

主論文

Foraging behavior of streaked shearwaters during the chick-rearing period
in relation to marine environments

(育雛期におけるオオミズナギドリの採餌行動と海洋環境の関係)

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Chapter 1:

General Introduction

1.1. Introduction

Seabirds are top predators and represent the top of the food web in the marine ecosystem; therefore, their behavior, breeding ecology, and population dynamics might be affected by changes in marine environments, including physical environments or lower trophic levels (Parsons et al. 2008). To understand the seabird reproductive and/or population dynamics, it is necessary to describe their foraging behavior and location in relation to marine environments. As seabirds are likely to be sensitive to changes in prey environments (Furness & Camphuysen 1997), their foraging behavior and location would change corresponding to changes in marine environments. In particular, as seabird parents should balance chick provisioning and self-feeding during the chick-rearing periods, their foraging behaviors are considered to be more likely to respond sensitively to the marine environment under constraints. Furthermore, there might be sexual differences in foraging behavior and location during their breeding season, because their flight performance can be affected by sexual size differences as well as environmental conditions such as wind fields. For instance, as heavier males have higher wing loading than females do, it might be hypothesized that seabird males can travel long distances and behave flexibly in response to changes in marine environment during their breeding season. Thus, seabird foraging behavior should be considered in terms of the relationship with the environments and/or behavioral

differences between males and females.

As seabirds are highly mobile animals, research methods pertaining to the study of seabird behavior, especially movement, had been limited to direct observation from vessels or coasts until the 1990s. However, research of seabird behavior has been advanced by the development of bio-logging techniques that allow the attachment of microelectronic recorders on the animal's body and record the animal's behavior and/or the surrounding environments. This technology can be used to record their locomotion; physiology; foraging behavior; physical activities such as wing motion; social activities; and ambient environments (Burger & Shaffer 2008, Takahashi & Yoda 2010). Therefore, it is now possible to clarify foraging behavior and locations in detail using the bio-logging techniques.

To reveal the behavioral response of seabirds to the marine environment, it might be a good research strategy to apply bio-logging techniques in characteristic marine environments. For example, it may be easier to determine areas where productivity is high in coastal regions with river plumes rather than in open oceans. Moreover, the relationship between the marine environment and seabird behavior should be examined by comparing interannual changes in seabird foraging behavior and marine environments. However, previous studies compared data recorded in limited years using small sample sizes. To understand seabird behavioral changes, in response

to changes in marine environments, it is necessary to use a multiyear data set.

The main aim of this thesis is to clarify the foraging behavior in relation to marine environments. I tracked the movements of streaked shearwaters *Calonectris leucomelas* (Figure 1.1) during their chick-rearing period using the bio-logging method to examine how they forage in response to marine environmental changes.

The streaked shearwater is a pelagic seabird that belongs to the Procellariiformes, breeding on islands distributed from 24–42°N and 121–142°E in East and Southeast Asia (Oka 2004). They return to the breeding colonies in mid-March following a migration to tropical regions: the seas off northern New Guinea, South China Sea, and Arafura Sea (Yamamoto et al. 2010). In mid-to late June, they lay a single egg in burrows and incubate it for 50–55 days (Yamamoto et al. 2012). Chicks hatch in early to mid-August, and parents provision them for 78–82 days (Oka et al. 2002). They fly to wintering regions in November (Figure 1.2). They represent sexual dimorphism: males wing spans are larger than those of females (Shirai et al. 2013, Yamamoto et al. 2016). They forage on pelagic fish such as Japanese anchovies, *Engraulis japonicus* (Kurasawa et al. 2012, Matsumoto et al. 2012). Streaked shearwaters are central-place foragers that move between their colony and foraging locations during the chick-rearing period, and tracking data including multiple foraging trips can be obtained from the same individuals.

The fieldworks were conducted on Meshima Island (31.6°N, 128.2°E) in Nagasaki Prefecture (Chapter 2) and Awashima Island (38.4°N, 139.2°E) in Niigata Prefecture Japan (Chapter 3), during the shearwaters' chick-rearing period. Meshima Island is in the East China Sea. The population of streaked shearwaters on Meshima Island is estimated to be a few thousand birds (Oka 2004). The Changjiang River is one of the largest rivers and discharges large amounts of fresh water into the East China Sea. It might be expected that the river discharge plume affects seabirds' foraging distributions. In contrast, Awashima Island is located in the Sea of Japan, within the Tsushima Current. The population of streaked shearwaters on Awashima Island is estimated to be approximately 84,000 birds (Yamamoto et al. 2011). The shearwaters on Awashima Island forage both in the Sea of Japan and the Pacific Ocean. The Sea of Japan and the Pacific Ocean differ in terms of foraging environments, and this difference is expected to emphasize differences in foraging behaviors of streaked shearwaters.

In Chapter 2, I examine the relationship between the foraging location of streaked shearwaters breeding on the island in the East China Sea and oceanographic features, such as large river discharges. In Chapter 3, I investigate the effect of wind condition and marine environment on sex differences in streaked shearwaters breeding in the Sea of Japan. Finally, in Chapter 4, I discuss the main results obtained in this

study and examine how seabirds forage in response to changes in marine environments.

1.2. Figures



Figure 1.1.

Streaked shearwater *Calonectris leucomelas* on its colony ground on Awashima Island, Niigata, Japan.

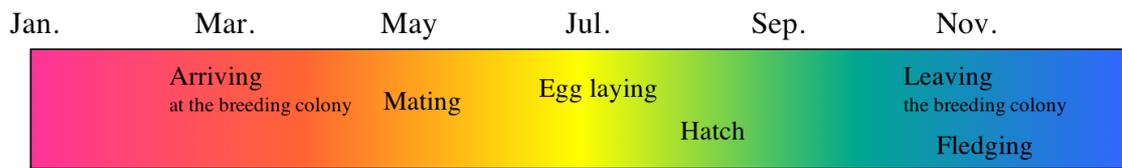


Figure 1.2.

A schematic diagram showing the annual cycle of streaked shearwaters.

Chapter 2:

The Changjiang River discharge affects the distribution of
foraging seabirds

2.1. Introduction

Freshwater discharge from large rivers (e.g. the Amazon and the Mississippi) is known to enhance oceanic primary production by supplying nutrients into the sea, inducing upwelling by convergent fronts, and/or generating vertical stability of the water column, thus influencing the marine ecosystem on the shelf (Lohrenz et al. 1990, Drinkwater & Frank 1994, Smith & Demaster 1996). Herbivorous zooplankton are often aggregated in enhanced primary production areas, which in turn generally attracts assemblages of forage fish and any predators that feed on them, such as seabirds (Hunt et al. 1999). Therefore, I expect that areas under the influence of river discharge should attract foraging seabirds, though only a few studies have considered the ecological role of such areas (Dias et al. 2012, Zamon et al. 2014).

The East China Sea (ECS) is one of the largest marginal seas, and 70% (0.9×10^6 km²) of its area is occupied by the continental shelf. The Changjiang River (Yangtze River) is the largest in Asia and discharges large amounts of water (an annual mean discharge of 30×10^3 m³ s⁻¹; Beardsley et al. 1985) with abundant nutrients into the upper layer of oceanic water in the ECS (Gong et al. 2003, Chen 2009), supporting high biological production (Gong et al. 2011). Here, I tracked a streaked shearwater breeding on an island in the ECS (ca. 600 km from the estuary of the Changjiang River) to examine how the river discharge plume affects their foraging distributions.

2.2. Materials and Methods

Fieldwork was conducted at Meshima Island in the Danjo-gunto archipelago (31.6° N, 128.2° E; Figure 2.1 a) on 8th September 2010. I attached a solar-powered GPS-PTT (GPS = Global Positioning System, PTT = Platform Transmitter Terminal) (28 g, 62 × 22 × 14.5 mm with 178 mm antenna, Microwave Telemetry) to the back feathers of 6 randomly chosen streaked shearwaters using Tesa® tape (Figure 2.2). During the breeding season, streaked shearwaters utilize large areas at sea and surface-feed on pelagic fish (Matsumoto et al. 2012). Although data are limited, anchovy were identified in the stomach contents from several individuals of the study colony that regurgitated at the time of their capture (S. Matsumoto unpublished data). The GPS-PTT was programmed to record fixes every 2 h during the daytime (06:00, 08:00, 10:00, 12:00, and 14:00 h). Two birds were tracked until 22nd September and 1st October 2010, respectively. For the rest of the birds, positions were recorded until 1st, 9th, 23rd, and 27th November 2010 (Figures 2.3 & 2.4, Table 2.1), respectively. Streaked shearwaters migrate southward to tropical oceans during their non-breeding period, and the start of migration was determined through analyzing the rapid southward movement by the tracked birds. I analyzed their positions during the chick-rearing period (9th September–20th October), including 33 ± 12 d of tracking data (Figure 2.5). All data

were pooled for further analysis (Figure 2.1 b). I estimated the 95% (foraging area) and 50% (core area) utilization distributions of tracked streaked shearwaters using the kernel estimation method in the ESRI ArcGIS 10.2.2 Spatial Analyst tool. The smoothing parameter (h) was determined by least squares cross validation using the Home Range extension for ArcView 3.3. Bird density close to a breeding colony is sometimes high due to geometric spreading because birds move to and from the island; therefore, I subtracted concentrically predicted density values from the kernel density estimation, following the formula in Yamamoto et al. (2015).

Monthly mean sea surface temperatures (SSTs) and chl *a* concentrations in September and October 2010 (0.025° resolution, measured by Aqua-MODIS) were downloaded from NOAA BloomWatch 180 (http://coastwatch.pfel.noaa.gov/coastwatch/CW_Browser_WW180.jsp), and the values in each cell were averaged. A generalized additive model (GAM) was used to identify the characteristics of shearwater oceanographic habitat (Yamamoto et al. 2015). Values for the kernel density (ranging from 0 to 1) using the kernel estimation method and oceanographic variables at each cell within the area 25–40° N and 120–135° E were determined, and a smoothed spline fit with predictors was used in the GAMs, assuming a binomial distribution with the logit link function. I treated kernel density as response variables and oceanographic parameters as explanatory variable in the models.

