Monte Carlo (MCMC) methods to estimate the posterior distribution of locations (Sumner et al. 2009). The locations for each bird were estimated (and 95% CI) from the pre-processed light data using a set of priors that included: (i) a spatial probability mask, to exclude locations on land, (ii) a movement model where the average speed of travel between successive locations was assumed to be Gamma distributed, the probability of distribution of speeds is estimated using the mean time intervals between twilights (in hours), limiting the distance between locations (set at 80 km h^{-1}), (iii) to improve accuracy of location data, SST was used to constrain the location estimation. The final estimated track was calculated using a Metropolis algorithm to run 12 000 iterations, and (iv) to account for twilight errors associated with tag shading, a log-normal probability distribution was applied to twilights, providing more accurate location estimation (Wotherspoon et al. 2013).

Spatial analysis of location data

For consistency, the migration phase was determined to have commenced when a bird moved north of 40° S, as movement beyond this latitude was associated with rapid and continuous changes in latitude, and ended when it moved north of 40° N, which coincided with the cessation of rapid continuous latitudinal movements. Using the complete set of daily posterior location estimates produced by SGAT, the proportion of time individual birds spent in each 20° latitude by 10° longitude grid cell (calculated as a proportion of the total time spent between 40° and 80° N and 125°–135° W) was determined, to identify the core areas used. This spatial resolution was chosen to account for (i) the known uncertainty associated with light level Geolocation and (ii) to maximise the number of cells in the analysis. Groups of birds with the same patterns of use of grid cells were identified using hierarchical cluster analysis using Ward's minimum variance method based on Euclidean distances (*hclust*, R Development Team). Only cells used by more than three individuals were included in analyses to provide an indication of general usage of cells.

Using the mean daily location estimates of the individuals, both the core and home range estimates were calculated for all birds and then for each cluster group using the *adehabitatHR* package (Calenge 2006). The 50% Kernel Utilisation Distribution (KUD) represented the core area and 95% KUD was considered the home range (Wood et al. 2000). These were calculated using the fixed Kernel Density Estimation method taken from the least-squares cross-validation bandwidth. The time individuals spent within their core areas was calculated as a proportion of the total time they spent within the non-breeding region ($> 40°N$).

Inter-annual site fidelity

We assessed the degree of inter-annual site fidelity for the subset of birds that recorded foraging trips in two consecutive winters using a bootstrap analysis (Wakefield et al 2015). Here, we calculated 95% KUDs for each year and then calculated the percentage overlap of the two KUDs. We then contrasted this with the percentage overlaps of 95% KUDs for 20 pairs of birds randomly drawn from the pool of birds which recorded only a single trip. If the degree of overlap was greater for repeat birds and the random pairs, we took this as evidence that individuals were more consistent between years than expected by chance.

Activity data

The birds in this study spent more time on the surface of the water at night ($t = - 19.477$, df $= 17,955$, $p < 0.0001$), most likely associated with time spent resting due to limited visibility (Phalan et al. 2007; Shaffer et al. 2009; Wilson et al. 2009). Consequently, we excluded night activity data, and used the time spent on the water during daylight (*pwet*) as an index of foraging activity. Although it is likely that a proportion of the time spent on the water surface during daylight hours could be associated with resting or moulting rather than foraging (Cherel et al. 2016), the amount of time a logger is wet is considered to provide an acceptable index of seabird foraging activity (Catry et al. 2009; Krietsch et al. 2017). Further, the occurrence of non-foraging activities should not compromise comparison between regions as we used the wet/dry data as an index to compare activity, unless there is a regional bias in these activities, which seems unlikely (Cherel et al. 2016).

Environmental data

We described the environmental characteristics of each core foraging area using available time series of: chlorophyll *a* concentration (Chl *a*) (2003–2016), SST °C (1983–2016), sea surface height (SSH) (1993–2016) and sea surface height anomaly (SSHa) (1993–2016). We selected variables that were previously identified as good predictors of the oceanic habitat of short-tailed shearwaters in the North Pacific (Yamamoto et al. 2015). Data were obtained from the Australian Antarctic Data Centre and extracted using the R package *raadtools* (Sumner 2017). The mean yearly value for each environmental variable was calculated from the daily values for the entire period that the short-tailed shearwaters were present in the North Pacific Ocean (May to October).

Statistical analyses

We used a two-sample *t* test to compare the body masses of instrumented and un-instrumented birds at the end of the migration. One-way ANOVAs were used to compare behavioural parameters between cluster groups: (i) the mean within year time spent in the core regions; (ii) the time taken on each annual migration to the North Pacific and whether these differed between years and (iii) the most northerly location reached each year and between years. All dependent variables were log transformed when necessary and significance levels were set at $p < 0.05$. To assess whether the proportion of the day spent in the water (*pwet*) varied between cluster groups, we used a linear mixed effects model (LME) (Bates et al. 2015) in the *nlme* package (Pinheiro et al. 2017). To account for temporal autocorrelation of the daily activity data, we used an autoregressive correlation [AR(1)] structure. The proportion of the day the logger was wet was logit transformed to obtain approximately normal distributions. All models had Bird ID as the random term and a Gaussian family distribution and the model fit was estimated using maximum likelihood.

Spearman's rank correlation coefficients were used to examine if environmental variables were correlated. Variables were weakly correlated, in all cases ($r_s < 0.5$), so all variables were included in analyses. To quantify the annual variation of marine environmental variables (Chl *a*, SST, SSH, SSHa), we compared the mean values from each year in the 50% core foraging area for each group of shearwaters using generalised linear models (GLM), where groups were included as covariates within models. With the *MuMin* package, the best models were elected using Akaike's Information Criteria (AIC) (Burnham and Anderson 2002) and Akaike's weight (wAIC), using the small sample size correction (AICc). Unless otherwise stated means ± standard error (s.e.) are presented. Statistical analyses were performed in R (version 3.5.1, R Development Team 2014).

