Foraging areas of streaked shearwaters in relation to seasonal changes in the marine environment of the Northwestern Pacific: inter-colony and sex-related differences

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ABSTRACT: As the spatial distribution of marine organisms is often affected by seasonal changes, pelagic seabirds may change their foraging areas in response to seasonal changes in the marine environment. Here, we examined the foraging area of streaked shearwaters *Calonectris leucomelas*, breeding at Sangan (SA) and Mikura Islands (MK), Japan, from spring to summer during pre-laying and incubation periods. Those colonies are located at the north and south of the Northwestern Pacific's Kuroshio-Oyashio transition area where high seasonal temperature changes are observed, and where, consequently, birds may show comparable responses to such changes. Our results showed that streaked shearwaters from both colonies shifted their foraging areas northwards as the season progressed. The seasonal shift of foraging areas appeared to coincide with the movement pattern of pelagic fishes that migrate northward in association with the increase in water temperature. However, the pattern of seasonal movement differed between the 2 colonies; shearwaters from SA moved their foraging area along the coastal area of the Kuroshio-Oyashio transition, while those from MK moved along the Kuroshio Extension. Our results also indicated sex-related differences in this general pattern: females showed clear seasonal changes in foraging area, while males did not. During the pre-laying period males returned to the colony frequently to defend their nests or mates, and spent less time at sea. Our results suggest that streaked shearwaters changed their foraging areas in response to seasonal changes in the marine environment, although colony location and sex-related differences in reproductive roles may constrain the birds' responses to seasonal change.

KEY WORDS: Streaked shearwaters · Northwestern Pacific · Seasonal change · Foraging · Kuroshio · Sex-related difference · Pre-laying

INTRODUCTION

Understanding the spatio-temporal dynamics of seabirds at sea is important, not only for describing their relationship with physical and biological processes in the marine environment, but also for identifying their responses to human-induced or climate-related changes in the system (González-Solís & Shaffer 2009). Seabirds breeding in polar or temperate oceans may experience great seasonal changes in the marine environment (Ashmole 1971, Weimerskirch 2007). It is also virtually certain that seasonal changes in the marine environment affect the spatial and temporal distribution of marine organisms, including

major fish or zooplankton that are prey for pelagic seabirds (Hunt 1990, Nihira 1996, Ballance et al. 2006, Iwahashi et al. 2006). Because pelagic seabirds may range widely over the ocean to reach distant foraging grounds, we expect that pelagic seabirds should track the spatial and temporal dynamics of their prey, induced by the seasonal changes in the marine environment.

Breeding seabirds, however, have some limitations in their foraging ranges because they have to return to the colony in order to engage in breeding activities, such as guarding nest sites, mating, incubating eggs, and provisioning chicks (Weimerskirch 2007). These breeding constraints may then lead to differences in a bird's selection of foraging area, depending upon the location of the colony in relation to productive feeding areas. Sex-related differences in flight morphology or reproductive roles may also constrain a bird's foraging range (Shaffer et al. 2001, Phillips et al. 2004b). For example, one sex may have higher wing loading and be better adapted for travelling over windy ocean areas, while individuals of another sex may assume a greater responsibility for incubating or chick-feeding and thus may have limited time available for foraging (Phillips et al. 2004b, Peck & Congdon 2006). Nevertheless, the manner in which individual seabirds respond to seasonal changes in the marine environment has remained elusive, because, due to their high mobility, information on their at-sea distribution is generally lacking.