Statistical analyses were done in R software, version 3.2.2 (R Development Core Team 2014), using the package mgcv.

All experiments were performed according to a protocol approved by the Institutional Animal Care and Use Committee of Nagoya University. This work was conducted with permits from the Ministry of the Environment.

2.3. Results

The foraging area (95% utilized area) of streaked shearwaters was distributed over large areas in the ECS and the Yellow Sea as well as a small area along the east coast of the Korean Peninsula, while the core foraging area (50% utilized area) was concentrated on the north of the ECS (Figures 2.5 & 2.6).

The tracked birds used areas with SSTs of 19.6 to 28.4°C and chl *a* values of 0.14–15.06 mg m⁻³ (Figures 2.7 & 2.8). According to the model response curves, the probability of occurrence was high in relatively productive water (peaked at 1.70 mg m⁻³) and SSTs of around 25°C (Figure 2.7).

2.4. Discussion

In this study, streaked shearwaters foraged mostly in the northern part of the ECS rather than searching in all directions including the warm waters influenced by the

Kuroshio. A small portion of the foraging area was also found along the east coast of the Korean Peninsula, as 1 individual concentrated foraging on this region (Figure 2.5). As I attached the GPSs to randomly selected individuals of unknown breeding status, this individual probably did not breed and occupied different areas from the breeders (Yamamoto et al. 2015).

Within the possible foraging range, the tracked birds foraged intensively in the offshore waters of the ECS. Previously, Kim et al. (2009) examined water mass characteristics in the ECS using salinity data measured by an oceanographic survey and chl *a* data measured by satellite and suggested that areas with relatively high chl *a* (0.49–1.82 mg m⁻³) can be considered as the Changjiang plume. The model results showed that streaked shearwaters concentrated their foraging in areas with high chl *a* (1.70 mg m⁻³) and SSTs of around 25°C (Figures 2.7, 2.8 & 2.9), which corresponded to conditions most likely associated with the outflow from the Changjiang River. In the continental shelf region of the western ECS, the hydrography is mainly characterized by the northeastward-flowing Taiwan Warm Current, which is a branch of the Kuroshio, and the southward-flowing Yellow Sea Coastal Current (Ichikawa & Beardsley 2002) (Figure 2.1 a). The intrusion of the Changjiang plume extends far offshore to the northeast in association with these currents in concert with summer monsoon winds (Beardsley et al. 1985, Lie et al. 2003). Freshwater discharge from a large river is

known to enhance oceanic biological production by supplying nutrients into the sea (Lohrenz et al. 1990, Smith & Demaster 1996). Enriched nutrient conditions and thus intensive primary production have been especially observed around the Changjiang River estuary and also as a tongue-like distribution toward offshore from the mouth of the river (Chen 2009, Figure 2.7), which represent major fish assemblage areas in the ECS (Gong et al. 2003, 2011, Chen et al. 2014). Japanese anchovy, the main prey for streaked shearwaters, is one of the most abundant forage fish species in the ECS and adjacent Yellow Sea (Iversen et al. 1993, Ohshimo 1996, Jin et al. 2003), estimated to make up ca. 3 million tons (Xianshi 2008). In the area off the Changjiang River, anchovy spawning takes place from April to October, with the peak season in May and June (Ohshimo 1996, Iseki & Kiyomoto 1997, Kim et al. 2005). Along with the northeastward extension of the Changjiang plume in the surface layer, a huge spawning ground develops offshore over hundreds of kilometers from the Changjiang River estuary, and early larval stages of anchovy are distributed along outflows of the Changjiang River (Iseki & Kiyomoto 1997, Jin et al. 2003, Kim et al. 2005, Chen et al. 2014). Hence, the abundance of prey should be high in the zones of the Changjiang plume. In addition to enhancing primary productivity, in the zones of the Changjiang plume, a strong vertical thermohaline front exists at the subsurface during the summer as a result of low-salinity fresh water (Kim et al. 2005, Park & Chu 2006). Schools of

anchovy are often distributed in the upper layers above the thermocline (Ohshimo 2004), which should be beneficial to surface-feeding streaked shearwaters and provide a favorable foraging spot for them in the ECS. This is possibly one of the reasons why shearwaters did not forage in all available productive waters, such as the coastal waters along the continent.

The results suggest that river discharge, which enhances oceanic primary and secondary productions (Gong et al. 2003, 2011, Chen et al. 2014), acts as a large spatial-scale physical oceanographic feature of prey availability, not only in coastal waters (Dias et al. 2012, Zamon et al. 2014) but also in offshore waters.

2.5. Figures and Tables

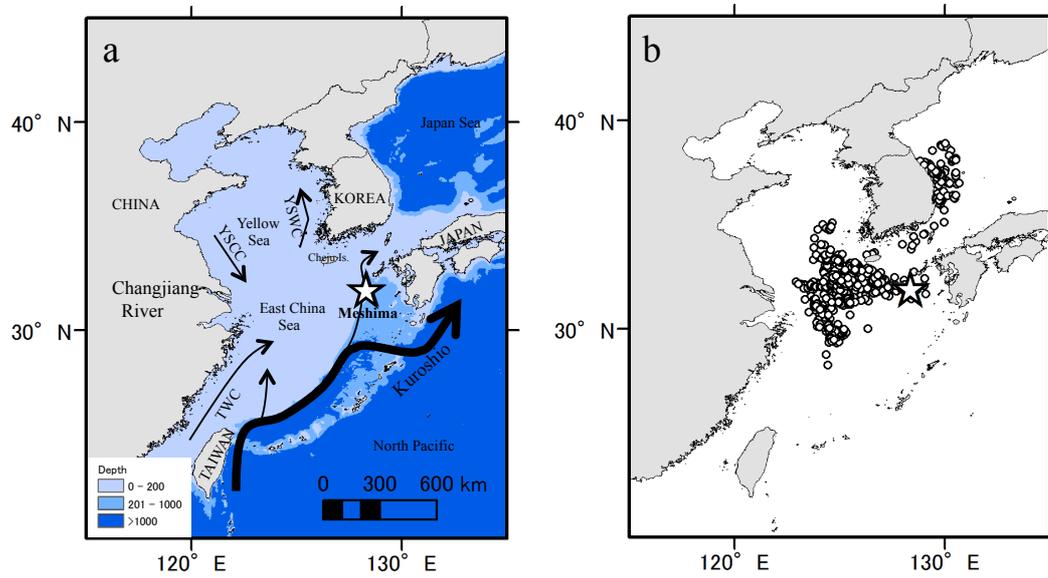


Figure 2.1.

(a) Oceanographic features in the East China Sea overlaid on its bathymetry (modified from Beardsley et al. 1985). Arrows indicate currents: Kuroshio, Taiwan Warm Current (TWC), Yellow Sea Coastal Current (YSCC), and Yellow Sea Warm Current (YSWC).

(b) GPS positions of streaked shearwaters during the chick-rearing period (9th September–20th October 2010). Star indicates the study colony.



Figure 2.2.

GPS-PTT attached on shearwater's back.

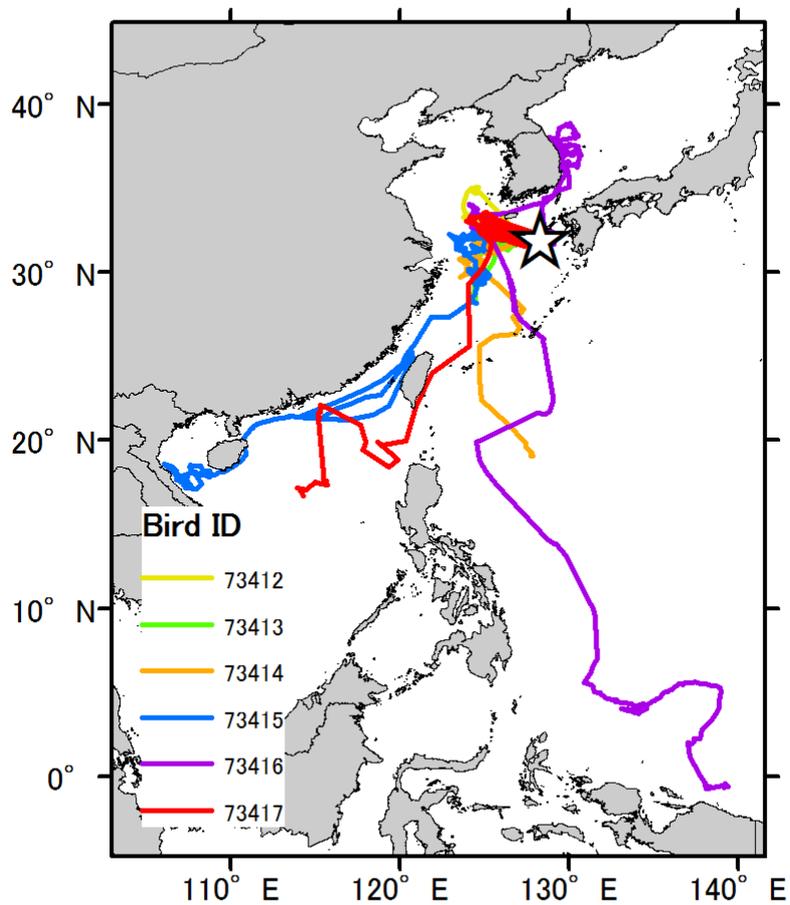


Figure 2.3.

GPS tracks of streaked shearwaters obtained from 8th September 2010 (next day of the GPS deployment) to the last position (22nd September–27th November).

