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Incomplete isolation in the nonbreeding areas of two genetically separated but sympatric short-tailed albatross populations

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ABSTRACT: The short-tailed albatross *Phoebastria albatrus*, a globally Vulnerable species recovering from near-extinction, breeds mainly on 2 island groups in the north-western Pacific: Torishima and Senkaku Islands. Recently, it became clear that this is a species complex, composed of 2 populations ('Torishima' and 'Senkaku' types) that are distinct from both genetic and morphological perspectives, and which mate assortatively on Torishima. We tested the hypothesis of premating isolation as a possible mechanism for genetic differentiation and shifted breeding date in short-tailed albatrosses. Using light-based geolocation and molecular analysis, we examined whether adults from the 2 populations breeding on Torishima differed in their at-sea distribution during the nonbreeding period (June–September) and in their return dates. From 22 bird tracks collected from 12 birds over 4 yr, we identified 2 distinct nonbreeding areas: around the Aleutian Islands in the Bering Sea and near the Kuril Islands in the Okhotsk Sea. All 6 tracks of Torishima-type birds migrated directly to the Bering Sea in all years. In contrast, most of the Senkaku-type birds migrated along northeast Japan to the Okhotsk Sea (9 tracks), with the others moving to the Bering Sea (7 tracks). There was no clear difference in the dates of return to Torishima between the 2 bird types. Overall, no absolute pre-mating isolation in space or time was observed in short-tailed albatrosses, but we highlighted notable divergences in the nonbreeding distribution of both types. This result suggests that Torishima- and Senkaku-type populations should be treated as separate management units.

KEY WORDS: *Phoebastria albatrus* · Isolation mechanism · At-sea distribution · Timing of breeding · Genetics · Management unit · Geolocator

1. INTRODUCTION

Genetical isolation between populations has been widely reported among seabird species (e.g. Friesen et al. 2007b, Smith & Friesen 2007, Wold et al. 2021). However, physical barriers to seabird movements (land, ice) seem to have little influence on this genetic structuring (Friesen et al. 2007a, Friesen 2015). In contrast, spatial divergence between population sub-groups in their respective at-sea distributions during the nonbreeding period is assumed to potentially reduce gene flow between these sub-groups (Friesen et al. 2007a, Friesen 2015). This mechanism would notably limit the opportunities for assortative mating. For example, 2 genetically distinct populations of Cook's petrel *Pterodroma*

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cookii breeding on islands about 1300 km apart spend the nonbreeding season in areas separated by 5000 km (Rayner et al. 2011). In addition, the birds return for breeding with 1 mo difference between the 2 populations, and such shifted timings of return to the colony may be another strong mechanism effectively precluding gene flow between the subgroups (Wold et al. 2021). Indeed, 2 populations of the band-rumped storm-petrel *Oceanodroma castro* were found to breed at distinct times on the same island in the Azores (Monteiro & Furness 1998), and are now genetically and morphologically recognized as separate species (Bolton et al. 2008).

Divergent distributions across nonbreeding areas, with the potential outcome of shifted return timings, may thus provide a robust framework to explain genetic structuring in sympatric bird populations. However, in the wild where instances of divergent distributions and/or shifted return timings have been observed, the genetic distance between those subgroups is generally unknown (Gunnarsson et al. 2006, Müller et al. 2015). Consequently, it remains difficult to understand the interplay among the spatial, temporal and genetic components of population structure.

The short-tailed albatross *Phoebastria albatrus* breeds mostly on 2 island groups in the northwestern Pacific Ocean: Torishima and Senkaku Islands (see Fig. 1; BirdLife International 2018). The global population suffered from intense harvesting at these sites and other islands where the species used to breed, and approached extinction at the beginning of the 20th century (ACAP 2009). Over recent decades, numbers have been recovering from an extremely reduced pool of breeders (25 individuals in 1954). The population breeding at Torishima is the only one being closely monitored over the long term, with systematic ringing of the chicks. The short-tailed albatross is now listed as Vulnerable on the IUCN Red List and tacitly regarded as a single management unit (US Fish and Wildlife Service 2008, ACAP 2009, BirdLife International 2018). However, Eda et al. (2020) showed that short-tailed albatrosses consisted of 2 cryptic species, from several lines of evidence. Based on the analysis of mitochondrial DNA (mtDNA) of zooarchaeological specimens, research revealed that this species indeed consisted of 2 genetically distinct populations (haplotype clades), with differences in morphological and isotopic variables that have persisted for at least 1000 yr (Eda et al. 2012). Remarkably, these 2 clades appear more distant from each other than other sister species of albatrosses, such as the black-browed *Thalassarche melanophrys* versus Campbell *T. impavida* albatrosses, and wandering *Diomedea exulans* versus Amsterdam *D. amsterdamensis* albatrosses (Eda & Higuchi 2012).

One of the 2 *P. albatrus* populations breeds mainly on Torishima ('Torishima type') and the other is likely to be mostly found on the rarely visited Senkaku Islands ('Senkaku type'; Kuro-o et al. 2010, Eda et al. 2011, Eda & Higuchi 2012). However, repeated observations of un-ringed birds in subadult plumage every year in the Torishima colony and the analysis of population structure at Torishima through mtDNA suggested an immigration of individuals from the Senkaku population (Kuro-o et al. 2010, Eda et al. 2010, 2011). Further, Eda et al. (2016a) found that individuals ringed as chicks on Torishima and un-ringed birds (likely immigrants from the Senkaku Islands) mate assortatively, despite incomplete pre-mating isolation, and suggested that a difference in the timing of breeding might prevent mating between the 2 types of birds and thus be 1 mechanism involved in maintaining a level of mating isolation between the 2 populations. However, it is unknown whether the 2 types differ in their timing of breeding. Field observations tend to support this hypothesis, showing that the birds breeding on the Senkaku Islands departed from the islands ~2 wk earlier than those on Torishima in 2002 (Hasegawa 2006). Moreover, although satellite tracking of albatrosses from Torishima showed variations in their at-sea distribution spread across the North Pacific during the nonbreeding period (Suryan et al. 2006, 2007, ACAP 2009), the genetic type of the birds from these previous studies is unknown.