Streaked shearwaters *Calonectris leucomelas* breed on islands in east and southeast Asia, and major breeding populations exist in the regions of the Kuroshio, Oyashio, and the Kuroshio-Oyashio transition area in the North Pacific east of Japan (Oka 2004). The Kuroshio is the western boundary current of the North Pacific subtropical gyre that is characterized by warm and nutrient-poor surface waters, while the Oyashio is the western boundary current of the North Pacific sub-Arctic gyre that is characterized by cold and nutrient-rich surface waters (Kawai 1972, Qiu 2001, Sakurai 2007; Fig. 1). The area between the Kuroshio and Oyashio is known as the Kuroshio-Oyashio transition area, where the warm Kuroshio water and cold Oyashio water converge, generating a variety of complex hydrographic features (Kawai 1972, Olson 2001, Yasuda 2003). As a consequence of this highly dynamic ocean environment, the Kuroshio-Oyashio transition area represents one of the most productive zones in terms of carbon in the World Ocean (Kimura et al. 1997, Qiu 2001, Yasuda 2003, Sakurai 2007). Streaked shearwaters from both Sangan (SA) and Mikura (MK) Islands — located ca. 640 km apart, to the north and south of the Kuroshio-Oyashio transition area, respectively — forage in the northern part of the
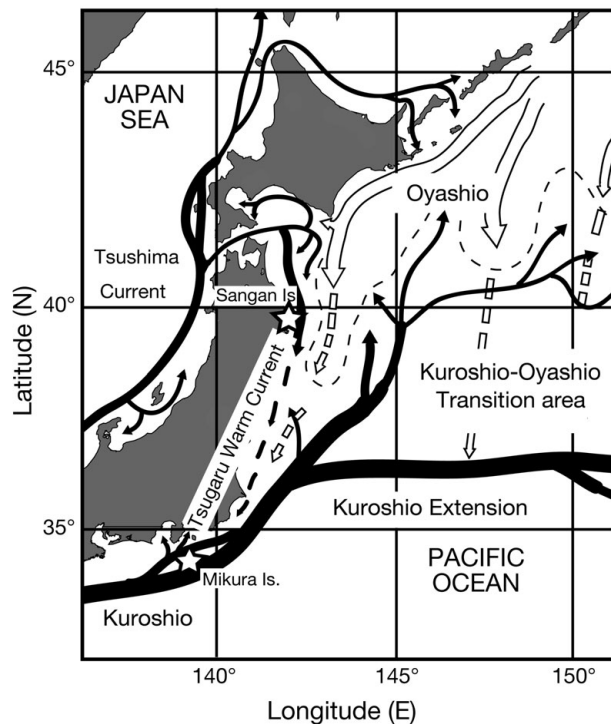

Fig. 1. Oceanographic features of the Northwestern Pacific along the eastern coast of Japan. Open arrows: Oyashio. Closed arrows: Kuroshio and Kuroshio Extension in the Pacific Ocean; Tsushima Warm Current and Tsugaru Warm Current in the Japan Sea and Pacific Ocean, respectively. Solid arrows: surface currents; dashed arrows: undercurrents. Stars: study colonies on Sangan and Mikura islands

Kuroshio-Oyashio transition area and the Oyashio frontal zone during the chick-rearing period (Matsumoto 2008). However, this previous study (Matsumoto 2008) was conducted only over a short period (from late August to late September) during the chick-rearing period, and did not examine the foraging area of shearwaters in relation to the seasonal changes in their marine environment.

In the Northwestern Pacific, the position of the cold Oyashio fluctuates seasonally, shifting northward in summer and southward in winter, affecting sea-surface temperature (SST) through warm/cold water advection (Kawai 1972, Qiu 2001). Thus, SST in the Northwestern Pacific reaches a minimum in March, and a maximum in August, showing one of the highest seasonal temperature changes (a range of 14°C) in the world (Kawai 1972, Iwahashi et al. 2006). These seasonal temperature changes may affect the distribution and availability of zooplankton, which in turn should affect pelagic fishes (Odate 1994, Mihara 1998, Iwahashi et al. 2006), and thus any predators feeding upon them. We therefore hypothesize that streaked shearwaters may change their foraging areas seasonally, moving in association with the migration of their fish

prey. In addition, we expect that patterns in the shift of foraging areas may differ according to sex as well as according to colony. Preferred foraging areas may be farther away from or closer to the colony depending on the time of the season and the location of the colony.

In the present study, we recorded the at-sea distribution of streaked shearwaters over 4 mo (April through July) using global location sensor loggers, and examined how seasonal changes in ocean conditions affected the foraging distribution of shearwaters. In addition, we examined inter-colony and sex-related differences in foraging area usage, the latter relating chiefly to nest attendance patterns.