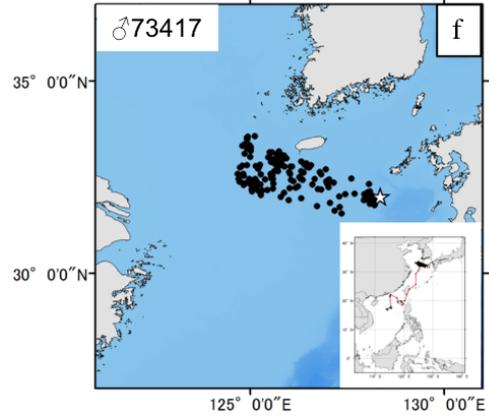
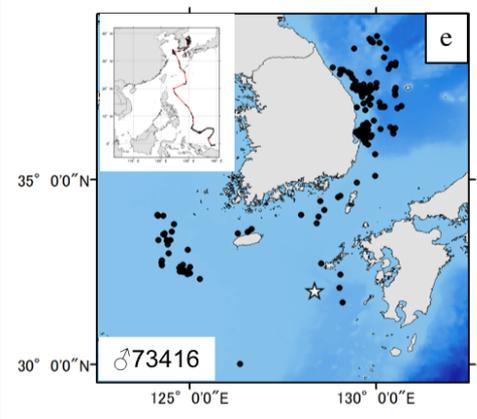
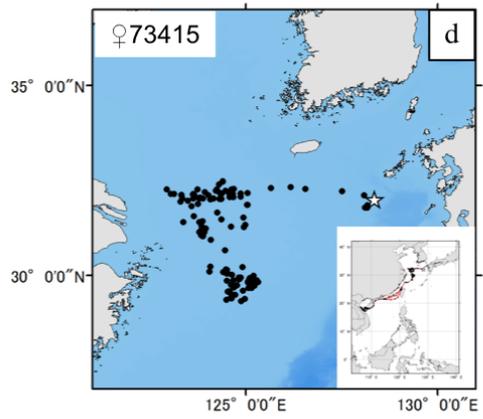
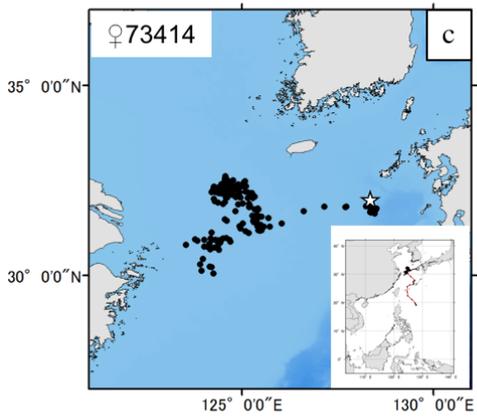
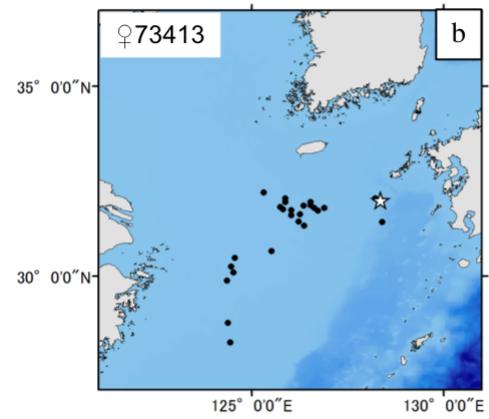
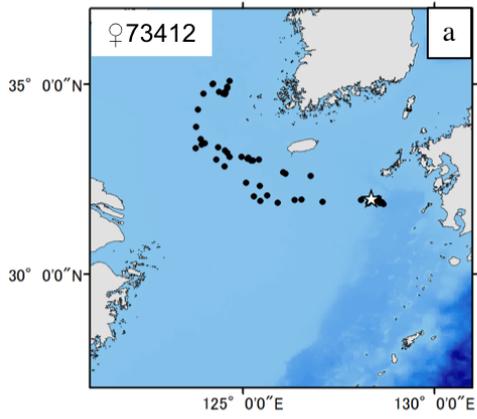


Figure 2.4.

Individual tracks of streaked shearwaters obtained from 8th September 2010 (next day of the GPS deployment) to the last position (22nd September–27th November).

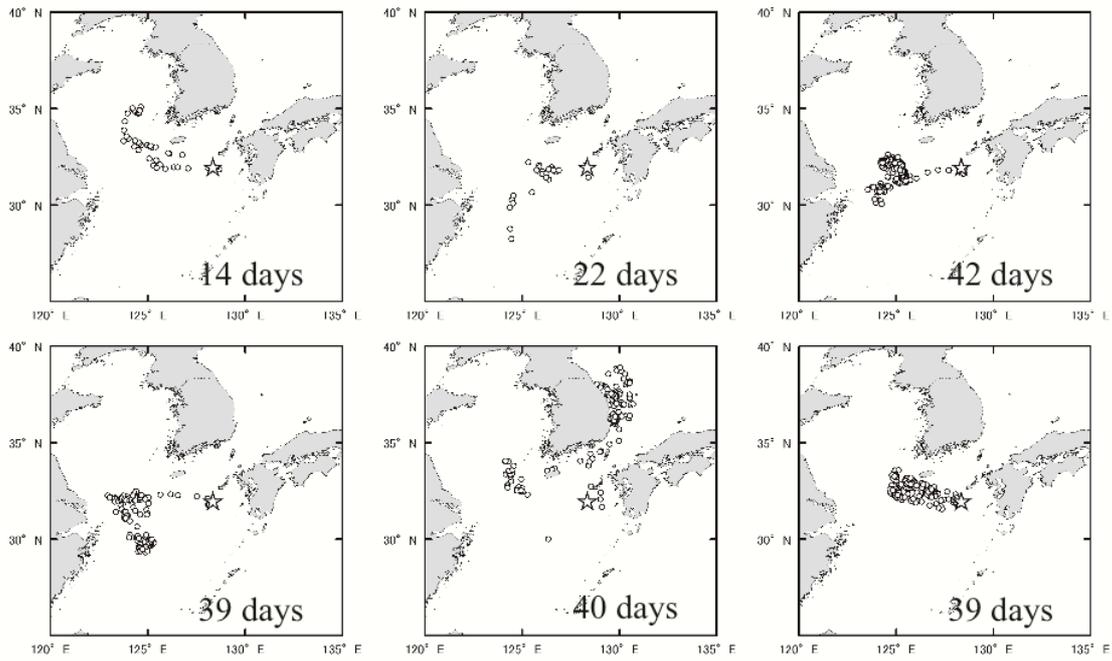


Figure 2.5.

Individual tracking maps of streaked shearwaters during the chick-rearing period from 8th September 2010 (next day of the GPS deployment) to the start of migration (18th–21st October). Days tracked for each individual are shown.

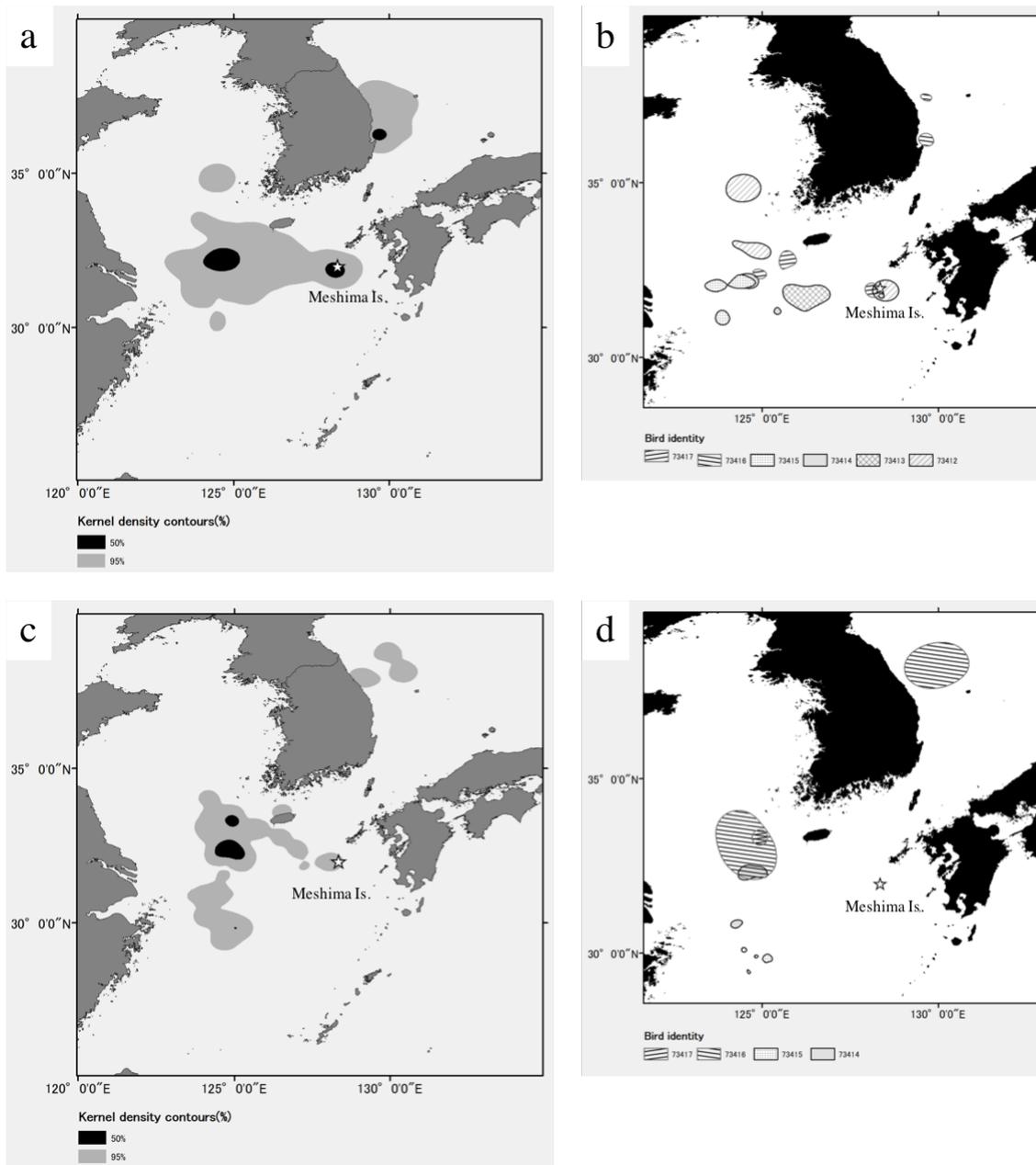


Figure 2.6.

Utilization distributions of pooled data (95% foraging area [grey] and 50% core area [black]) of streaked shearwaters in (a) September and (c) October. 95% foraging area of individuals in (b) September and (d) October.