In this study, we hypothesized that Torishima-type and Senkaku-type birds breeding on Torishima spend the nonbreeding period over divergent geographic areas and accordingly return to Torishima on different dates for breeding. To test this hypothesis, we studied adult birds that were each genetically typed through sequencing of blood cell mtDNA. We concomitantly tracked their individual year-round movements at sea using light-based geolocation loggers attached to leg bands. We finally examined whether adults of the Torishima type versus the Senkaku type, breeding sympatrically on Torishima, differed markedly in their nonbreeding areas and their timing of return to Torishima.

2. MATERIALS AND METHODS

2.1. Field study

We conducted fieldwork in the Hatsunezaki colony on Torishima (described in detail by Eda et al. 2016a,

2020) during the 2014–2018 breeding seasons in February–March. The colony is located in the north-west of the island and was established in 1995 by artificially attracting albatrosses using decoys and audio recordings (Sato 2009). Only 1 pair was known to breed at this colony until 2003–2004, but from that point, the observed number of breeding pairs increased rapidly; it reached 389 pairs in the 2018–2019 breeding season (Hasegawa 2020). In addition to Hatsunezaki, short-tailed albatrosses breed at 2 other colonies (Tsubamezaki and Komochiyama) on Torishima. Because most of the birds in all colonies on Torishima were ringed with a metal ring or both metal and color rings as chicks, un-ringed birds were suspected to originate from the Senkaku Islands (Eda et al. 2011).

We captured 9 un-ringed and 5 ringed short-tailed albatrosses using a dip net and attached a light-based geolocation logger to each bird in 2014–2018 (see Table 1). The geolocation loggers were fitted to the metal or color ring of the studied birds. The loggers used were Biotrack® model MK3005 or MK3006 (both models: 18 × 14 × 6 mm, mass 2.85 g; total mass 6.14 g with a metal or color ring). The total mass was equivalent to 0.13 ± 0.02% (0.10–0.18%) of the birds' body mass. We recaptured the tagged birds after 1 to 4 yr and retrieved the loggers; new loggers were then deployed on some of the same studied birds (see Table 1). We collected blood samples from each bird for a molecular phylogenetic analysis and sex determination (results in Eda et al. 2020). The mtDNA control region 2 sequence confirmed that all of the 9 unringed birds were Senkaku-type individuals, whereas all of the 5 ringed birds were Torishima-type individuals. Molecular sexing confirmed that all birds from both types were males.

2.2. Migratory movements and chronology

The data loggers record time and ambient light intensity every 5 (MK3005) or 10 (MK3006) min, allowing us to infer sunset and sunrise times, from which 2 estimates of latitude and longitude can be derived per day. The loggers also record sea temperature after 20 min of continuous immersion. The logged data sets were analyzed separately for each individual and each year, using the 'Solar/Satellite Geolocation for Animal Tracking' (SGAT; https://rdrr.io/github/SWotherspoon/SGAT/) library for R (v.3.4.2, R Core Team 2017). This approach relies on Markov chain Monte Carlo simulation of animal movement (Sumner et al. 2009). The initial location estimates are then refined using a species-specific movement model, as well as a land mask to prevent location estimates over land, and a sea-surface temperature (SST) matching process between the logger's continuous records and remotely sensed SST data to correct latitude estimates (especially important for the equinox periods, when latitude is not reliable from light). The movement model was based on an average daily speed of 3 m s^{-1} based on satellite tracking of migrating albatrosses (Suryan et al. 2007). The SST data were weekly means over a grid of 1.0 spatial degree, downloaded from NOAA's Optimum Interpolation Sea Surface Temperature V2 data set (https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html). The movement model ultimately provides daily, most likely positions.

From the final set of estimated locations, we calculated the dates of migration as the dates when a significant change-point occurred in daily distance to the colony. These multiple dates of abrupt changes between staging and sustained movement phases (or vice versa) were objectively inferred using a 'broken stick' modeling approach applied on the daily distance to the colony. This approach relies on optimized regression and maximum likelihood in R (package 'betareg', Cribari-Neto & Zeileis 2010); here we followed the process and R script provided by Thiebot et al. (2014). The most likely dates of departure from, and return to, the colony area, and dates of arrival and departure to/from the nonbreeding area were inferred following this approach.

2.3. Statistical analysis

At-sea distribution data were pooled per population type to estimate the respective utilization distributions of the 2 albatross groups, using the kernel estimation method in QGIS 2.18 (QGIS Development Team 2017). Kernel density contours of 25–75% were computed with a smoothing parameter of 1°.

We then assigned each bird track to 1 of the 2 nonbreeding areas highlighted in our study (see Section 3), using a *k*-means clustering analysis in R. This method aims to partition the data points into *k* groups (in our case 2) such that the sum of squares from points to the assigned cluster centers is minimized. For each bird track, we thus calculated the latitude and the longitude of the distribution centroid for the portion comprised between the arrival to and departure from the predominant nonbreeding area. The *k*-means clustering analysis was first run on the latitude values and then on the longitude values of the nonbreeding centroids of the bird tracks. We then com-

pared the clustering performance in each case (ratio of the between-clusters sum of squares divided by the total sum of squares) to evaluate which factor (latitude or longitude of the centroids) provided the clearest partitioning of the distribution areas.