MATERIALS AND METHODS

Study site. We conducted fieldwork on SA (39° 18′ N, 141° 58′ E, Iwate, Japan) located near the Kuroshio-Oyashio transition area, and on MK (33° 52′ N, 139° 14′ E, Izu Islands, Japan) located in the Kuroshio area (Fig. 1). Approximately 109 000 streaked shearwaters are estimated to breed on SA and from 17.5 to 35 million shearwaters on MK (Oka 2004, Matsumoto et al. 2007). Streaked shearwaters are monogamous seabirds. They return annually to their breeding colony beginning in late March, following their migration from southern wintering areas, and lay a single egg in mid-to-late June (Yoshida 1981, Yamamoto et al. 2010). The pre-laying period lasts ca. 3 mo, from April to June. The birds incubate eggs for ca. 51 d, and feed chicks for ca. 82 d (Yoshida 1981, Oka et al. 2002).

Logger deployment. We captured 48 chick-rearing birds (24 males and 24 females) at SA in mid-September 2006 and 16 chick-rearing birds (7 males and 9 females) at MK in early October 2006, by hand, from nest burrows. A Global Location Sensor logger (GLS-Mk4, $25 \times 18 \times 7$ mm, 4.5 g, British Antarctic Survey) was attached to the tarsus of each bird using a plastic leg ring (Takahashi et al. 2008). The total mass of the GLS logger, including the leg ring, was 7 g. This represents ca. 1.2% of the mean body mass of all study birds (mean ± SD = 570.4 ± 74.9 g) and ca. 1.6% of the body mass of the smallest bird (435 g). The attachment of GLS on a species from the same genus (the Cory's shearwater *Calonectris diomedea*) did not show any adverse effects on foraging behaviour or breeding success of these birds (Igual et al. 2005). We recaptured 38 of the 48 birds from SA in early August and late September 2007, and 7 of the 16 birds from MK in mid August 2007, either in their nest burrows or nearby. Three more MK birds were recaptured in early October 2008. Upon recovery, we removed the logger and plastic leg ring from each individual. We did not observe any injuries to their legs. To examine the effect of tag attachment on the birds' feeding success, we weighed the equipped and non-equipped birds at the time of recapture using a spring balance calibrated to the nearest 1 g. We further determined the sex of all birds based on their vocalizations during handling. The calls of males are high-pitched whereas those of females are low-pitched (Arima & Sugawa 2004).

Data analysis. The GLS loggers record time, light intensity, percentage of time immersed in seawater, and water temperature. The loggers were programmed to measure light levels at 60 s intervals, and to record the maximum value during each 10 min period. Time of immersion in seawater was measured every 3 s and data were compiled over each 10 min recording period. Water temperature was recorded only after continuous immersion for 20 min, as the temperature sensors require 10 min to stabilize. We estimated the geographic location using the light data as follows: Sunset and sunrise times were estimated from thresholds in the light curves; we then derived the latitude based on day/night length, and longitude from time of local midday/midnight with respect to Greenwich Mean Time and Julian day, providing 2 locations per day (Hill 1994, Phillips et al. 2004a). Simultaneous deployment of geolocators with satellite tags (ARGOS Platform Terminal Transmitters) in polar and temperate regions have shown a mean location error of 186 km (Phillips et al. 2004a) and 202 km (Shaffer et al. 2005), respectively. Location errors were minimised by comparing the water temperature records with available satellite remotely sensed 8 d composite SST images from Aqua-MODIS (Moderate Resolution Images Spectroradiometer). This allowed us to estimate latitude on a daily basis, following the methods of Teo et al. (2004). During processing, any locations that were derived from light curves with obvious interruptions around sunset and sunrise, or that required unrealistic flight speeds (>35 km h^{-1} sustained over a 48 h period) were identified and later excluded, following Takahashi et al. (2008).

For our analysis, we determined the breeding status of the birds either by direct observation of eggs or chicks at the time of recapture, or by examining whether the GLS data included repeated periods of darkness lasting longer than 4 d, presumably representing time spent in incubation within nest burrows (see 'Results').