Results

### Migratory pathways and non-breeding distribution

Carrying a GLS device did not influence the return body masses of tracked birds (567.8 ± 6.9 g) when compared

with those of control birds (572.0 ± 6.0 g, $t = -0.46$, df = 113.3 $p = 0.65$). The onset of the migration to the North Pacific varied by up to 4 weeks between individuals, with birds commencing the migration between 3 and 29 April. Birds dispersed upon reaching the North Pacific: utilising the Sea of Japan, the Sea of Okhotsk, the North Pacific Ocean, the Bering Sea, the Gulf of Alaska and the Chukchi Sea (Fig. 1).

Individual spatial foraging distribution

From the cluster analysis, we identified two groups of birds with similar spatial usage patterns (Fig. 2) defined here as the Western and Eastern groups (Fig. S1). The core area (the 50% KUD) of the Western group ($n = 25$) incorporated areas of the Sea of Japan/Sea of Okhotsk and the North Pacific Ocean (Fig. 3). On average, 61 ± 4.2% of the locations of birds in the Western group were in this core area. The core area (50% KUD) of the Eastern group ($n = 35$) incorporated areas of the southeast Bering Sea, the Aleutian Islands


Fig. 1 The post-breeding movements (April–October) of 60 short-tailed shearwaters tracked from Wedge Island (2012–2016). Arrows indicate direction of travel. *SoJ* Sea of Japan, *OK* Sea of Okhotsk, *BS* Bering Sea, *CK* Chukchi Sea, *GoA* Gulf of Alaska, *NPO* North Pacific Ocean. The locations south of −50 degrees show the post-breeding foraging trip to the Southern Ocean just prior to the winter migration
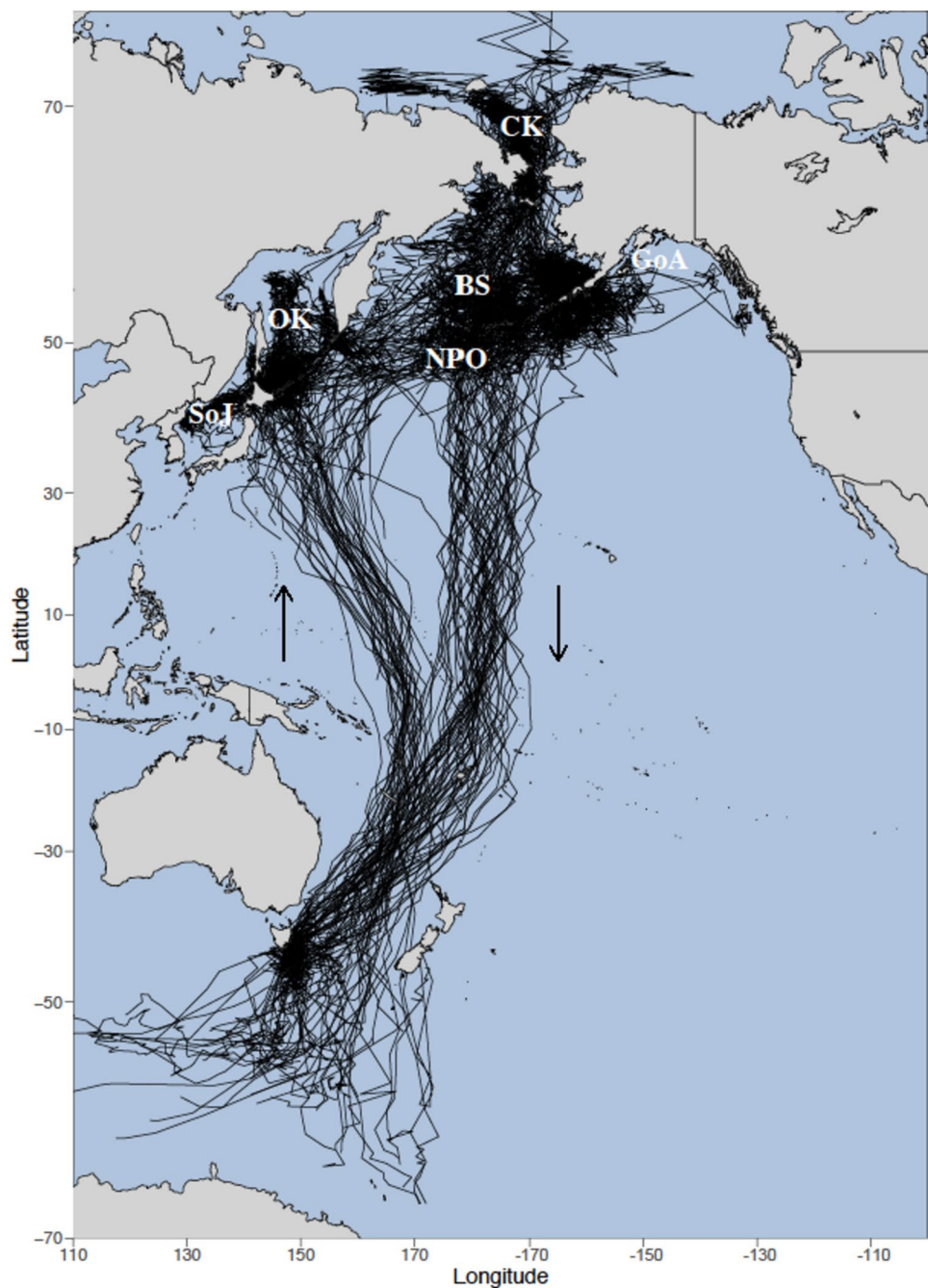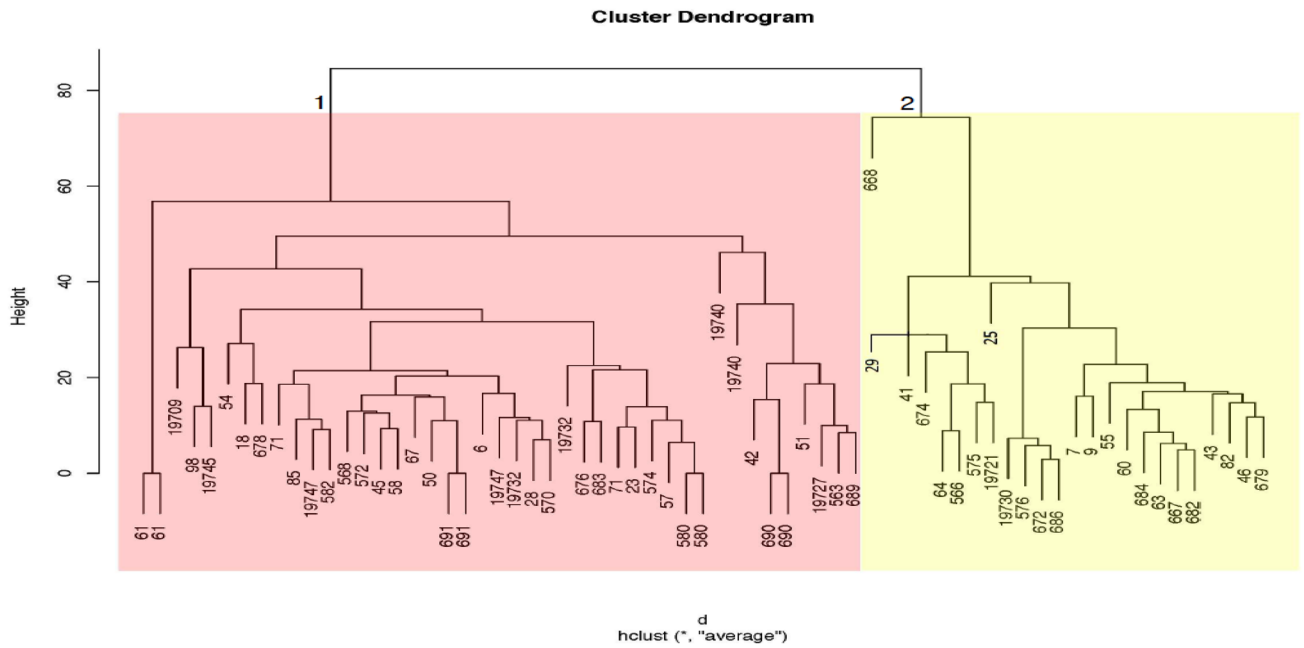
Fig. 2 Cluster groups of short-tailed shearwaters from Wedge Island during the non-breeding period (2012–2016), determined by Ward's minimum variance method: (1) Eastern group (southeast Bering Sea/ North Pacific; and (2) Western group (Sea of Okhotsk/North Pacific Ocean). Individual Bird IDs are shown
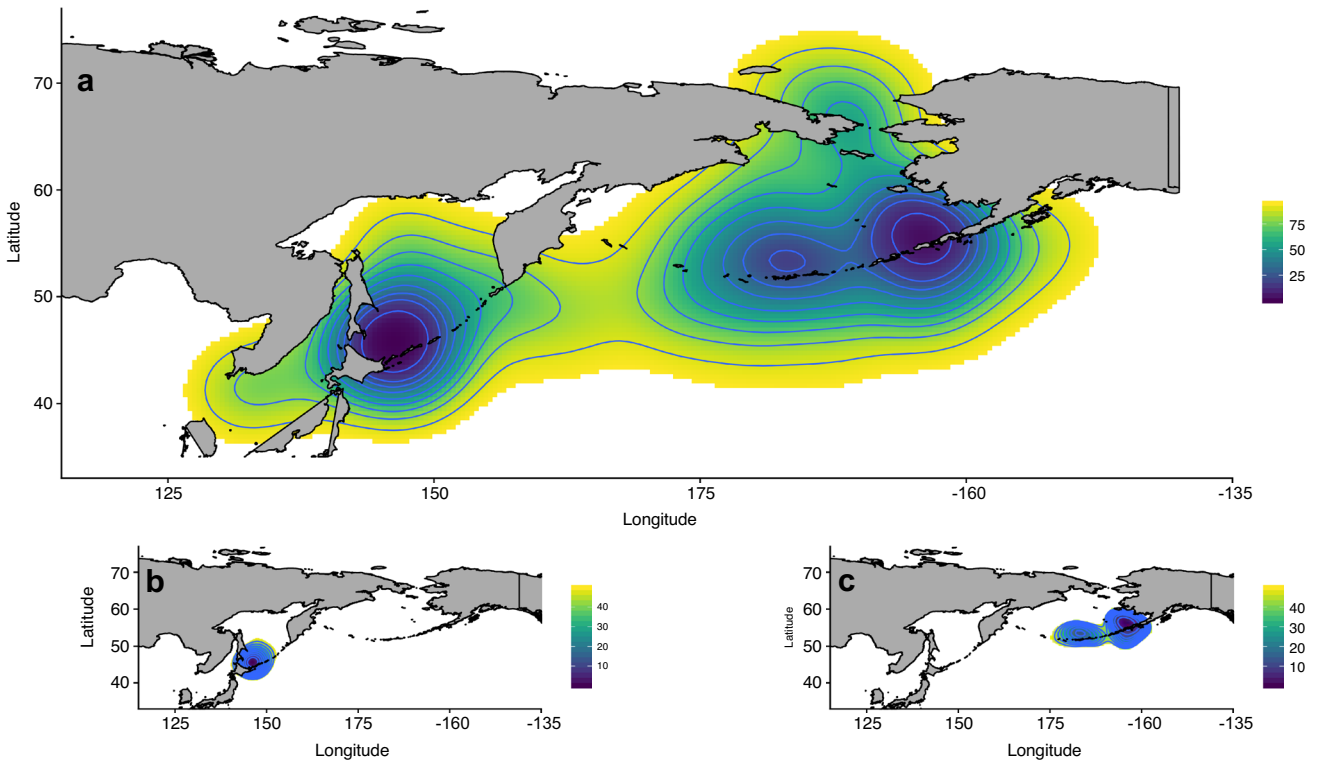
Fig. 3 **a** The 95% KUD home range of 60 short-tailed shearwaters tracked from Wedge Island, during the non-breeding season (2012–2016); and the 50% kernel KUD core foraging areas for; **b** the Western group ($n = 25$); and **c** the Eastern group ($n = 35$)