Finally, we compared the migration timing of the birds according to genetic type and the nonbreeding area that was exploited. We used linear mixed models (LMMs) where the day of year of departure from the breeding colony area, arrival at the nonbreeding area, departure from the nonbreeding area, and return to the breeding colony area (within <500 km) were response variables, assuming a Gaussian distribution. In the case of the return date to the colony area, a different approach was used, because the locations suggested that birds tended to move away and back towards the colony again at the onset of breeding, and the loggers' immersion data were not always available until the birds were established on dry land to inform on their actual return date. We therefore defined the date when the birds were back in their breeding colony area as a 500 km radius around the colony. This 500 km range was arbitrarily set as a compromise between a value small enough to accurately reflect when the birds approached the colony, while providing a sufficient buffer around that location to account for 2 factors: (1) the fact that the returning birds may be moving at sea near the island before finally settling in, and (2) the inherently large spatial error of location estimates derived from light-based geolocation (185 km, Biotrack Geolocator User Manual; although this could be as low as 43.3 km when data are processed using track optimization approaches incorporating a movement model, such as in this study; Rakhimberdiev et al. 2016). The chosen range thus corresponded to a minimum of less than 3 times the spatial error of the location estimates, which was assumed to be adequate in this case. In the LMMs, 'bird type and its nonbreeding area' was set as a fixed factor, and 'bird ID' and 'year' were included as random factors. We then compared models with and without the effect of the fixed factor using a likelihood ratio test (LRT). We used the 'lme4' package in R (v.4.0.2, R Development Core Team 2020) for LMMs.

3. RESULTS

3.1. Logger retrieval

The loggers were retrieved from 12 of 14 birds across years: 4 birds of the Torishima type and 8 birds of the Senkaku type (Table 1). The other 2 birds could not be recaptured because they were not seen again at the colony. The loggers from 8 birds provided data over 2 or 3 yr (Table 1). In total, 22 nonbreeding distribution data sets were available across birds and years, including 6 from the 4 Torishima-type birds and 16 from the 8 Senkaku-type birds; however, in 6 cases, the loggers reached full memory capacity or failed early, and as a consequence, it was not possible to estimate the movements of these birds until their return to Torishima.

3.2. Nonbreeding areas

During both the late breeding (March–May) and early breeding (October–February) seasons, all birds of both types concentrated mainly between about 140° and 145° E, from Torishima to northern Japan (Fig. 1; Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/n053p213_supp.pdf).

However, during the nonbreeding period (June–September), the albatrosses' at-sea distribution spread widely across the North Pacific, from about 140° to 200° E (Fig. 1). Two distinct areas were used: the area around the Aleutian Islands to the outer shelf and shelf slope of the Bering Sea (hereafter, Aleutian–Bering), and the area around the Kuril Islands to the central Okhotsk Sea (hereafter, Kuril–Okhotsk). These 2 main distribution areas are about 2500 km apart (Fig. 1), and the *k*-means clustering analysis showed that these were clearly partitioned according to longitude (sum of squares ratio = 96.6%; Table 1), with a minimum in the birds' utilization overlap occurring around 165–166° E (Fig. 2). On the other hand, the partitioning of these 2 areas based on latitude was less clear (sum of squares ratio = 79.2%). Importantly, in most cases, the data showed that the birds spent the nonbreeding period in only 1 of these 2 areas, although this was not always the case. All 6 data sets available for the 4 Torishima-type birds showed a migration over the North Pacific Basin to the Aleutian–Bering area (Figs. 3a,b & 4a; Fig. S1), whereas in the 16 individual-year data sets available for the Senkaku-type birds, 8 (50%, from 5 birds) showed movements along the northeast Japan coast over the shelf to the Kuril–Okhotsk area (Figs. 3c & 4b; Fig. S2), 5 others (31%, from 3 birds) reached the Aleutian–Bering area (Figs. 3d & 4b; Fig. S2), and the last 3 (19%, from 3 birds) covered both areas (Fig. S2). However, the latter tracks to both areas were predominantly directed to either one of these areas, and

Table 1. Predominant nonbreeding areas and dates of movement inferred from optimized regression of 2 population types in short-tailed albatrosses: departure from the breeding colony area, arrival at the nonbreeding area, departure from the nonbreeding area, and return to the breeding colony region (within 500 km from Torishima). Estimated age from plumage pattern for the Senkaku-type birds (Konno et al. 2018) and exact age from metal rings attached at the chick stage for the Torishima-type birds. Dates are given as year/month/day. Dash indicates no data available (cases when the loggers stopped recording prematurely)