The foraging distribution of both male and female shearwaters from each colony was established by generating kernel density maps using the ESRI® ArcGIS Spatial Analyst Density tool with a cell size of 25 km and a search radius of 100 km. A previous study had suggested that streaked shearwaters travel with a mean flight speed of 19.3 km h^{-1} (Matsumoto 2008).

Thus, we defined the maximum potential daily foraging range of streaked shearwaters to be <250 km from the island (Figs. 2 & 3). To compare the difference in at-sea distribution between sexes as well as between months, we calculated the mean latitude, mean longitude, and mean distance from the breeding colony of the daily bird locations. We identified the day of return

to the breeding colony using the light and immersion data (Rayner et al. 2008). Streaked shearwaters generally come ashore only at night. Most shearwaters land at the breeding colony after sunset, and depart from the colony before dawn (Yoshida 1981, T. Yamamoto pers. obs.). Periods spent in the nest burrow were also identified from the light and immersion data. Day and
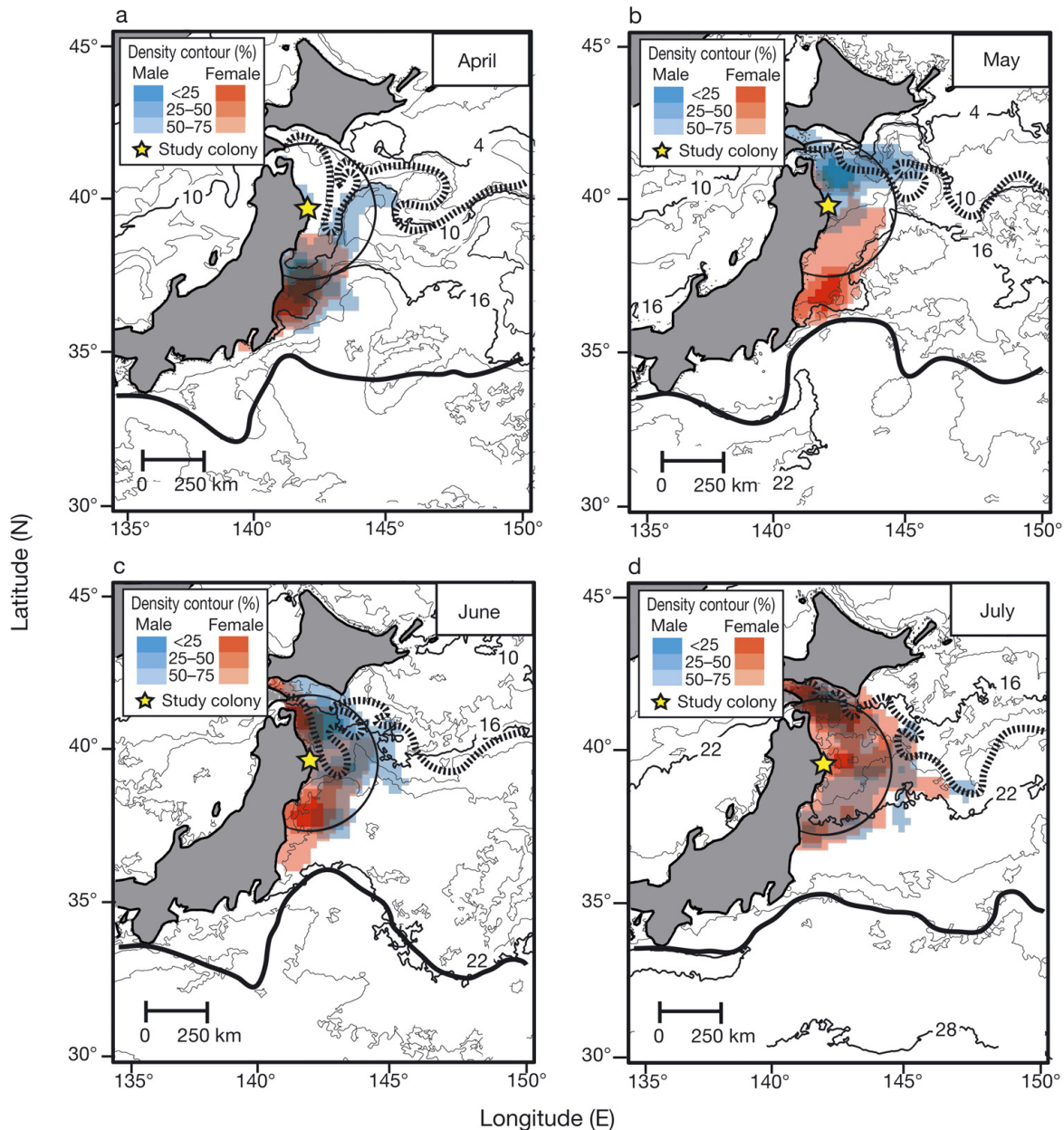