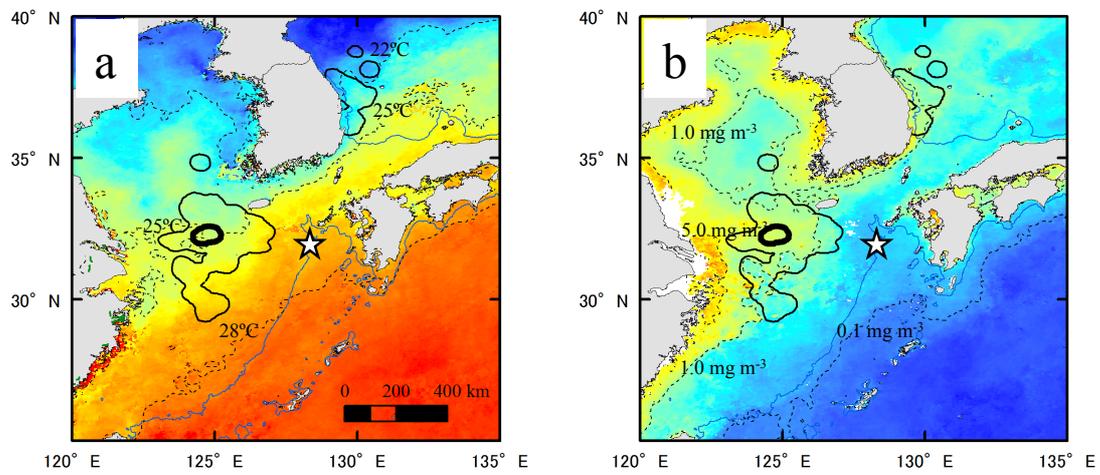


Figure 2.7.

Utilization distributions (95% foraging area [thin line] and 50% core area [thick line]) of streaked shearwaters overlaid on (a) mean sea surface temperature (SST) in September and October 2010 and (b) mean chl *a* concentration in September and October 2010 in the area within 25–40°N, 120–135°E. Broken lines indicate 22, 25, and 28°C SST in (a) and 0.1, 1.0, and 5.0 mg m⁻³ chl *a* in (b); star indicates the study colony; blue line indicates 200 m depth.

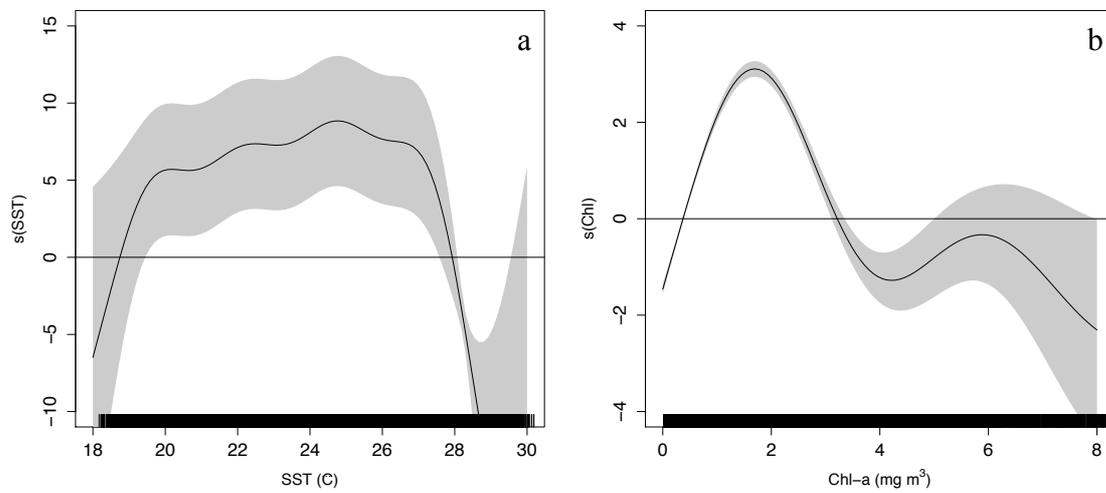


Figure 2.8.

Response curves of environmental variables in the oceanographic habitat model (generalized additive model) of streaked shearwaters foraging in the East China Sea: (a) sea surface temperature (SST) and (b) chl *a* concentration. Solid line: regression estimated by the model; shading: 95% confidence intervals.

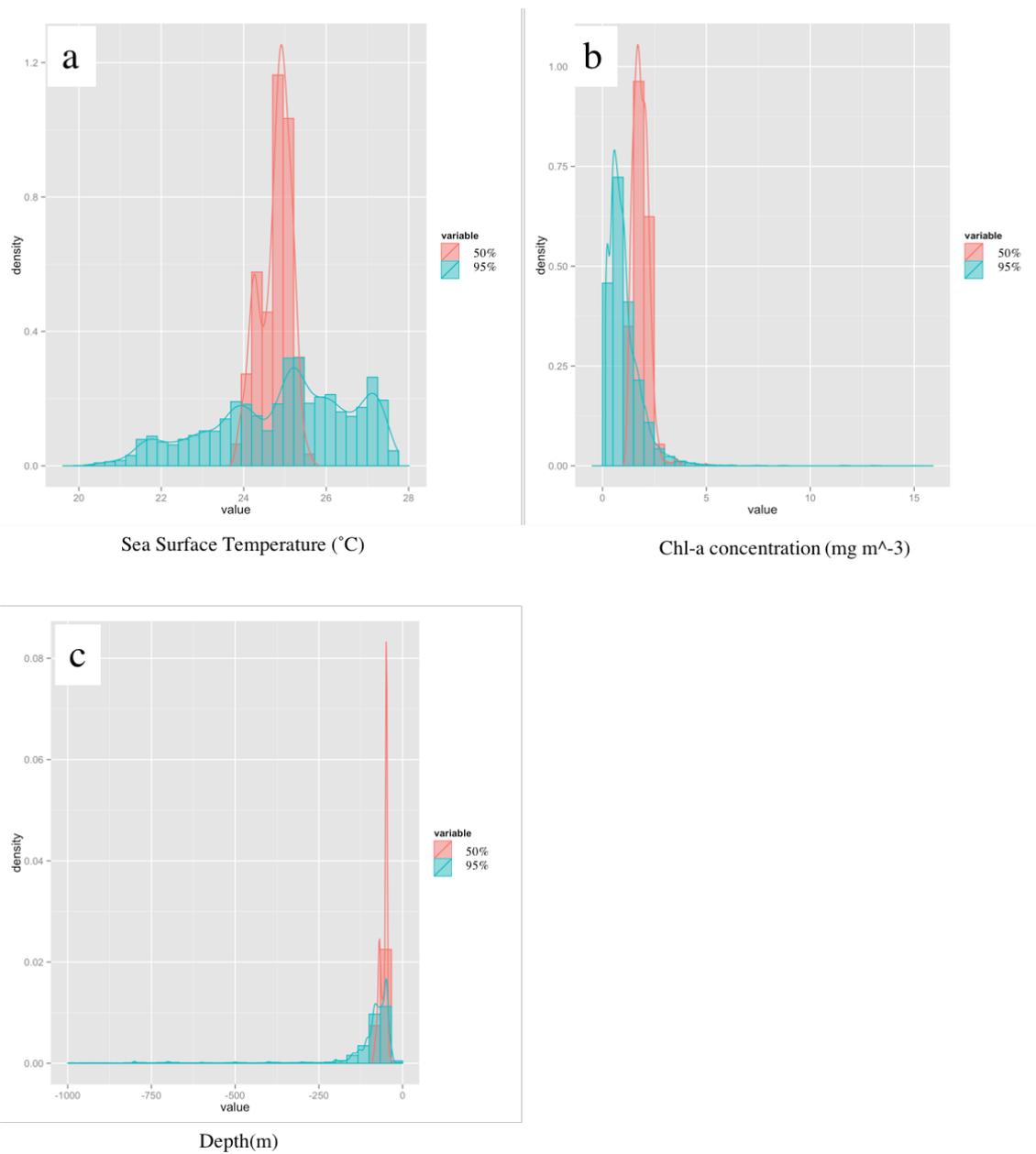


Figure 2.9.

Histograms of (a) mean sea surface temperature (SST) in September and October 2010, (b) mean chl *a* concentration in September and October, and (c) depth within 95% foraging area [green] and 50% core area [red].

Table 2.1.

Summary of the data obtained from GPS-PTT tracked streaked shearwaters.

Shearwaters ID	Sex	Weight (g)	Date of equipment	Date of first position	Date of last position	Tracking duration (day)	Max flight distance (km) (chick-rearing period)	Total distance traveled (km)	Date of migration start
73412	Female	500	08/09/2010	09/09/2010 10:00	22/09/2010 9:00	14	510	2365	-
73413	Female	522	08/09/2010	10/09/2010 17:00	01/10/2010 11:00	22	561	1872	-
73414	Female	515	08/09/2010	09/09/2010 12:00	01/11/2010 8:00	54	477	4919	21/10/2010
73415	Female	477	08/09/2010	09/09/2010 6:00	27/11/2010 16:00	80	490	8908	18/10/2010
73416	Male	490	08/09/2010	09/09/2010 10:00	23/11/2010 8:00	76	780	10872	19/10/2010
73417	Male	565	08/09/2010	09/09/2010 14:00	09/11/2010 15:00	62	364	10510	18/10/2010

Chapter 3:

Sex-related differences in the foraging movement of
streaked shearwaters breeding on Awashima Island
in the Sea of Japan

3.1. Introduction

Identifying at-sea foraging habitat is an essential aspect of the biology of seabirds (Ballance 2007, González-Solís & Shaffer 2009). Seabirds rely on various physical oceanographic features to predict enhanced resource availability (Hunt & Schneider 1987, Hunt 1990, Hunt et al. 1999, Pinaud & Weimerskirch 2007, Weimerskirch 2007, Chapter 2). Foraging habitats are not equally utilized by individual birds and both inter-and intra-specific habitat segregation are known to occur (Cairns 1989, González-Solís et al. 2000, Lewis et al. 2002, Grémillet et al. 2004, Votier et al. 2011, Yamamoto et al. 2011).