ID	Type	Year	Age	Presence of chicks	Logger attachment date	Predominant nonbreeding area (Jun–Sep)	Start of migration	Arrival at nonbreeding area	Departure from nonbreeding area	Date of return (< 500 km)
A54	Senkaku	2014	9	Yes	2014/2/27	Aleutian–Bering	2014/4/27	2014/7/8	2014/10/7	2014/10/21
A54	Senkaku	2015	10	Yes	Continued	Aleutian–Bering	2015/4/22	2015/7/5	–	–
A54	Senkaku	2016	11	Yes	2016/2/26	Aleutian–Bering	2016/4/23	2016/6/29	2016/10/5	2016/10/21
A55	Senkaku	2014	6	None	2014/2/28	Kuril–Okhotsk	2014/4/22	2014/6/23	–	–
A55	Senkaku	2017	9	None	2017/2/18	Kuril–Okhotsk	2017/4/12	2017/6/16	2017/10/14	2017/10/21
A56	Senkaku	2014	12	Yes	2014/3/2	Kuril–Okhotsk	2014/4/21	2014/6/29	–	–
A56	Senkaku	2015	13	Yes	2015/2/26	Kuril–Okhotsk	2015/4/19	2015/6/2	2015/10/8	2015/10/15
A57	Senkaku	2014	5	None	2014/3/3	Kuril–Okhotsk	2014/4/22	2014/6/4	2014/10/2	2014/11/29
A57	Senkaku	2015	6	None	2015/2/25	Kuril–Okhotsk	2015/4/8	2015/7/14	2015/10/21	2015/11/5
A58	Senkaku	2014	5	None	2014/3/5	Kuril–Okhotsk	2014/5/13	2014/6/9	–	–
A58	Senkaku	2016	7	None	2016/2/29	Kuril–Okhotsk	2016/4/11	2016/6/11	2016/10/19	2016/10/25
A62	Senkaku	2015	7	None	2015/2/26	Aleutian–Bering	2015/4/19	2015/6/1	2015/10/24	2015/11/8
A62	Senkaku	2016	8	None	Continued	Aleutian–Bering	2016/4/18	2016/7/1	2016/10/20	2016/10/31
A63	Senkaku	2015	3	None	2015/2/26	Not retrieved	–	–	–	–
A64	Senkaku	2015	5	None	2015/2/26	Aleutian–Bering	2015/4/27	2015/5/24	2015/10/24	2015/11/5
A64	Senkaku	2016	6	Yes	Continued	Aleutian–Bering	2016/4/29	2016/7/9	2016/10/9	2016/10/28
A67	Senkaku	2016	9	Yes	2016/2/23	Kuril–Okhotsk	2016/4/13	2016/6/26	2016/9/30	2016/10/10
A59	Torishima	2014	4	None	2014/3/8	Not retrieved	–	–	–	–
A60	Torishima	2014	7	Yes	2014/3/11	Aleutian–Bering	2014/4/25	2014/7/2	–	–
A60	Torishima	2015	8	Yes	2015/2/26	Aleutian–Bering	2015/4/22	2015/8/6	2015/10/12	2015/10/20
A60	Torishima	2016	9	Yes	2016/2/21	Aleutian–Bering	2016/4/17	2016/6/22	2016/10/7	2016/10/20
A61	Torishima	2014	3	None	2014/3/16	Aleutian–Bering	2014/4/6	2014/5/29	–	–
A65	Torishima	2016	11	Yes	2016/2/21	Aleutian–Bering	2016/4/17	2016/5/10	2016/10/6	2016/10/17
A66	Torishima	2016	9	Yes	2016/2/23	Aleutian–Bering	2016/4/16	2016/6/27	2016/10/10	2016/10/20

only marginally to the other. Overall, we found a marginally significant statistical difference in the odds of the birds distributing predominantly over one or the other nonbreeding area, according to their genetic type (Fisher's exact test for count data, p = 0.07; Torishima-type birds: n = 4 versus 0, Senkaku-type birds: n = 3 versus 5, distributing predominantly in the Aleutian–Bering versus the Kuril–Okhotsk areas, respectively; Table 1, Figs. S1 & S2).

All 8 birds whose tracks were collected over multiple years used predominantly the same nonbreeding area for 2 or 3 study years, regardless of type (Table 1; Figs. S1 & S2). More specifically, the single Torishima-type bird tracked over 3 successive years consistently used the Aleutian–Bering area, and only that area, during the nonbreeding period. However, among the 7 Senkaku-type birds tracked over multiple years, 4 visited the same nonbreeding area year after year (3 birds to the Kuril–Okhotsk area and 1 bird to the Aleutian–Bering area), and the other 3 showed more variable distribution across years. In these latter 3 birds, 2 that initially used the Aleutian–Bering area only then also briefly visited the Kuril–Okhotsk area on their outbound migration during the following year; and 1 bird that initially visited the Aleutian–Bering area in addition to predominantly using the Kuril–Okhotsk area only used the Kuril–Okhotsk area during the following year.

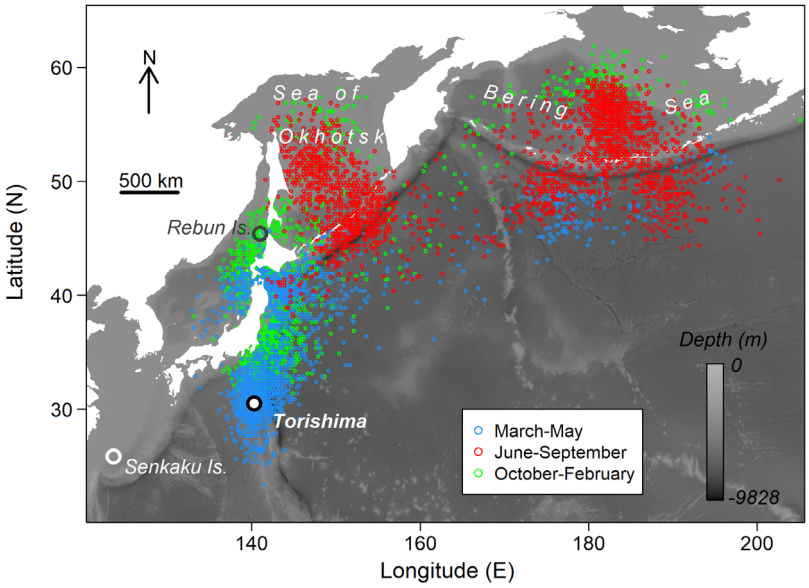

Fig. 1. At-sea distribution of short-tailed albatrosses tracked from Torishima with geolocators (n = 22 tracks collected from 12 birds). Blue circles indicate locations during March to May (late breeding season), red circles during June to September (nonbreeding season), and green circles during October to February (early breeding season)

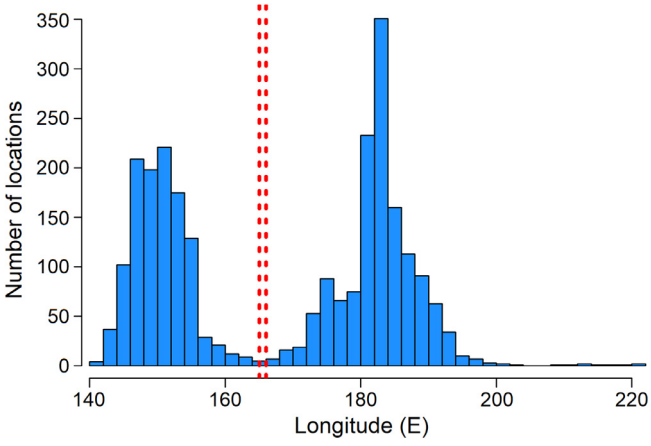

Fig. 2. Longitudes during the June–September period (nonbreeding season) of all GLS-tracked short-tailed albatrosses from Torishima, showing a bimodal pattern with a minimum between 165 and 166° E (indicated by red lines)