Fig. 2. *Calonectris leucomelas.* Kernel density distribution of breeding streaked shearwaters from Sangan Island in (a) April, (b) May, (c) June, and (d) July 2007, including (a–c) the pre-laying and (d) incubation periods. Density distributions are overlaid on the monthly composite sea surface temperature map (Aqua-MODIS) with contours at 2°C intervals (thin lines) and 6°C intervals (thick lines). The heavy solid black line indicates the approximate location of the Kuroshio (defined by the 14°C isotherm at 200 m depth), while the dashed line represents the approximate location of the Oyashio (defined by the 5°C isotherms at 100 m depth) from April to July in 2007, based on information supplied by the Japan Meteorological Agency (www.jma.go.jp). The approx. semicircle shows the potential maximum foraging range of streaked shearwaters for a daily round trip (250 km from the colony, based on information in Matsumoto 2008)

night were identified using the light data, whilst visual examination of immersion data confirmed when birds returned to the colony, as immersion data were not recorded over a substantial period of the night. Therefore, we were able to calculate the foraging trip duration (at the accuracy level of 1 d) and thus the attendance pattern at the colony.

Water temperatures recorded by the loggers were averaged daily to determine the SST of the foraging areas, because streaked shearwaters typically dive to <3 m (Matsumoto 2008). We then compared tempe-