Further, sex-related differences in foraging areas are well-known among seabirds. Such sex-specific foraging areas have been attributed to the different reproductive roles and energy or nutrient requirements of the sexes (Phillips et al. 2004, Ruckstuhl & Neuhaus 2005, Peck & Congdon 2006, Yamamoto et al. 2011) or niche specialization owing to sexual differences in morphology (Shaffer et al. 2001, Lewis et al. 2002, 2005, Weimerskirch et al. 2012), thereby resulting in competitive exclusion between the sexes (González-Solís et al. 2000, 2008). In addition, winds are likely to increase the effect of sexual dimorphism in size on flight performance, which determines the accessibility of foraging habitats for flying seabirds (Shaffer et al. 2001, Phillips et al. 2004, Weimerskirch et al. 2012).

Previous studies of streaked shearwater population breeding on Awashima Island in the Sea of Japan have been found that only males transited the Tsugaru Strait into the Pacific Ocean during the incubation period (Yamamoto et al. 2012). In this study, I investigated the sex-related differences in foraging movements during their chick-rearing period. Male streaked shearwaters are larger bodied and have higher wing loading than females (Shirai et al. 2013, Yamamoto et al. 2016); thus it was considered possible that differences in foraging habitat might become obvious when shearwaters traveled long distances to the Pacific Ocean, owing to differing flight abilities or energy requirements because of their sexual size dimorphism. The wind characteristics of the Tsugaru Strait are also considered as another factor possibly driving the sexual difference. Strong winds prevail in the strait, resulting from a large thermal contrast between the cooler air over the Pacific Ocean and the warmer air over the Sea of Japan (Shimada et al. 2010). The wing loading of seabirds is considered to be a key characteristic in relation to wind strength (Shaffer et al. 2001, Suryan et al. 2008, Navarro et al. 2009); hence, winds in the strait might act as an environmental barrier (Suryan et al. 2008, Navarro & González-Solís 2009) restricting foraging movements, especially of females.

The aim of this study is first to describe sex-related differences in shearwater foraging trips in relation to differing environmental and wind conditions, and second to

determine the effect of wind velocity on the passage of the Tsugaru Strait, as a determination of sex-related differences in foraging habitat.

3.2. Material and Methods

Fieldwork was performed on Awashima Island (38°28'N, 139°14'E; Niigata, Japan) located in the Sea of Japan between mid-August and early October in 2011, 2012, and 2013 (Figure 3.1). GPS loggers (GiPSy-2, 37 × 16 × 4 mm or GiPSy-4, 37 × 19 × 6 mm; TechnoSmArt, Roma, Italy) were attached to the back feathers of chick-rearing streaked shearwaters with Tesa® tape (Beiersdorf AG; GmbH, Hamburg, Germany) and cyanoacrylate glue (Loctite®401; Henkel Ltd., Hatfield, UK) (Figure 3.2). The loggers were housed in waterproof heat-shrink tubing and set to record one fix per minute. The total weight of the unit was 25 g, which was less than 5% of the mean mass of the birds in my study (mean±SD: 555±68 g, $N = 112$) in accordance to the suggested load limit for flying seabirds (e.g., Phillips et al. 2003). The sex of the birds was determined based on their vocalizations during handling because males give high-pitched calls, while females give low-pitched calls (Arima et al. 2014).

One hundred and fifty-one GPS loggers were deployed: 34 in 2011 (on 17 males, and 17 females), 59 in 2012 (31 males; 28 females), and 58 in 2013 (30 males; 28 females). After approximately 11 days (range 4–20 days) of deployment, the loggers

recaptured and retrieved. The recovery rate was 75–100%, with 29 recovered in 2011 (16 males; 13 females), 52 recovered in 2012 (31 males; 21 females), and 51 recovered in 2013 (25 males; 26 females) (Table 3.1). Some of the retrieved loggers had failed to record data; hence location points were only available for 25 birds in 2011 (12 males; 13 females), 46 birds in 2012 (28 males; 18 females), and 41 birds in 2013 (18 males; 23 females).

During fieldwork in 2011, I randomly selected 50 streaked shearwaters (26 males and 24 females) to estimate wing loading. For each individual, body mass was measured using a 1 kg spring balance, and wing area was estimated by spreading the right wing over a board (a ruler was placed along side for reference) and photographing it. The inter-wing area (i.e., the root box) was measured using a ruler.

Foraging trips was defined as the time during which birds spent beyond a 3-km buffer zone around the colony. The buffer zone was set in order to exclude location fixes of birds resting on the sea surface of the island's coast after departing from and before arriving at the nest. To determine the effects of wind on shearwaters passing into the Pacific Ocean, I first selected tracks that reached a distance of 100 km from the line between Cape Tappi (the tip of the Tsugaru Peninsula) and Cape Shirakami (the southernmost tip of the Oshima Peninsula; Figure 3.1) represents a gateway into the windy Tsugaru Strait (Matsuzaka et al. 2003, Yamaguchi et al. 2006).

Next, I divided foraging trips into two types, based on whether the birds crossed (assigned as 1) or did not cross over (assigned as 0) the entrance to the strait. Some birds approached the entrance line, but did not immediately cross it, and returned later and crossed it during the same trip. Hence, some trips included “crossed” or “not crossed” more than once (the time between approaches was 29.7 ± 17.3 h; range 6.5–68.5 h, $N = 13$) excluding an extraordinary case of 173.5 h.

The 30-min mean wind direction and speed data corresponding to the time of each approach to the line were obtained from the Japan Oceanographic Data Center (at the Tappizaki and Matsumae meteorological stations: http://www.jodc.go.jp/jodcweb/index_j.html, accessed on 16th December 2018). There was a strong correlation between the wind velocities recorded at the two meteorological stations (Pearson’s $r = 0.86$, $P < 0.01$) (Figure 3.3); the data were averaged for further analysis. Westerly and easterly winds are dominant in the Tsugaru Strait (Yamaguchi et al. 2006); therefore, I calculated westerly (assigned as negative values) and easterly (assigned as positive values) wind components following the formula reported by Garthe et al. (2007). The difference between the flight direction of the birds and the wind direction was considered to be 60° in the formula, which represents the angle of the strait between the Sea of Japan and the Pacific Ocean. Westerly winds correspond to downwind and easterlies to upwind, for birds heading to the Pacific Ocean. The monthly mean sea surface temperature (SST)

within 100 km of the colony in September 2011–2013 (0.025° resolution; Aqua-MODIS) was also downloaded via NOAA's BloomWatch180 (http://coastwatch.pfeg.noaa.gov/browsers/cwbrowser_global180.html, accessed on 16th December 2018) to compare the marine environment condition among the years.

The total wing area (S) is the area of the wing (photographed) $\times 2$ + inter-wing area (Pennycuick 2008) (Figure 3.4). Wing area was estimated using Image J (Wayne Rasband, US). Wing loading (a measure of force per unit area) was calculated as [(mass \times gravity)/S], and expressed as Newton (N) \cdot m⁻² (assuming gravity = 9.81 m \cdot s⁻²).

Spatial data were analyzed using ArcGIS 10.2.2 (ESRI, Redlands, CA, USA), and statistical analyses were performed using R version 3.2.2 (R Development Core Team 2014). The area of 100 km from the line between capes Tappi and Shirakami was generated using the ArcMap Buffer tool. Foraging trip duration, maximum foraging distance, and the probability of crossing the line in relation to wind velocities, were all analyzed using generalized linear mixed models (GLMMs), using Gamma, Gaussian, and binomial distributions, respectively. The maximum foraging distance was log-transformed before the statistical analysis. Sex and year were treated as explanatory variables and individuals as random factors in the models. I used R package lme4 (Bates et al. 2015) for the linear models. The sex-related differences in the proportion of trips

in which the line was crossed were assessed using the proportion test. Annual differences in wind velocity were analyzed using the Kruskal–Wallis test and pairwise Wilcoxon comparisons with Bonferroni correction, and SST was analyzed using ANOVA followed by Tukey’s post hoc multiple comparison. The difference in wing loading between males and females was compared using t-test. The normality and homoscedasticity in data were first checked using the Shapiro–Wilk and Bartlett tests. Values are presented as mean \pm SD, and statistical significance was set as < 0.05 .

All experiments were performed according to a protocol approved by the Institutional Animal Care and Use Committee of Nagoya University. This work was conducted with permits from the Ministry of the Environment.

3.3. Results

Over the three year study period, I recorded 243 foraging trips for males and 241 for females (Table 3.1 & Figure 3.5). The mean duration of foraging trips did not differ between males and females (GLMM, $t = -0.90$ $P = 0.37$) (Figure 3.6), but trips were longer in 2012 than in 2011 ($t = -3.23$, $P < 0.01$). The maximum foraging distance from the colony did not differ between the sexes or the years (GLMM, both $t > 1.18$, $P > 0.08$). Most foraging trips ($> 70\%$) were within 250 km of the colony (Figure 3.7). The proportion of trips during which shearwaters crossed into the Tsugaru Strait relative

to all trips obtained in each year was: in 2011, 7.8% (5/64 trips) for males, and 0% (0/65 trip) for females; in 2012, 21.7% (20/92 trips) for males, and 12.1% (7/58 trips) for females; and in 2013, 10.3% (9/87 trips) for males and 3.4% (4/118 trips) for females. Males foraged into the Pacific Ocean more frequently than females in 2011 and 2013 (proportion test, $\chi^2 = 5.28$, $P < 0.05$ in 2011 and $\chi^2 = 4.08$, $P < 0.05$ in 2013), but the frequency did not differ between the sexes in 2012 ($\chi^2 = 2.25$, $P = 0.13$). The probability of crossing the line was not related to wind velocity (GLMM, $Z = 0.48$, $P = 0.63$) for males or females ($Z = -1.15$, $P = 0.25$). Wing loading was greater in males (46.3 ± 3.7 N·m⁻²) than in females (41.0 ± 2.4 N·m⁻²; t-test, $t = -6.1$, $P < 0.01$).