and Bristol Bay (Fig. 3). For birds in the Eastern group, $64.3 \pm 2.9\%$ of their locations were in this core area. Except for four individuals, birds in the Eastern group did not forage in the Western core area (Sea of Japan/Okhotsk Sea); instead they travelled in an easterly direction after reaching the North Pacific. The number of days taken to migrate to the non-breeding region (Eastern group 11.4 ± 0.7; Western group 10.9 ± 0.5), days spent in the non-breeding region (Eastern group 149.9 ± 2.0; Western group 145.5 ± 2.3) and the most northerly latitude the birds moved to (Eastern group $67 \pm 1.0°$N; Western group $62 \pm 1.7°$N) were all similar between the groups (Table 2; $p > 0.05$ in all cases).

Within-season foraging movements

The proportion of time birds stayed within their core area varied between individuals but not amongst groups ($F_{1,66} = 0.90$, $p = 0.37$) (Western $61 \pm 4.2\%$; Eastern $64.3 \pm 2.9\%$ Table 2). Overall, birds spent between 15 and 99% ($63 \pm 1.7\%$) of their time in their core areas. Eight birds from the Western group first moved into the Sea of Japan upon reaching the North Pacific, where they spent between 26 and 46 days, before moving to the Sea of Okhotsk. Of the Eastern group, four birds spent between 3 and 8 weeks foraging in the Western core area (Sea of Okhotsk, Sea of Japan, Kuril Islands and eastern Japanese coastline) before moving to the Eastern core area in the southeast Bering Sea. An additional three birds from the Eastern group foraged in the eastern North Pacific/Gulf of Alaska following their arrival (for > 4 weeks) and then moved back into the Eastern core area. By the end of August, 10 Western birds and 20 birds from the Eastern group shifted to the Chukchi Sea, where they remained (mid-August–early-September) until they commenced the southern migration (Fig. 4). Further, two birds from the Western group and three birds from the Eastern group shifted to the North Bering Sea/Bering Strait in August.

Foraging behaviour of birds tracked for 2 years

The eight birds that were tracked in 2 successive years all used the same areas in both years (Fig. 5). We tested this by comparing the percentage overlap in 95% KUD of each

year for all 8 birds, with a random sample of 20 pairs drawn from the sample of birds that made a single trip. For the repeat birds, the mean overlap was $51.3 \pm 11.0\%$ compared to $37.7 \pm 17.0\%$, which were significantly different ($t = 2.49$, df $= 19.93$, $p = 0.021$). This indicates that the birds had broadly overlapping home ranges in both years. However, the timing of arrival, the proportion of time spent in the area and the western and northern extents reached varied between years for some of the birds (Table 3).

Foraging effort amongst groups

The proportion of time in the water (*pwet*) in the core 50% KUD areas was similar for each group (wAIC = 0.4) (Table 4). The *pwet* for the Western group was $71 \pm 0.5\%$, and the *pwet* for the Eastern group was $66 \pm 0.5\%$.

Relationship between environmental variables and core foraging areas

Sea surface temperature was ~ 2 °C warmer in the Western core area than the Eastern core area (Table S2). The SST fluctuated between years but increased between 1983 and 2016 (Fig. 6). Neither region nor year were found to influence mean annual Chl *a* (2003–2016) (wAIC = 0.5) (Table 5; Fig.). Over time, SSH and SSHa (1993–2016) trended upward in both core areas (Fig. 6). However, SSH varied between core areas and years (wAIC = 0.4) and SSHa varied between years but not core areas (wAIC = 0.5). Chl *a* showed a distinct seasonal pattern in both core areas (May–October 2003–2016). In the Eastern core area, Chl *a* was highest during May and gradually declined through October, whereas the Western core area had two peaks in May and October (Fig. S2).

Discussion

The birds tracked in this study used two primary foraging regions: the Sea of Okhotsk/North Pacific Ocean and the southeast Bering Sea/North Pacific. The eight individuals tracked for 2 years showed fidelity to foraging sites and returned to the same core foraging area in subsequent years.

Table 2 The number of days short-tailed shearwaters took to migrate, the number of days spent in the non-breeding region and the most northern point visited by birds (latitude) and the proportion (%) of the non-breeding stage that was spent in the core 50% KUD region by birds in each group

Region	Northern migration	Southern migration	Non-breeding stage	Northern latitude (°)	Proportion of time (%) spent in core foraging area	n
Western	10.9 ± 0.5	12.8 ± 0.8	144.5 ± 3.3	62 ± 1.7	60 ± 4.2	25
Eastern	11.4 ± 0.7	12.5 ± 1.7	149 ± 2.0	67 ± 1.0	64.3 ± 2.9	35