3.3. Migration timing

Change-points were detected in the individual time series of distance from the colony, with an estimated 95% confidence interval of ±5.2 d on average (Fig. S3). There was no significant difference in migration timing according to genetic type and the nonbreeding area that was exploited for either date of departure from the breeding colony area (LMM with LRT, $\chi^2 = 2.644$, p = 0.267), arrival at the nonbreeding area (LMM with LRT, $\chi^2 = 0.330$, p = 0.848), departure from the nonbreeding area (LMM with LRT, $\chi^2 = 2.078$, p = 0.354), or return to the breeding colony region (within <500 km) (LMM with LRT, $\chi^2 = 1.478$, p = 0.478) (Fig. 5).

4. DISCUSSION

We found that 2 genetically distinct populations of the short-tailed albatross (Torishima and Senkaku types), breeding in sympatry at the same colony on Torishima, used 2 areas during the nonbreeding period (June–September). First, all tracks collected from Torishima-type birds revealed the utilization of the Aleutian–Bering area only. Although we cannot exclude the possibility that this population type may in fact use a wider range of areas than we were able to reflect in this study from just 4 birds (6 tracks), and larger sample sizes are desirable to strengthen our

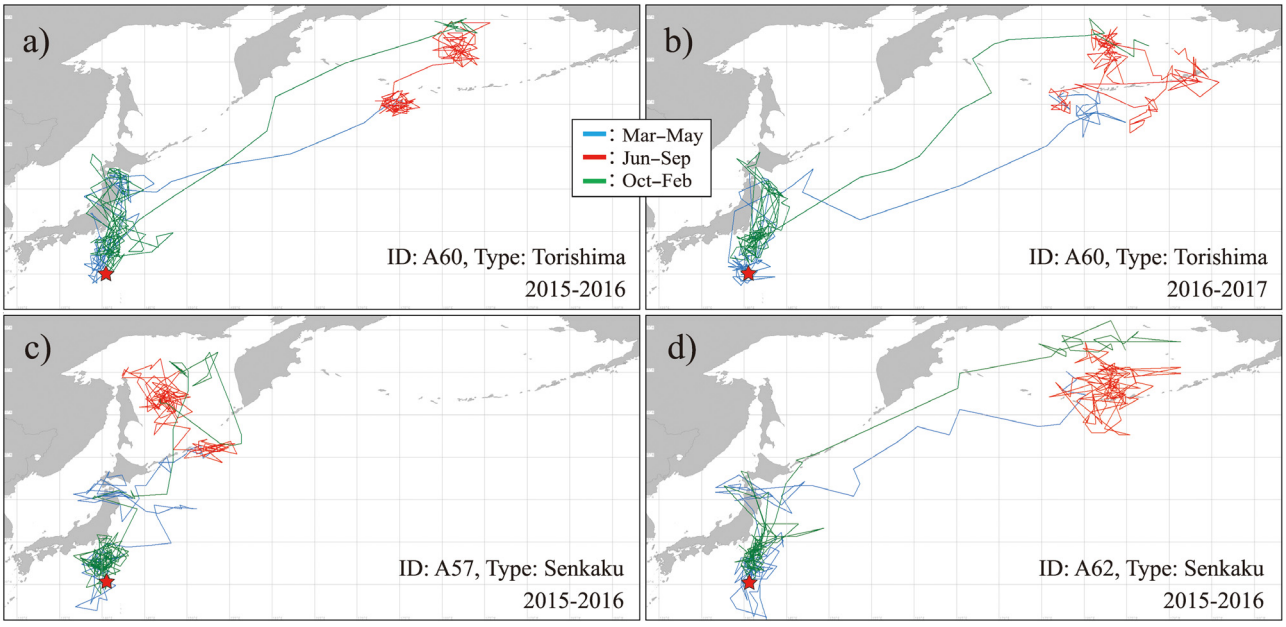

Fig. 3. Examples of individual-year migration tracks of short-tailed albatrosses of the (a,b) Torishima type, (c) Senkaku type using the Kuril–Okhotsk area, and (d) Senkaku type using the Aleutian–Bering area. Blue lines indicate migration tracks during March to May (late breeding season), red lines during June to September (nonbreeding season), and green lines during October to February (early breeding season). The star indicates the colony location on Torishima

findings, this area was previously known to be used extensively by short-tailed albatrosses tracked from Torishima (Suryan et al. 2006, 2007, ACAP 2009), hence supporting the geolocation estimates from our study. Although the genetic type of the satellite-tracked birds from these previous studies is unknown, most of them are likely to be of the Torishima type, since this type is estimated to constitute about 93% of the short-tailed albatrosses breeding on Torishima (Kuro-o et al. 2010). These results are also supported by ancient DNA analysis of archaeological short-tailed albatross specimens from the Yuquot site in British Columbia, Canada, that documented the historical presence of the short-tailed albatross in the Northeast Pacific (Royle et al. 2022). In particular, that study indicated that cytochrome b sequences obtained from 40 of the 43 specimens belonged to the same clade as the Torishima-type birds, thus further confirming the distribution of this type. The outer shelf and slope region of the Bering Sea and both sides of the Aleutian