The speed of the easterly winds (headwinds for birds moving toward the Pacific Ocean) differed significantly among the years; it was highest in 2012, moderate in 2011, and lowest in 2013 (Kruskal–Wallis test, $\chi^2 = 97.23$, $P < 0.01$ with pairwise Wilcoxon comparisons, $P < 0.01$ for all combinations). SST around the colony was $24.1 \pm 0.5^\circ\text{C}$ in 2011, $27.7 \pm 0.3^\circ\text{C}$ in 2012, and $25.3 \pm 0.4^\circ\text{C}$ in 2013 (Figure 3.8), indicating significantly warm conditions in 2012 (ANOVA, $F = 20689$, $P < 0.01$ with Tukey's post hoc multiple comparison, $P < 0.01$).

3.4. Discussion

In this study, I showed that male streaked shearwaters travel to the Pacific

Ocean during the chick-rearing period, as males do during the incubation period (Yamamoto et al. 2012). In addition, my results indicate that while females also transit the Tsugaru Strait, males are more likely to do so. This frequency was higher for males than females in both 2011 and 2013, but was similar in 2012. Sex-related differences in habitat use have been reported in seabird species and are often attributed to differences in reproductive roles or niche segregation resulting from sexual size dimorphism (González-Solís et al. 2000, Shaffer et al. 2001, Lewis et al. 2002, Phillips et al. 2004, Elliott et al. 2010, Cleasby et al. 2015). However, despite foraging trip duration often being considered related to the respective reproductive roles of males and females (Phillips et al. 2004, Yamamoto et al. 2011), trip duration did not differ between male and female streaked shearwaters in this study. Larger bodied male shearwaters (Yamamoto et al. 2016) with greater wing loading than those of females (Shirai et al. 2013, this study) may perhaps have greater tolerance to wind and so be better able to cope with stronger winds (Suryan et al. 2008, Navarro et al. 2009). Nevertheless, I found that wind strength did not affect the probability of shearwaters transiting the Tsugaru Strait where strong winds prevail (Shimada et al. 2010). Thus, the question remains: what is responsible for the difference between the sexes in the proportion of shearwaters foraging in the Pacific Ocean?

Greater wing loading functionally enables birds to fly faster (Pennycuik

1989, Shaffer et al. 2001). Thus, males are potentially more mobile and may tend to reach distant areas. Alternatively, greater wing loading needs higher energy for flying (Freed 1981, Navarro & González-Solís 2007); therefore, males may need to travel into the Pacific Ocean to obtain energy-rich Pacific Saury *Cololabis saira* (Kurasawa et al. 2012). Saury are more energy-rich prey species than Japanese Anchovy (14.6 KJ·g⁻¹ for saury, versus 7 KJ·g⁻¹ for anchovy: Ochi et al. 2016), shearwaters' dominant prey in the Sea of Japan (Maki Yamamoto unpublished). Such foraging behavior may be similar to the dual foraging strategy (Weimerskirch et al. 1994, Baduini & Hyrenbach 2003), involving the alternation of short-range trips to maximize the frequency of food deliveries to young, and long-range trips to recover their own energy reserves. In fact, males were more likely to show a stronger bimodality in foraging distance than females (Figure 3.7).

The proportion of trips to cross the line into the Tsugaru Strait did not differ between females and males in 2012, even though winds that year were the strongest among the three years. This result counters my assumption (discussed above) that males might have more opportunities to reach distant areas owing to their greater mobility.

The Japanese Anchovy, the dominant prey species of streaked shearwater in the Sea of Japan, prefers SST from 12°C to 18°C (Mihara 1998), and migrates northward in association with the northern expansion of the Tsushima Warm Current

(Watanuki et al. 2009). In 2012, SSTs in the Sea of Japan (measured within 100 km of the colony) were warmer than those in the other years (see also Figure 3.8). The availability of anchovy around the study colony was probably reduced in 2012, because the sea became warmer than the anchovy's optimal temperature range. However, it is still unclear why shearwaters traveled through the windy Tsugaru Strait into the Pacific Ocean rather than northward in the Sea of Japan to the western coast of Hokkaido. One possibility is that foraging efficiency becomes lower in warmer water. Streaked shearwaters are surface-feeding seabirds and are likely to forage with predatory fish such as yellowtails and skipjacks (Oka 1994, Takahashi 2000). Yellowtail *Seriola* spp. are common in the Sea of Japan (Lee et al. 2009), and are greatly influenced by the Tsushima Warm Current, migrate northward to northern Hokkaido as well as into the Tsugaru Strait (Mitani 1959, Watanabe 1979, Tian et al. 2006, 2012), although the proportion of fish migrating into each region is yet not known. Hence, both male and female streaked shearwaters were perhaps more likely to go into the Pacific Ocean in 2012, which could account for the difference in the foraging trip duration between warmer 2012 ($27.7 \pm 0.3^\circ\text{C}$) and cooler 2011 ($25.3 \pm 0.4^\circ\text{C}$). Foraging trip duration is generally related to the distance traveled (Weimerskirch 2007), but the maximum foraging trip distance and duration did not differ significantly between the sexes in streaked shearwater, even though males made a higher proportion of their trips into the

Tsugaru Strait. This is probably because most trips were within 250 km of the colony (i.e., trips into the Pacific Ocean were considerably fewer relative to the overall number of trips).

My results suggest that whereas male streaked shearwaters may forage more frequently in the Pacific Ocean in order to recover their body condition, females enter the Tsugaru Strait when environmental conditions (e.g., high SST) in the Sea of Japan were unfavorable, generating a condition-dependent difference between sexes in foraging habitat.

Previous studies have suggested that wind strength and direction mediate the movements of seabirds, such as the direction of foraging excursions, migratory routes, and timing (e.g., Felicísimo et al. 2008, González-Solís et al. 2009, Paiva et al. 2010, Nourani & Yamaguchi 2017). Optimal use of wind enables seabirds to save their energy for traveling (González-Solís et al. 2009). Furthermore, I might expect a trade-off between the cost of traveling with unfavorable winds and energy intake, especially during the breeding period, when the energy spent for breeding and survival should be balanced. Future studies need to consider energy expenditure as well in order to better understand the effect of wind on the foraging habitat selection of seabirds.

3.5. Figures and Tables

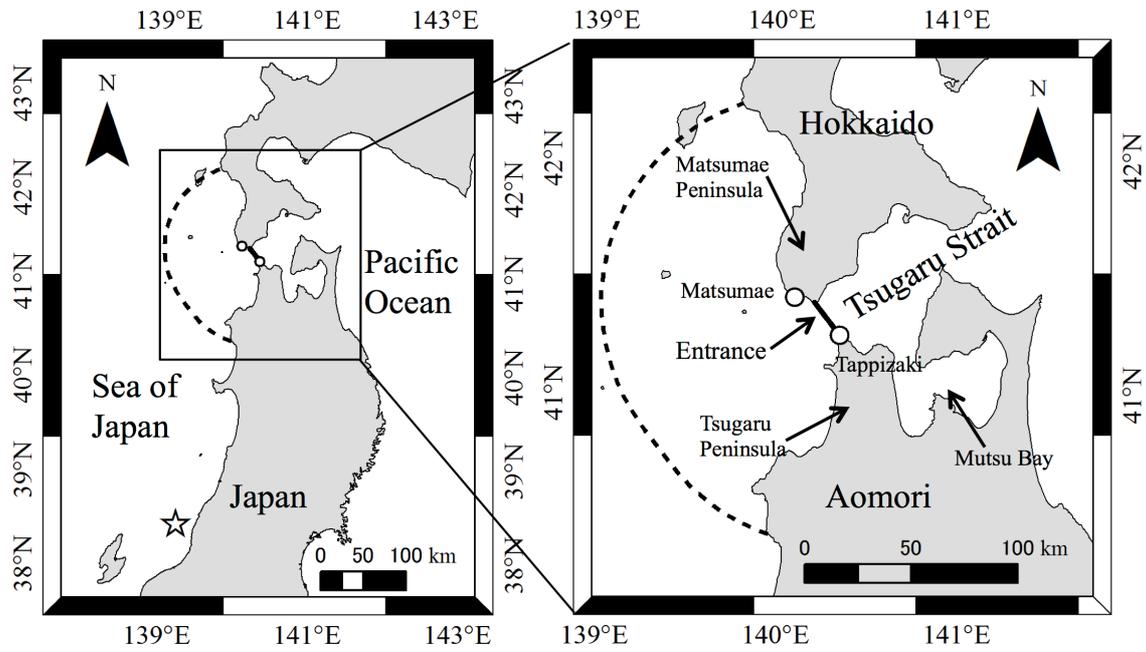


Figure 3.1.

The location of the Tsugaru Strait. The study colony is indicated by a star; open circles indicate the Matsumae and Tappizaki meteorological stations; the heavy line marks the entrance of the Tsugaru Strait, and the dashed line, a distance of 100 km from the line.



Figure 3.2.

GPS logger attached on shearwater's back.

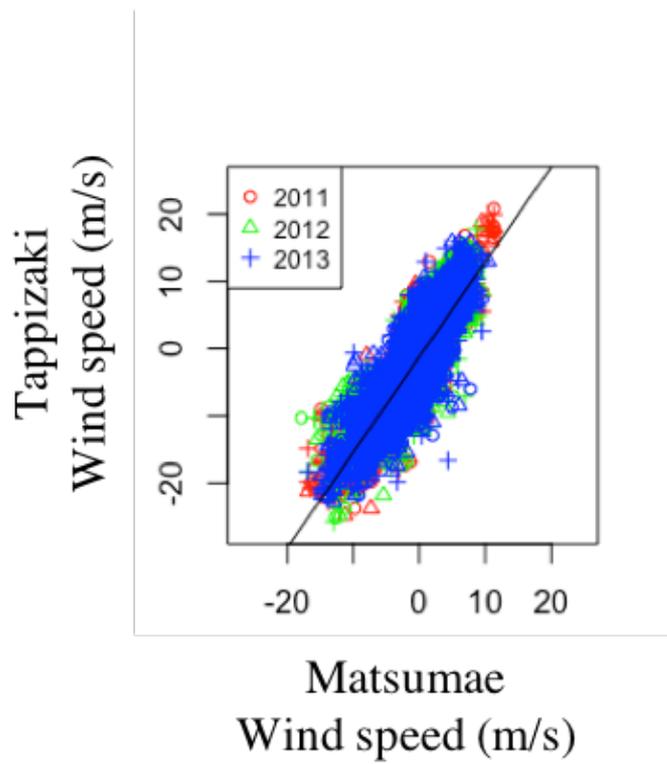


Figure 3.3.