All values are mean $\pm$ SD
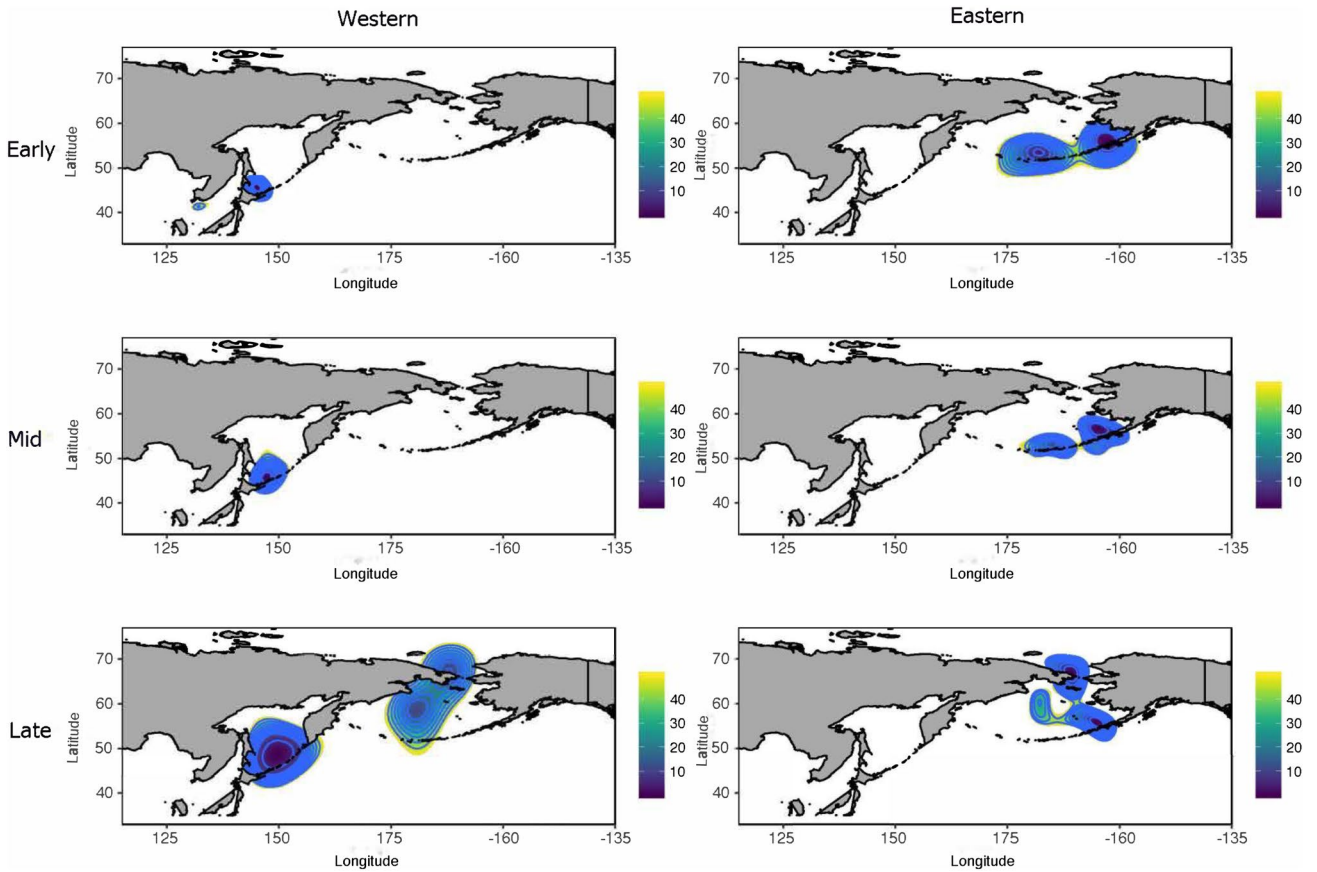
Fig. 4 The seasonal distribution (50% KUD) of short-tailed shearwaters in the Western and Eastern core foraging areas during the non-breeding stage. Early (May–June), mid (July–August) and late (September–October)
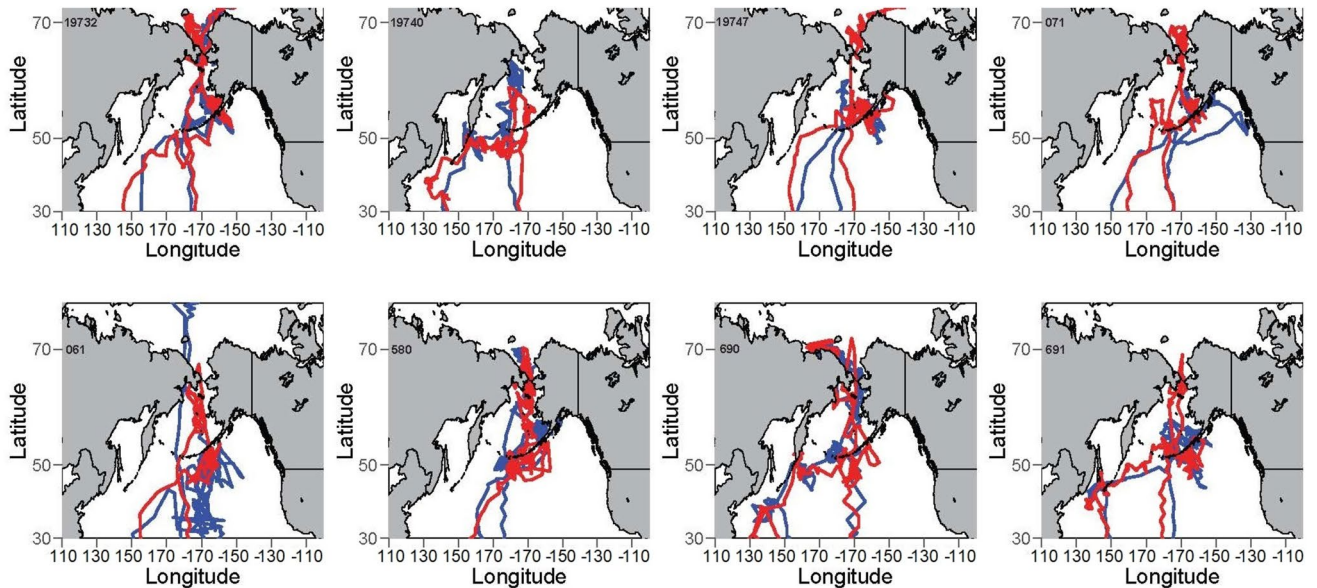
Fig. 5 Successive non-breeding season movements of eight short-tailed shearwaters in the North Pacific Ocean. Bird IDs:061 (2015/blue and 2016/red), 071 (2013/blue and 2014/red), 580 (2015/blue and 2016/red), 690 (2015/blue and 2016/red), 691 (2015/blue and 2016/red), 19,732 (2012/blue, 2013/red), 19,740 (2012/blue, 2013/red) and 19,747 (2012/blue, 2013/red)