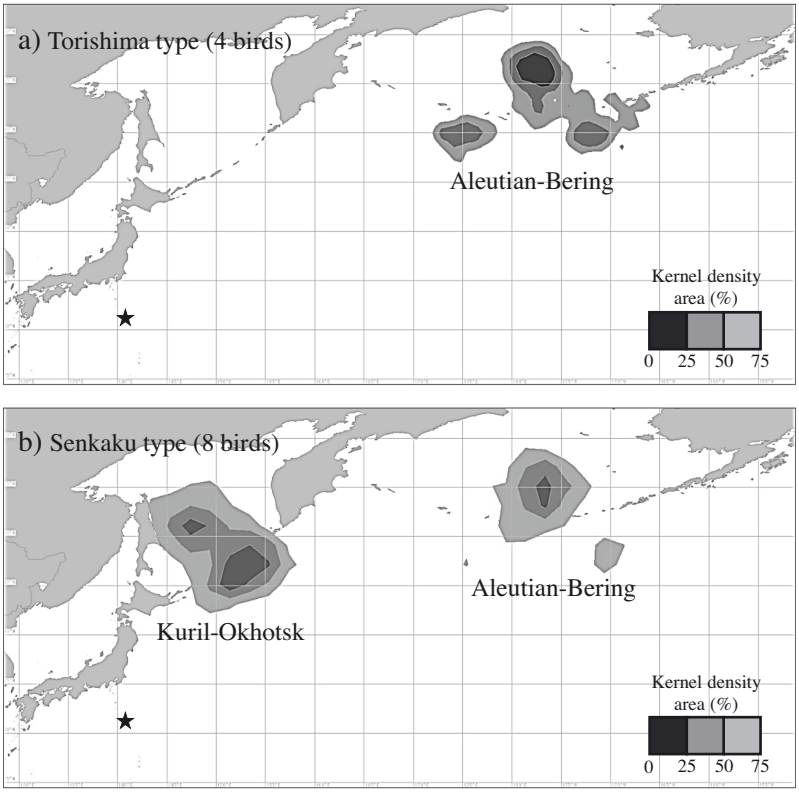

Fig. 4. Predominant nonbreeding areas of 2 population types of short-tailed albatrosses during June to September: (a) Torishima type, (b) Senkaku type. Kernel density areas encompass 25 (dark grey) to 75% (light grey) of the total distribution. The star indicates the colony location on Torishima

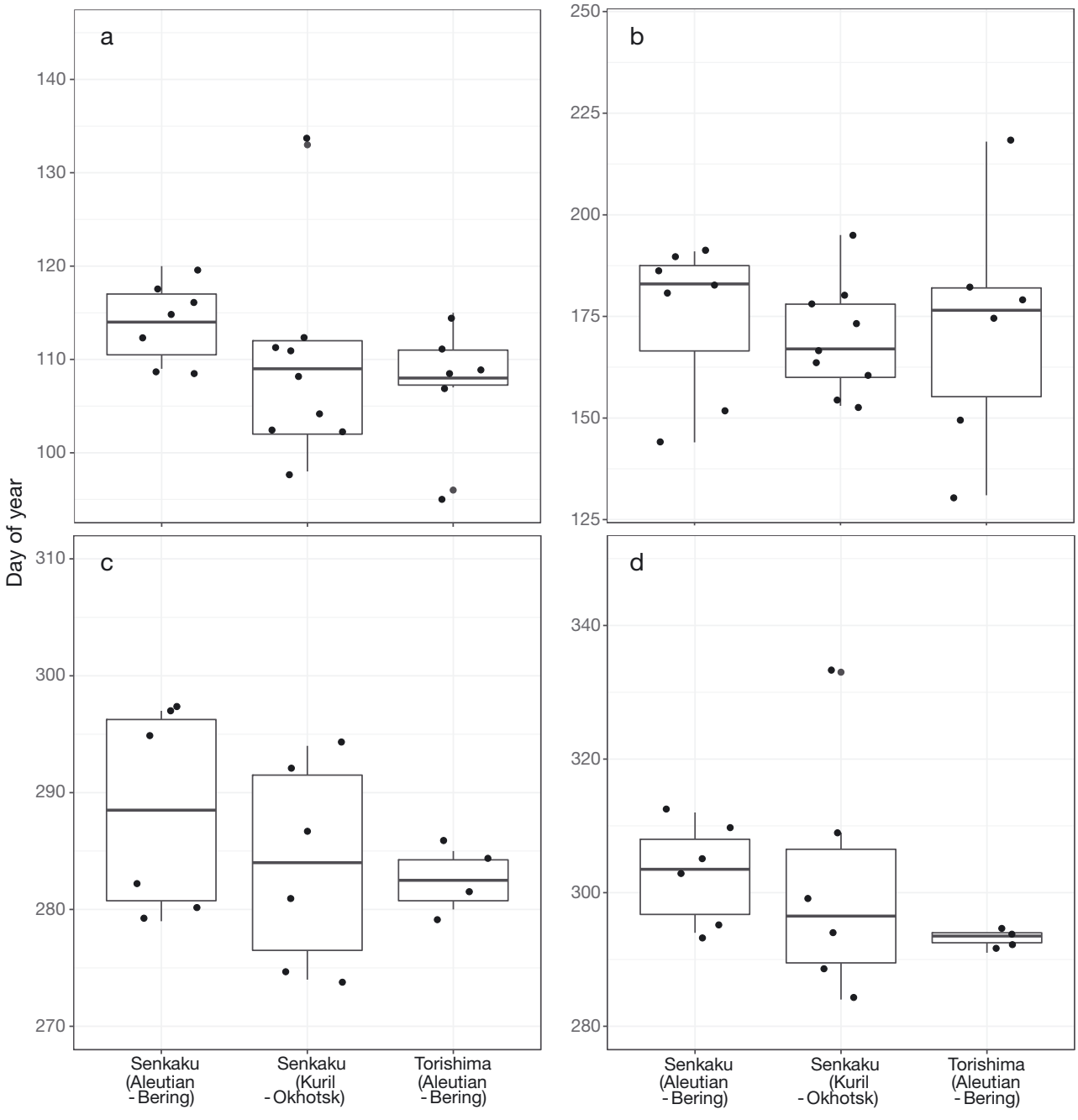

Fig. 5. Dates (day of year) of (a) departure from the breeding colony area, (b) arrival at the nonbreeding area, (c) departure from the nonbreeding area, and (d) return to the breeding colony region (within < 500 km) differed among albatrosses of the Torishima type, Senkaku type that used the Kuril–Okhotsk area, and Senkaku type that used the Aleutian–Bering area. Boxplots show the median (bold line) with box endpoints at the 25th and 75th percentiles, and whiskers show the 90th and 10th percentiles

Islands are known to be highly biologically productive areas (Springer et al. 1996, Hunt & Stabeno 2005), providing key foraging areas for several seabird species, including the short-tailed albatross during the nonbreeding period (Suryan et al. 2006, Suryan & Fischer 2010), and more generally throughout the year (Piatt et al. 2006).