Relationship of wind speeds (m/s) between Tappizaki and Matsumae meteorological stations. The solid line indicates the regression line.



Figure 3.4.

The white dotted line indicates the midline; the red area indicates the area of the wing, and the blue area, the inter-wing area.

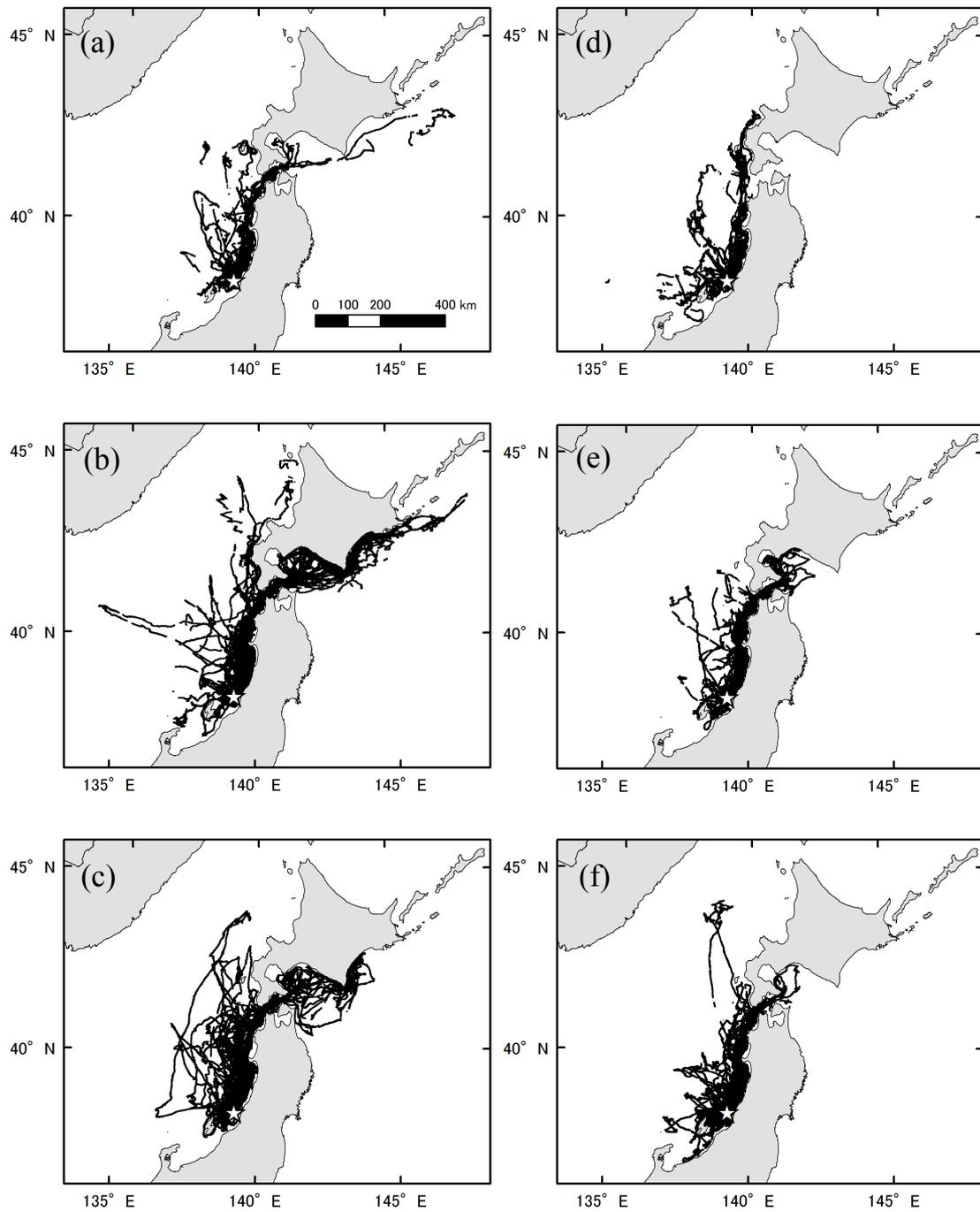


Figure 3.5.

GPS positions of streaked shearwaters in (a) 2011, (b) 2012, and (c) 2013 for males, and in (d) 2011, (e) 2012, and (f) 2013 for females. The study colony is indicated by a star.

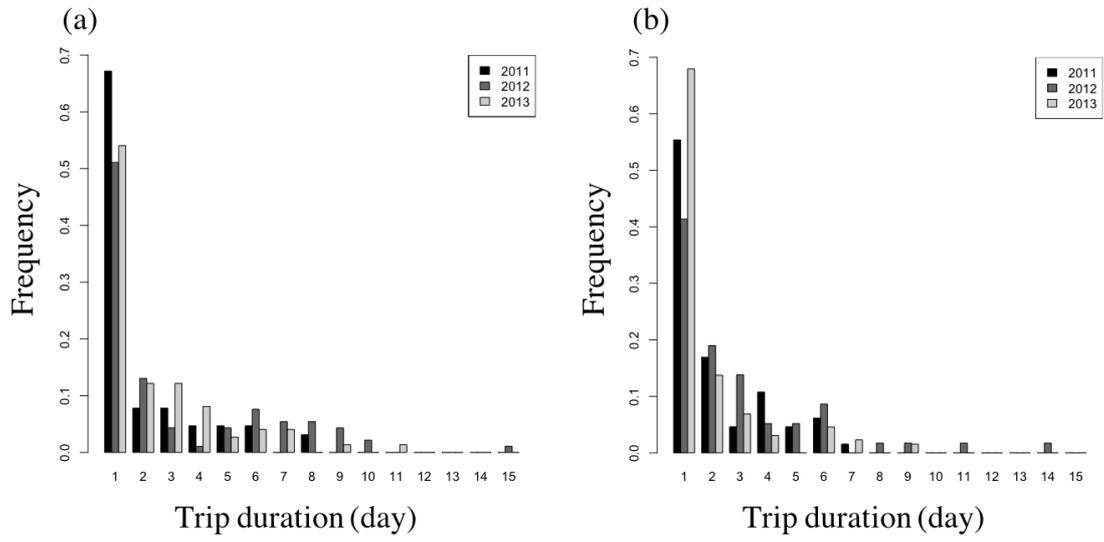


Figure 3.6.

Histograms of the trip duration of (a) males and (b) females.

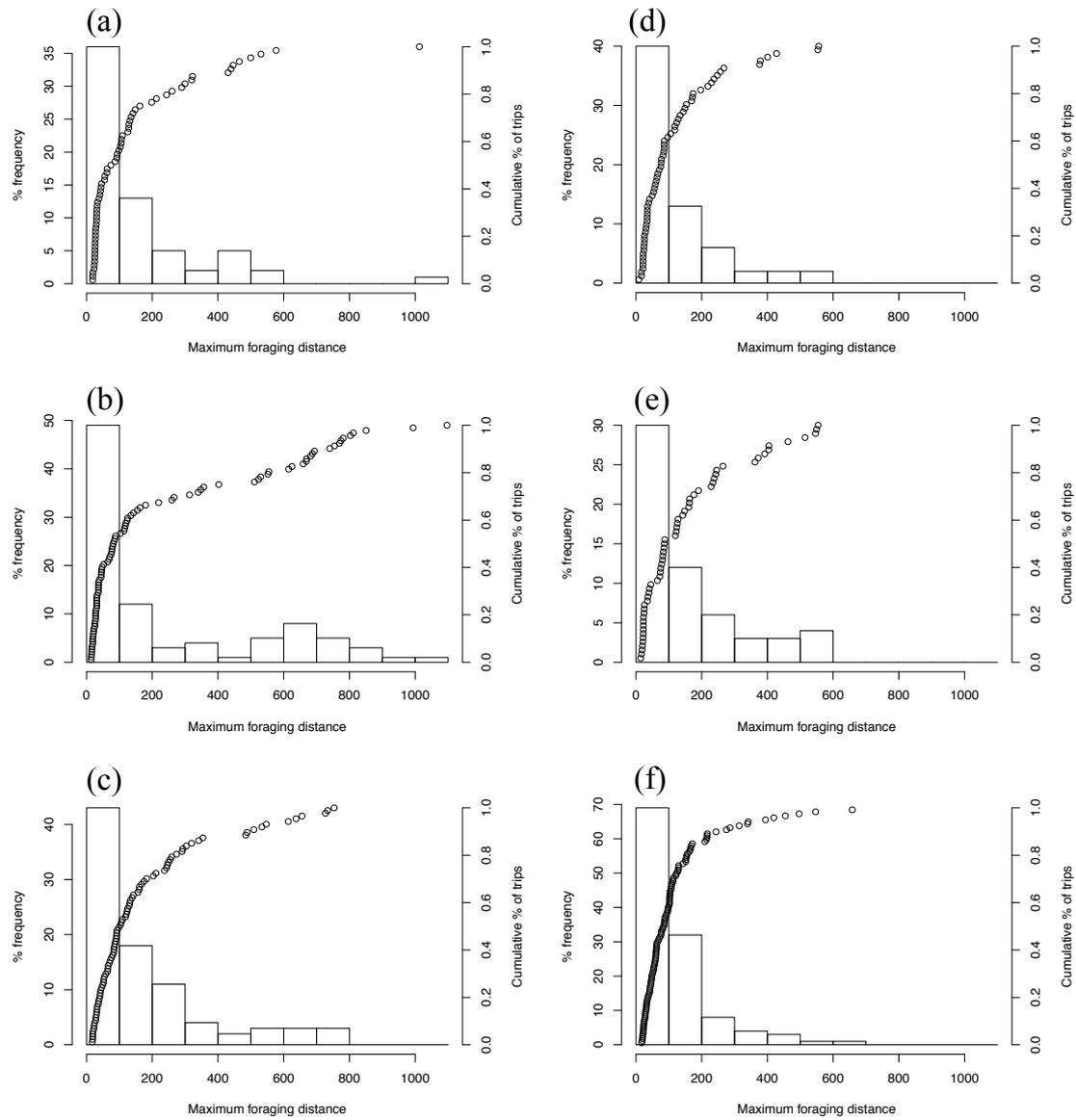


Figure 3.7.