rature values with those obtained from monthly composite SST data (resolution of 9 km, measured by Aqua-MODIS). We also obtained monthly composite chlorophyll a (chl a) concentrations (resolution of 9 km, measured by Sea-viewing Wide Field-of-View Sensor (SeaWiFS) to examine productivity within the foraging areas. The oceanographic data were obtained from http://oceancolor.gsfc.nasa.gov, and extracted using the SeaWiFS Data Analysis System (SeaDAS, version 5.2). The locations of the Kuroshio front (14°C isotherm at 200 m depth) and Oyashio front (5°C isotherm at
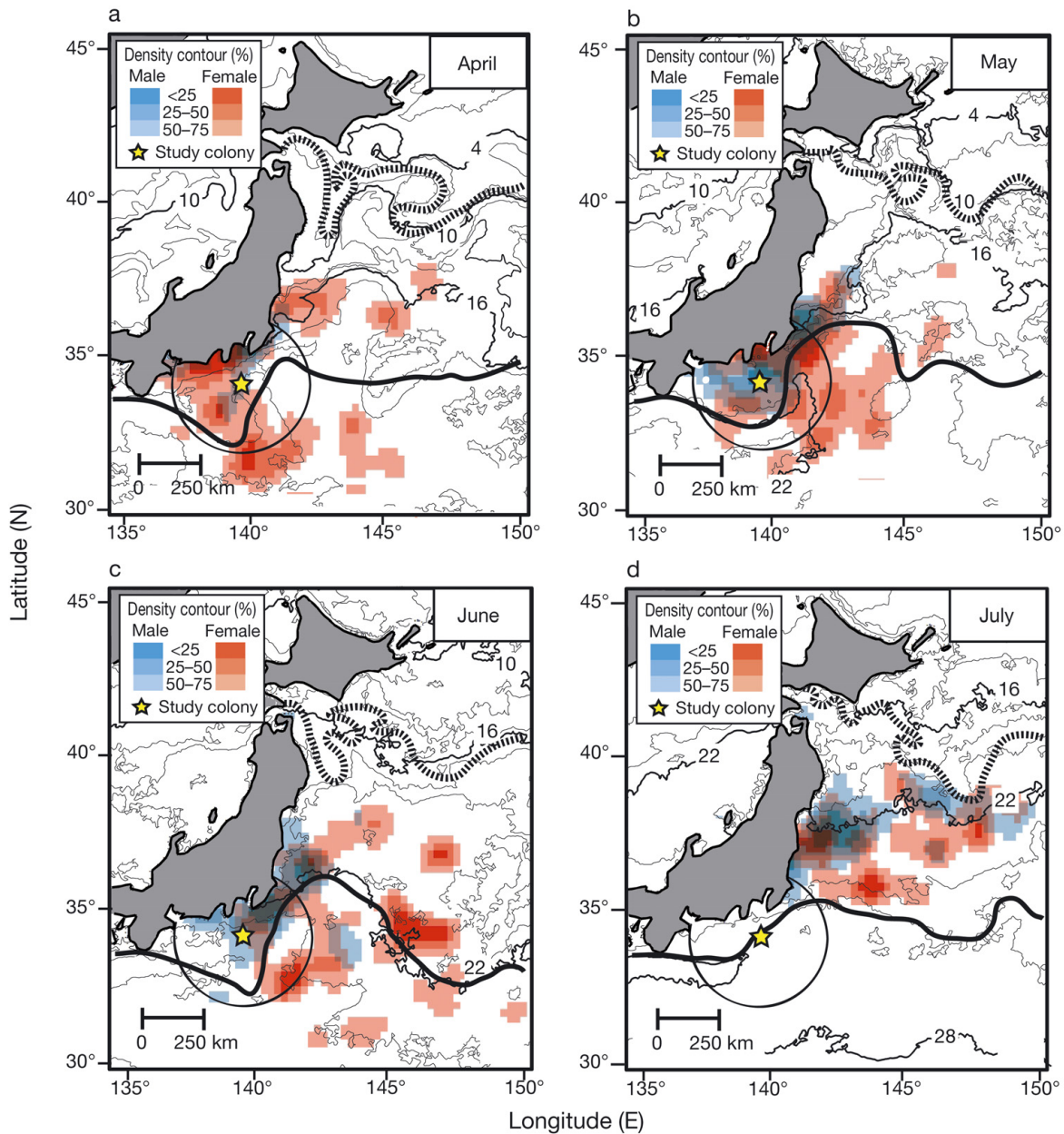

Fig. 3. *Calonectris leucomelas*. Kernel density distribution of breeding streaked shearwaters from Mikura Island in (a) April, (b) May, (c) June, and (d) July 2007, including (a–c) the pre-laying and (d) incubation periods. The background lines are the same as in Fig. 2

100 m depth, Kawai 1972) were obtained from information supplied by the Japan Meteorological Agency (www.jma.go.jp).

Statistical analysis. All statistical analyses were performed in R software, version 2.5.1 (R Development Core Team 2007). To test the differences in foraging behaviour between the sexes as well as from month to month, we fitted a Generalized Liner Mixed Model (GLMM) with either a Gaussian error distribution or a Poisson error distribution. Bird identity was set as a random factor in the models. The models with and without information on sex or month were compared using a likelihood ratio test. We also examined differences of daily bird locations (latitude, longitude and distance from the colony) between the sexes and by month, including individual bird identity as a random factor. The differences in attendance patterns and in chl a concentration within core foraging areas between the sexes were compared using ANOVA. The percentages of nights that individuals appeared at the breeding colony were arcsine-transformed prior to analysis. We used R package lme4 and function lmer for the linear models. Values are presented as mean ± SD. Statistical significance was set at <0.05.

RESULTS

Data from the recovered 48 GLS loggers (38 from SA and 10 from MK) were successfully downloaded. However, 8 loggers from SA had recording errors and the data were partially or completely unusable. For our analysis of data from SA birds, we used 21 breeding birds (9 males and 12 females) and 9 non-breeding birds (4 males and 5 females). For our analysis of data from MK birds, we used 8 breeding birds (4 males and 4 females) and 2 non-breeding birds (2 males). There was no difference in body mass between birds with and without GLS loggers at the time of recapture at SA

(Yamamoto et al. 2008) or MK (2-way ANOVA: sex: $F_{1,18} = 14.92$, p < 0.01; equipment: $F_{1,18} = 0.23$, p = 0.64).