Table 3 The day of year (DOY) the core foraging region was reached, the most western longitude, the most northern latitude and the proportion of the non-breeding period spent in their core foraging region by eight birds that were tracked over 2 successive years

ID	Year	Core foraging region	Arrived into core foraging area (DOY)	Western longitude	Northern latitude	Time in specialist area** (%)
19,732	2012	Eastern	129	178°E	72°N	66
19,732	2013	Eastern	124	174°E	72°N	60
19,740	2012	Eastern	191	151°E	69°N	16
19,740	2013	Eastern	173	130°E	60°N	26
19,747	2012	Eastern	117	157°E	59°N	90
19,747	2013	Eastern	134	155°E	72°N	76
71	2013	Eastern	121	159°E	58°N	66
71	2014	Eastern	120	160°E	70°N	60
61	2015	Eastern	136	177°W	81°N	32
61	2016	Eastern	113	165°E	64°N	72
580	2015	Eastern	111	167°E	70°N	66
580	2016	Eastern	117	167°E	70°N	65
690	2015	Eastern	162	131°E	71°N	43
690	2016	Eastern	161	131°E	71°N	50
691	2015	Eastern	143	136°E	69°N	90
691	2016	Eastern	160	131°E	69°N	50

**The proportion of days spent in specialist area calculated from the total days spent in the non-breeding region ($> 40°N$)

DOY day of year

Table 4 Linear mixed effects models for determining the relationship between the time the Western and Eastern groups of short-tailed shearwaters spent in the water (*pwet*) during the non-breeding period

Candidate models	LogLik	AIC$_C$	ΔAIC	wAIC
1. Null	**− 6929**	**13,864.1**	**0**	**0.6**
2. Group ~ *pwet*	− 6928.6	13,865.1	1.03	0.4

pwet = proportion of time the logger was wet

LogLik, log likelihood, ΔAIC$_C$ is the difference in AIC of the models to the best fitting model

wAIC, indicates the probability of the best model

The top ranked model is in bold

Interestingly, all the birds for which return trips were available had core foraging areas in the eastern North Pacific, and therefore may not be representative of the whole population's behaviour. However, for these eight birds, these core regions likely provide a predictable supply of prey allowing the birds to quickly replenish reserves lost during their transhemispheric migration. Whilst these core areas are clearly important to the birds, given the high degree of overlap in successive years, they did use a larger area to feed in and shifted core areas as the season progressed, most likely in response to changing prey availability (Charnov 1976). Nevertheless, we do concede that this interpretation needs to be treated with some caution, because; (i) we do not have direct observations linking movements to prey fields and (ii) because the timing of these movements occurs around the equinox when location accuracy is notoriously poor (Hill 1994).

Within-population foraging strategies

Most birds that used the Eastern core area did not forage in the Western core area and vice versa. It is unlikely that this is the result of sex-specific habitat requirements given males and females display similar migratory behaviours (Carey et al. 2014). Rather, birds most likely select where to forage based on past experience, as most individuals directly navigated to their core foraging area. Further, birds tracked in previous studies were found to use the same regions we have identified here (Watanuki et al. 2015; Yamamoto et al. 2015).

For long-lived species, such as short-tailed shearwaters, an extended immature phase (Skira 1991) allows individuals to thoroughly explore foraging habitats, leading to foraging site specialisations as individuals learn where to find food (Guilford et al. 2011; Missagia et al. 2015; Wakefield et al. 2015). Familiarity with an area should increase foraging success (Irons 1998), which is important after the long migration undertaken by the shearwaters over the less productive waters of the central Pacific (Baduini et al. 2001). Additional energy required for moult of the flight feathers shortly after arrival would place further pressure on birds to find food (Lindström et al. 1993; Hedenström and Sunada 1999). Of the Eastern group, four individuals foraged to the west of their core area before reaching the Eastern core area.
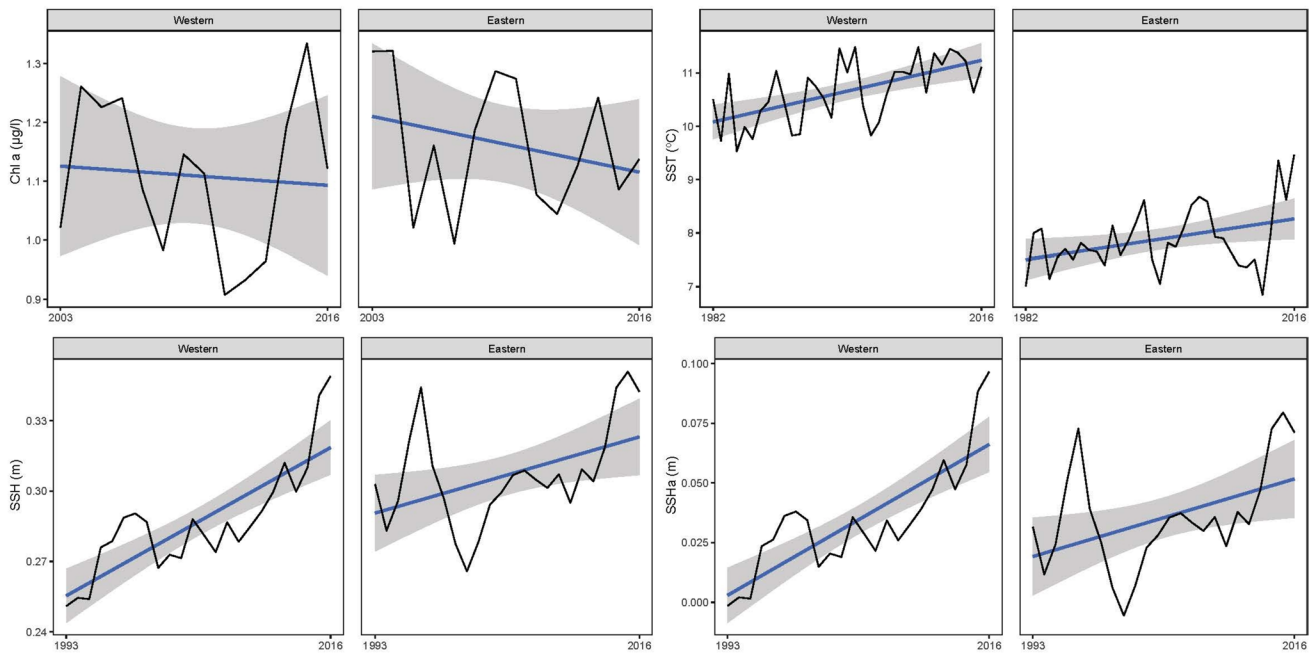
Fig. 6 The relationship identified by generalised linear models between; **a** chlorophyll *a* (Chl *a* μg/l; 2003–2016); **b** sea surface temperature (SST °C; 1982–2016); **c** sea surface height (SSH m; 1993–2016) and **d** sea surface height anomaly (SSHa; 1993–2016) and year and the core foraging regions used by short-tailed shearwaters during the non-breeding stage. 95% confidence interval is indicated by the grey shading. Yearly means (May–October) are indicated by the trend lines