Histogram of the maximum foraging trip distance and cumulative proportion of trips relative to the maximum foraging trip distance in (a) 2011, (b) 2012, and (c) 2013 for males, and in (d) 2011, (e) 2012, and (f) 2013 for females.

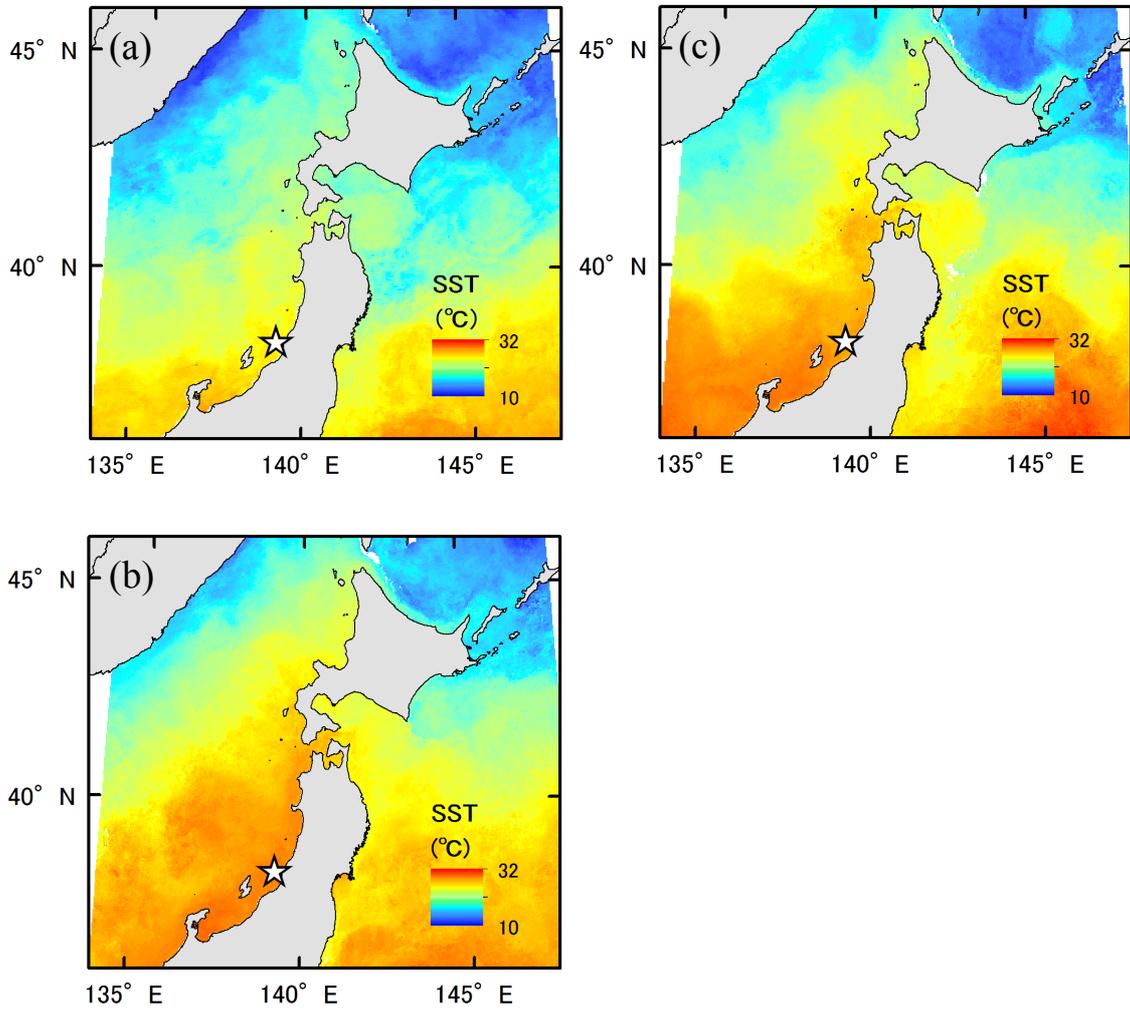


Figure 3.8.

The mean surface temperatures in September (a) 2011, (b) 2012, and (c) 2013. The study colony is indicated by a star.

Table 3.1.

Summary of streaked shearwater foraging trip parameters: attachment and recovery numbers of GPS data-loggers, numbers of foraging trips, trip duration, and maximum foraging distance from the colony. Foraging trip duration and distance are presented as mean \pm SD with ranges in parentheses.

Year	Sex	No. of recover/attachment	No. of foraging trips	Foraging trip duration	Maximum foraging distance from the colony
2011	Male	16/17	64	2.0 \pm 1.8 days (1–8 days)	149 \pm 184 km (19–1013 km)
	Female	13/17	65	2.2 \pm 1.7 days (1–7 days)	121 \pm 127 km (9–556 km)
2012	Male	31/31	92	3.2 \pm 3.1 days (1–15 days)	244 \pm 292 km (14–1097 km)
	Female	21/28	58	2.9 \pm 2.7 days (1–14 days)	158 \pm 157 km (14–554 km)
2013	Male	25/30	87	2.3 \pm 2.0 days (1–11 days)	178 \pm 188 km (17–753 km)
	Female	26/28	118	1.9 \pm 1.8 days (1–9 days)	115 \pm 114 km (17–658 km)

Chapter 4:

General Discussion

This study demonstrates that streaked shearwaters adjusted their foraging behavior in relation to marine environments such as the river discharge and sea surface temperature around the colony, and that sexual differences in foraging area and foraging behavior might be related to the marine environment.

In general, seabirds depend on various physical oceanographic features such as oceanographic fronts, eddies, ocean currents, and upwelling (Hunt & Schneider 1987, Hunt 1990, Hunt et al. 1999, Pinaud & Weimerskirch 2007, Weimerskirch 2007). My results indicate that river discharge assumes a key role as an oceanographic feature in offshore waters. Freshwater discharge from large rivers (e.g. the Amazon or the Mississippi) enhances oceanic primary production by supplying nutrients into the sea, inducing upwelling by convergent fronts, and/or generating vertical stability of the water column, thus influencing the marine ecosystem on the shelf (Lohrenz et al. 1990, Drinkwater & Frank 1994, Smith & Demaster 1996). I suggest that river discharge enhances oceanic primary and secondary production (Gong et al. 2003, 2011, Chen et al. 2014). Thus, river discharge acts as a large spatial scale physical oceanographic feature influencing prey availability, not only in coastal waters (Dias et al. 2012, Zamon et al. 2014), but also in offshore waters. The marine areas under the influence of river discharge would attract foraging seabirds; therefore, similar movement strategies might

be better examined for species such as wintering Magellanic penguins *Spheniscus magellanicus* that utilize the area around the mouth of the Rio de la Plata (Yamamoto et al. in press).

In my study, the frequency of traversing the Tsugaru Strait was higher for males than females in some years, and sex-related differences were observed in habitat use. The sex-specificity of the foraging areas has been attributed to competitive exclusion and social dominance by the larger sex (González-Solís et al. 2000, 2008), or the different reproductive roles and energy or nutrient requirements of the sexes (Phillips et al. 2004; Ruckstuhl & Neuhaus 2005; Peck & Congdon 2006; Yamamoto et al. 2011), or niche or habitat specialization due to differences in morphology (Shaffer et al. 2001; Lewis et al. 2002, 2005; Weimerskirch et al. 2012). The sex-related differences in the foraging behavior and location of seabirds are likely to be frequently affected by marine environments. Male wandering albatrosses, *Diomedea exulans*, have a higher wing loading than females. Wing loading determines flight speed. The males fly to the regions of the Sub-Antarctic/Antarctic where it is windier. Conversely, females exploit the lighter winds of the subtropical and tropical regions (Shaffer et al. 2001). Seasonal sexual segregation in grey-headed albatrosses, *Thalassarche chrysostoma*, and black-browed albatrosses, *T. melanophrys*, is attributable to niche divergence via

differences in flight performance, which is affected by wind conditions (Phillips et al. 2004). I investigated sex-related differences in shearwaters' trips in relation to differing environmental and wind conditions, and the effect of wind velocity on the passage of the Tsugaru Strait, as a determination of sex-related differences in foraging habitat. I showed that wind strength did not affect the probability of shearwaters traversing the Tsugaru Strait, where strong winds prevail (Shimada et al. 2010). My results suggest that, whereas male streaked shearwaters may forage more frequently in the Pacific Ocean to recover their body condition, females enter the Tsugaru Strait when environmental conditions (e.g., high SST) in the Sea of Japan are unfavorable, generating a conditional sex-related difference in foraging habitat.

Some variables could not be measured or calculated in the present study. First, I did not calculate and measure the body condition of birds using some indexes such as a scaled body mass index (Peig & Green 2009), and/or using physiological loggers such as heart rate loggers (Müller et al. 2018), which might help to investigate foraging strategy of males and females in relation to their body condition. In future, given the integration of behavior and physiology, the sex-specific strategy of seabirds might be better understood. Second, some seabirds show sexual differences in the allocation of foraging efforts and chick provisioning rate during the chick-rearing period (Thaxter et

al. 2009, Phillips et al. 2017). However, as I did not investigate meal mass and provisioning rate, further study would be required using automatic weighing system (Ochi et al. 2010), which can reveal the frequency of parent access in and out of their nest, and the mass of food provided to the chick. Third, although I compared foraging trips for three years, the associated reproductive success and/or prey species might be affected by changes in the climate or the marine environment on a long-term or decadal scale (e.g., northern gannets *Sula bassana*; Montevecchi & Myers 1997, auklets *Aethia* spp; Bond et al. 2011, Japanese cormorants *Phalacrocorax filamentosus*, rhinoceros auklets *Cerorhinca monocerata*, black-tailed gulls *Larus crassirostris*; Watanuki & Ito 2012). Future studies are needed to compare interannual changes in foraging behavior, prey species, reproductive success, and population dynamics to understand the strategies that seabirds adopt for successful foraging and reproduction and to reduce environmental risks such as food shortage.

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