On the other hand, only about half of the birds of the Senkaku type used the Aleutian–Bering area during the nonbreeding period, while the other half were unique in distributing in the Kuril–Okhotsk area. This region, although geographically distant from the former, shares similarities with the Bering Sea in terms of oceanographic habitats available for the birds: it

supports high biological productivity associated with spring ice-edge blooms as well as autumn blooms (Mustapha et al. 2009, Radchenko et al. 2010). Both regions also experience dynamic movements of these cold-water masses with enhanced biological productivity, under the influence of important water currents, notably the Bering Slope Current for the Bering Sea, which in turn generates the East Kamchatka Current flowing towards the Kuril Islands (Kinder & Coachman 1978). Similarly to the Bering Sea, the Kuril—Okhotsk region thus provides important habitats for seabirds, across seasons (e.g. Suryan et al. 2007, Fleishman et al. 2019). Although the Kuril—Okhotsk area is a part of the historical distribution range of short-tailed albatrosses (Hasegawa & DeGange 1982, Eda et al. 2012, 2016b), there have been only a few observations of this species in the Sea of Okhotsk through the years 1940—2012 (ACAP 2009). Such scarcity is coherent with the small estimated numbers of Senkaku-type birds, assuming that only these birds would visit this area as suggested from our limited sample sizes. The fact that all studied birds from both types appeared to be males helps to make our study more conclusive by eliminating sex as one potential confounding factor of the variability observed in the movement patterns from these small sample sizes.

Sex-specific patterns have been highlighted in the at-sea distributions of albatrosses (e.g. Weimerskirch & Jouventin 1987), including in the short-tailed albatross. Suryan et al. (2007) found that males spent more time in the Aleutian—Bering area, while females distributed mostly offshore Japan and the Kuril Islands, in addition to the Aleutian chain region, during the nonbreeding season. A conservative hypothesis, based on both our results (from both genetic groups, but only males) and those of Suryan et al. (2007; from likely Torishima-type birds only, but both sexes), would be that Senkaku-type birds may distribute in the Kuril—Okhotsk area during the nonbreeding period, at least to the same extent as their male counterparts. However, because such differences in movement patterns between sexes may vary among genetic groups (e.g. more prevalent sedentary behaviour observed in female wandering albatrosses of one group, Weimerskirch et al. 2015), tracking females of both types will be needed in the future. For now, our study newly reveals differences in the at-sea distribution of birds between the 2 types, even if this result may be within a single sex; this finding was not foreseen from previous studies.

These results are in line with the general hypothesis that divergent at-sea distribution patterns during the nonbreeding season maintain genetic structuring between seabird populations (Friesen et al. 2007a). However, the 2 short-tailed albatross groups did not have fully distinct spatial distributions. This result is remarkably coherent with previous research (Eda et al. 2016a) showing that birds from Torishima and the Senkaku Islands mate assortatively but with an incomplete pre-mating isolation. In our study, it was unclear why 3 Senkaku-type birds used the Aleutian—Bering area, similarly to the Torishima-type birds. This result reflected a higher inter-individual flexibility than expected in the destination of their migrations, within a genetic type. Such flexibility has previously been highlighted in comparative studies on the migration strategies of 2 genetically similar, neighboring populations of the wandering albatross *Diomedea exulans*: one population showed consistently extensive migrations during the nonbreeding period, while in the other, a range of diverse strategies was noted (Weimerskirch et al. 2015). The flexibility of migration strategies among individuals within a group may thus vary extensively between groups; importantly, in the latter study, as in ours, each bird was consistent in its movement strategy across years, suggesting that this flexibility is nevertheless limited on an individual level.

However, the inter-individual variation in at-sea distribution that was observed in our study is likely not the result of age-specific differences. Previous studies showed that first- and second-year birds that fledged from Torishima and Mukojima used several areas, including the Kuril—Okhotsk and Aleutian—Bering areas, in June—August, while adults only used the shelf slope and outer shelf of the Aleutian—Bering area (Suryan et al. 2007, Orben et al. 2018). In our study, 11 of all 12 tracked birds were over 5 yr old and the other bird was 3 yr old, based on metal rings attached at the chick stage, and on the plumage pattern (Konno et al. 2018). All study birds were thus adults, and we can consequently rule out the age-class factor here, which is known to increase the diversity of destinations observed in younger birds.

Previous studies suggested that in the Senkaku Islands, short-tailed albatrosses started their migration ~2 wk earlier than their counterparts breeding at Torishima (Kuroiwa 1900a,b, Miyajima 1900, Hasegawa 2006). In our study, we did not find clear differences in the timing of migration between the 2 types breeding at Torishima, based on their at-sea distribution rather than on direct observation of colony attendance. Recent large-scale analyses on oceanic migratory birds showed that individuals were able to adjust their time spent at the nonbreeding area, which allowed to buffer the variation in timing of migration