The lipid reserves of migrating shearwaters are depleted following the migration and so birds which used the Eastern region may have 'stopped over' to feed before continuing to the Eastern core region (Baduini et al. 2001; Goymann et al. 2010).

Secondary foraging regions

The timing of intra-North Pacific movements of the shearwaters corresponded approximately with the seasonal cycle of primary production which is influenced by changing daylight hours, temperatures, sea ice extent and spring phytoplankton blooms (Hirota and Hasegawa 1999; Saito et al. 2002; Liu et al. 2004; Kasai and Hirakawa 2015). We hypothesise that this results in changes in the distribution and abundance of prey, leading to the birds moving to new locations. Krill (*Thysanoessa raschii and T. inermis*) is the principal prey of short-tailed shearwaters during their occupation of the North Pacific Ocean and the Bering Sea (Hunt et al. 2002; Nishizawa et al. 2017). Fish such as sandlance (*Ammodytes hexapterus*), age-0 gadids (likely walleye pollock (*Theragra chalcogramma*) and copepods can also be important in their diet (Jahncke et al. 2005). Higher densities of short-tailed shearwaters have been associated with the abundance of large-bodied krill (Nishizawa et al. 2017), age-1 pollock (Suryan et al. 2016), and also with frontal systems and

shallow waters where euphausiid *spp*. can become trapped (Hunt et al. 1996).

There are seasonal shifts in the distribution of the prey of shearwaters associated with the changing environmental conditions in this region. Euphausiid *spp.* and sand lance move from inshore/inner-shelf areas to offshore through early spring to late summer and this shift has been associated with the distribution of short-tailed shearwaters (Jahncke et al. 2005; Hunt et al. 2014; Nishizawa et al. 2017). Like Yamamoto et al. (2015), we also found that towards the end of the non-breeding stage (mid—late August) that at least 50% of the shearwaters had moved northwards into the North Bering Sea and the Chukchi Sea, where earlier ice retreat and a longer open water period are promoting phytoplankton blooms. These blooms are attractive to the zooplankton on which the shearwaters feed (Gall et al. 2017; Kuletz et al. 2020).

Such within season shifts have also been observed for long-tailed skuas (*Stercorarius longicaudus*) (van Bemmelen et al. 2017), brown skuas (*Catharacta antarctica*) (Krietsch et al. 2017), and the yelkouan shearwater (*Puffinus yelkouan*) (Raine et al. 2013), which also return to the same sites amongst years but then move locally in response to environmental conditions. Resolving how the birds in this study are responding to changes in their environment is difficult using broad proxies of productivity such as Chl *a*. Specialised instrumentation that measures in situ behaviour

Table 5 Generalised linear model (GLM) results examining the relationship between region, year and environmental variability

Candidate models	DF	LogLik	AIC$_C$	ΔAIC	wAIC
Chla					
1. Null	**2**	**18.3**	**− 32.2**	**0.0**	**0.5**
2. Chla ~ region	3	18.8	− 30.7	1.5	0.2
3. Chla ~ year	3	18.4	− 28.1	2.4	0.2
4. Chla ~ region + year	4	18.9	− 28.1	4.1	0.1
SST					
1. SST ~ region + year	**4**	**− 52.2**	**113.0**	**0.0**	**0.7**
2. SST ~ region + year + region:year	5	− 51.7	114.3	1.4	0.3
3. SST ~ region	3	− 61.6	129.6	16.7	0.0
4. SST ~ year	3	− 126.7	259.7	146.8	0.0
SSH					
1. SSH ~ region + year + region:year	5	129.1	− 246.7	0.0	0.6
2. SSH ~ region + year	**4**	**127.2**	**− 345.6**	**1.2**	**0.4**
3. SSH ~ year	3	120.2	− 233.9	12.8	0.0
4. SSH ~ region	3	114.4	− 222.2	24.5	0.0
SSHa					
1. SSHa ~ year	**3**	**127.3**	**− 248.0**	**0.0**	**0.5**
2. SSHa ~ region + year	5	129.1	− 246.8	1.2	0.3
3. SSHa ~ region + year + region:year	4	127.3	− 245.6	2.4	0.2
4. Null	2	114.4	− 222.2	23.5	0.0

The top model for each of the four (Chl *a* = chorophyll *a*; SST = sea surface temperature; SSH = sea surface height; SSHa = sea surface height anomaly) environmental covariates is in bold

Chl *a* = chlorophyll *a* (May–September 2003–2016); SST = sea surface temperature (May–September 1983–2016); SSH = sea surface height (May–September 1993–2016); SSHa = sea surface height anomaly (May–September 1993–2016). LogLik, log likelihood, ΔAIC$_C$ is the difference in AIC of the models to the best fitting model. wAIC indicates the probability of the best model

and biological activity can provide insight (McMahon et al. 2021). However, further miniaturisation of such instruments is required before they can be fitted to small animals such as shearwaters, and until then we rely on proxy measures and correlation analysis such as those presented herein.