(van Bemmelen et al. preprint https://doi.org/10.1101/2023.05.27.542544). In the latter study, birds with more distant areas spent gradually more time on migration and less time at their nonbreeding areas: thus, despite large individual variation in migration distances, the sympatric birds were able to arrive at their breeding area synchronously. In our study, sample sizes were likely too small to clearly identify such adjustments, but it is plausible that the albatrosses may be able to time their movements as well according to migration distance from/to the nonbreeding area, which would explain that their observed timing of departure from or return to the colony was not clearly different among groups. It is thus desirable to increase sample sizes in future studies to clarify the trend in this non-significant difference among bird types, especially in their timing of return into the breeding area. As of now, this coherent timing does not support the hypothesis that divergent migration strategies during the nonbreeding period are associated with genetic differentiation in the short-tailed albatross. Our results showed only partial segregation of the areas used by the 2 bird types, with common movement patterns shared by individuals from both types (see above). The absence of absolute spatial segregation in this case, with instead a partial mixing of the 2 groups over the Aleutian–Bering area, is thus likely to minimize the potential difference of timing between the 2 groups. Indeed, as could be expected from more samples being available for the Senkaku-type birds, the dates of return to the breeding colony region varied more within the Senkaku type (10 October to 29 November, n = 12) than within the Torishima type (17–20 October, n = 4; Table 1). However, this observation may also be related to our limited sample sizes overall, which may prevent us from detecting any difference in these timings. Moreover, the migration of seabirds in the north-west Pacific has been shown to closely follow the timing of surface biological productivity over successive areas (Takahashi et al. 2015), presumably reflecting the birds adjusting to the seasonal profitability of the foraging areas. In this context, the lack of significant difference in movement timing between the 2 bird groups is coherent with the fact that phytoplankton blooming phenology does not differ greatly between the Okhotsk and Bering Seas (Sasaoka et al. 2011). Indeed, the birds generally left their nonbreeding areas in October, immediately following the second, i.e. autumn, bloom occurring in both regions at that time (Hunt et al. 2002, Takahashi et al. 2015).

Thus, yet another isolation mechanism between the 2 groups (e.g. courtship behavior) is likely to be more important as a proximate factor than the timing of migration. Some differences in courtship displays between the Torishima and Senkaku types have been observed (F. Sato pers. obs.), which may contribute to disassortative mating and genetic isolation. In particular, it is suggested that 'duet' behavior, i.e. displaying simultaneous 'yapping' and uttering gruff sounds or slightly opening the bill, may be particularly important in strengthening the pair-bond in albatrosses, as it could be used for individual recognition (Jouventin & Lequette 1990, Tickell 2000, Pickering & Berrow 2001). At this point, further field studies are therefore needed to clarify the mechanism responsible for genetic structuring in this colony.

New knowledge on the ecology of these 2 cryptic types is likely to benefit their conservation and/or more adequate management of their habitats. It was previously established that the 2 short-tailed albatross sub-groups, breeding at the same colony, have distinct genetic structure (Eda et al. 2020). The Senkaku-type birds are assumed to have immigrated from another population, likely from the Senkaku Islands. For that source population, the combination of (1) historical records, (2) genetic typing of bones of this species found at the Hamanaka 2 and Funadomari sites on Rebun Island in the northern Japan Sea off Hokkaido (Eda et al. 2012, 2016b; Fig. 1) and at the Yuquot site in British Columbia, Canada (Royle et al. 2022), and now (3) the finding of their migration route to the Kuril–Okhotsk area after breeding (this study) suggests that the birds breeding in the Senkaku Islands may also use the Kuril–Okhotsk area during the nonbreeding season. This provides an important insight for defining the relevant management units of this species. Previous studies on other Procellariiformes have shown that divergent at-sea distribution of sub-groups can lead to differential threat levels on their respective individual survival rates, with contrasted exposure to stressors such as fisheries and pollutants (Watanuki et al. 2015, Weimerskirch et al. 2015). Short-tailed albatrosses, like many other albatrosses and petrels, are threatened by commercial fisheries including longline, trawl, and gillnet fisheries (Suryan et al. 2007, Melvin et al. 2011, Žydelis et al. 2013, Orben et al. 2021). Japanese salmon gillnet fisheries were operating intensively in 1950–1990 in both regions utilized by the Senkaku-type birds tracked in our study (DeGange et al. 1985, Ogi 2008). After the closure of gillnet fishing in international waters in 1993, Japanese salmon gillnet fisheries operated in the Russian Exclusive Economic Zone in the Okhotsk Sea until 2016 (Nagasawa 2011), while

demersal longline fisheries from the USA have operated intensively in the Aleutian–Bering area (Fischer et al. 2009, Phillips et al. 2010). Such spatial discrepancies in the additional risk of mortality at sea across the distribution areas of short-tailed albatross populations might have historically affected one population of birds more than the other, as already suspected in other sister species of albatrosses (Weimerskirch et al. 1997). In addition, the concentration of bioaccumulative organochlorine pesticides including DDTs and HCHs in organs of salmon species from the Western Bering Sea is known to be higher than that in salmon from the Okhotsk Sea (Tsygankov et al. 2016). In contrast, mercury concentrations in the primary feathers of short-tailed shearwaters *Ardenna tenuirostris* that spent the nonbreeding period in the Okhotsk and northern Japan Seas were higher than in birds that used the eastern Bering Sea (Watanuki et al. 2015). Finally, the total anthropogenic load including marine litter and exploration levels of marine resources (i.e. mineral, gas, and oil) in the Okhotsk Sea is expected to be higher than in the West Bering Sea (Kachur et al. 2019). These area-specific variations in the intensity of stressors may hence impact short-tailed albatrosses differentially, according to their at-sea distribution and thus to their genetic type. Such differential risk levels have previously been reported in several albatross and shearwater species (e.g. Barbraud et al. 2013, Leat et al. 2013, Weimerskirch et al. 2015, Cherel et al. 2018, Dias et al. 2019). Thus, echoing previous recommendations based on genetic, mate choice, and morphology studies in this species (Eda et al. 2016a, 2020), the results collected in this study on the at-sea distribution of birds during the nonbreeding period strongly suggest that, despite small sample sizes, the short-tailed albatross of the Torishima and Senkaku types should be treated as different management units, for the sake of effective conservation actions.

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