Implications of individual foraging strategies in a changing climate

The overall time spent in the core foraging areas and the proportion of time spent in the water during the day were similar between groups. However, the time birds spent within their core foraging area varied between individuals. Theory predicts that when food availability becomes low, individuals should expand their foraging habitats to compensate for lower overall food densities (Stephens and Krebs 1986). We found that the physical conditions within the core foraging areas used by shearwaters are changing, and predict that those birds with a more flexible foraging strategy will benefit when resources are scarce (Switzer 1993; Phillips et al. 2017) in accordance with theoretical predictions (Stephens and Krebs 1986). However, there are also advantages of long-term foraging site fidelity, primarily that it maximises net energy gain over a lifetime (Perry and Pianka 1997).

Although if the productivity of a region decreases progressively in response to changes in the climate, then individuals that maintain fidelity to that region will have diminished fitness (Hindell et al. 2017). The short-tailed shearwater population may be resilient in a changing climate because they use a wide range of foraging sites and they demonstrate plastic foraging behaviour. Further, if the persistence of open water areas in the Chukchi Sea results in increased primary production that supports shearwaters prey, this may present an alternative foraging site if prey availability declines in their more southern foraging areas (Gall et al. 2017).

Although our results suggest that some individuals may use the same core areas longitudinally, we cannot be certain that these strategies endure over a shearwater's lifetime (Carneiro et al. 2017). There is evidence that some seabirds repeatedly use the same non-breeding staging areas over the long-term, such as Atlantic puffins (*Fratercula arctica*) (Fayet et al. 2016a). In contrast, some common (*Uria aalge*) and thick-billed murres (*U. lomvia*) switched core winter foraging areas after 2 to 3 years (Tranquilla et al. 2014). Further, Cory's shearwaters (*Calonectris diomedea*) have extreme foraging site plasticity, switching between ocean basins and hemispheres (Dias et al. 2011). However, the tendency of short-tailed shearwaters to leave their core foraging

area within a season indicates that the foraging decisions of the birds are intertwined with conditions they encounter and the knowledge of alternative productive foraging sites.

Long-term environmental trends in the core foraging regions

The environmental variables measured in this study fluctuated considerably through time, but we observed a gradual annual increase in SST (0.03 °C; 1983–2016), SSH (0.002 m; 1993–2016), and in SSHa (0.002 m; 1993–2016), but a slight annual decrease in Chl *a* (− 0.005 µg/l; 2003–2016) in the core foraging regions. Overall, SST was warmer in the Western core area (0.04 °C increase annually), but the increase in SSH and SSHa over time was similar between regions. The increase in SST in the core areas mirrors the general warming trend of the North Pacific, which is significantly changing the dynamics of sea ice and primary productivity (Johannessen et al. 2004; Overland and Stabeno 2004; Markus et al. 2009; Wood et al. 2015).

Reduced sea ice extent and warmer SST in the southeast Bering Sea can reduce the spring phytoplankton bloom and subsequently zooplankton abundance over the shelf (Hunt et al. 2011; Stabeno et al. 2012; Sigler et al. 2014; Duffy-Anderson et al. 2017). This is thought to deprive large-bodied lipid rich zooplankton of ice algae, which is needed for reproduction and growth (Hunt et al. 2011; Stabeno et al. 2012; Sigler et al. 2014). When warm stanza events occur in the Bering Sea, the reduction in zooplankton cascades up to higher trophic levels (Moss et al. 2009; Coyle et al. 2011; Mueter et al. 2011). If the observed warming trend continues, it is possible that seabirds and other top predators could decline in the southeastern Bering Sea if the prey on which they depend becomes less abundant (Renner et al. 2016).

Sea ice extent and duration have fluctuated significantly in the Bering Sea in recent years but have remained relatively more stable (Brown et al. 2011; Frey et al. 2015), than sea ice in the Sea of Okhotsk and the Chukchi Seas where the extent and persistence of sea ice have both declined (Stroeve et al. 2012; Ogi et al. 2015; Paik et al. 2017). In years when production in the core foraging areas is reduced, increased open water areas in the Chukchi Sea may present highly mobile species such as short-tailed shearwaters with alternate foraging areas. Indeed, earlier sea ice retreat and an increase in the availability of open water in the Chukchi Sea are thought to contribute to more favourable conditions for large-bodied euphausiid spp. and copepods, and this has been associated with increasing densities of shearwaters in this region in recent decades (Gall et al. 2017; Kuletz et al. 2020). How these complex environmental changes will affect shearwaters remains to be explored in full, but here we have provided some information on which to build a more comprehensive understanding of the long-term effects on shearwater performance.

Conclusion

From our multi-year study of post-breeding shearwater foraging behaviour in the North Pacific Ocean, we found that short-tailed shearwaters tend to return to known foraging areas in successive years (*i.e.* they show forging site fidelity). However, despite this initial fidelity to known foraging grounds, the birds do not necessarily stay at these sites and will move to alternative areas within their broader foraging habitats to find food. Such behaviour shows that the birds follow a hierarchical foraging strategy whereby, as theory may predict, they initially return but will subsequently move if the resources are not available or are depleted in accordance with the marginal foraging theorem. In other words, the birds follow some simple rules to optimise their foraging success: (i) return to the same area and stay there and feed if food is abundant and (ii) if food is not available at the known feeding site, move until food is found. These findings suggest that hierarchical foraging strategies may provide the behavioural plasticity to respond to changing environments across large temporal and spatial scales for this highly migratory species.

Declarations

Conflicts of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethical approval All animal handling and instrumentation were conducted under Research Permits (Department of Primary Industries, Parks, Water and Environment (DPIPWE): FA10212, FA13009, FA14063, FA15083, FA16077) and University of Tasmania Animal Ethics Committee permits (A11338, A128942, A15572).

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