Foraging areas

Female streaked shearwaters from SA changed their major foraging areas, moving from south to north of the breeding colony along the coast in the Kuroshio-Oyashio transition area as the season progressed (from month to month, likelihood ratio test, all p < 0.001; Fig. 2, Table 1). Males from SA also changed their foraging areas, moving northward from April to May, and southward from June to July (likelihood ratio test, p < 0.01 for April vs. May, June vs. July; Fig. 2, Table 1). Thus males, unlike females, did not show a steady northward movement in their foraging areas from April to July. Core foraging areas (50% kernel area) overlapped to a relatively high degree between the sexes in April and July, but less so in June, and they were completely segregated in May (Table 2). The daily mean distance from the colony for bird location was shorter for males than females only in May (likelihood ratio test, p < 0.01; Table 1).

Female streaked shearwaters from MK changed their major foraging areas by moving eastward from April to June along the Kuroshio and Kuroshio Extension (from month to month, likelihood ratio test, p < 0.001 for April vs. May, and May vs. June) and northward from June to July (likelihood ratio test, p < 0.001 for June vs. July; Fig. 3, Table 1). Males from MK changed their foraging areas by moving northward from April to July along the coast (likelihood ratio test, all p < 0.05), and also eastward from May to July (likelihood ratio test, p < 0.05 for May vs. June, and June vs. July; Fig. 3, Table 1). Core foraging areas overlapped between the sexes from April to July, and the proportion of overlap in the foraging areas was larger for males (from 34.7 to 62.1%) than for females (from 9.0 to

Table 1. *Calonectris leucomelas*. Summary of the mean latitude, mean longitude, and mean distance from the colony for daily bird locations at Sangan Island (9 males, 12 females) and Mikura Island (4 males, 4 females) from April to July 2007. Values calculated using individual bird data. Distance is presented as mean ±SD

Breeding colony	Month	Male Latitude (N)	Male Longitude (E)	Male Distance (km)	Female Latitude (N)	Female Longitude (E)	Female Distance (km)
Sangan Island	April	37°48′	141°57′	298 ± 38	36°53′	141°46′	335 ± 71
	May	40°09′	142°23′	243 ± 38	37°38′	142°04′	319 ± 72
	June	40°11′	142°39′	249 ± 29	39°06′	141°38′	277 ± 86
	July	39°37′	142°59′	284 ± 50	39°41′	143°02′	261 ± 44
Mikura Island	April	34°14′	140°06′	287 ± 53	33°25′	139°55′	492 ± 219
	May	34°51′	140°07′	244 ± 16	33°44′	142°10′	363 ± 39
	June	35°29′	141°13′	350 ± 93	34°15′	144°10′	496 ± 60
	July	37°16′	143°21′	589 ± 138	36°41′	144°31′	641 ± 130

36.3%; Table 2). The daily mean distance from the colony for bird location differed between the sexes in May and June (likelihood ratio test, both p < 0.05; Table 1).

Females from SA generally appeared to occupy areas with a restricted range of SSTs (from 14 to 17°C) from April to July as the birds changed their foraging areas (Fig. 4a−d). In contrast, males of SA tended to use the areas around the colony, within their daily foraging range from May to July, without regard to SST, though they generally used areas cooler than those immediately around the colony. In May and June, males used the areas with SSTs significantly lower than those of females (likelihood ratio test, both p < 0.05). At SA, chlorophyll a concentration within the core foraging area was higher for females than for males in April and May, but not in June and July (Table 3). Females from MK also appeared to use areas with a restricted range of SSTs (from 20 to 22°C) from April to July (Fig. 4e−h). Males from MK frequently used areas around the colony, or areas cooler than those around the colony. Males and females used different SST areas in May and June (likelihood ratio test, both p < 0.05), but not in April and July. From April to June, females used areas with lower chlorophyll a concentrations than those used by males, but in July, areas used by each sex had similar chlorophyll a concentrations (Table 3).

Core foraging areas overlapped slightly between the colonies in April, May, and July, but were completely segregated in June (Table 2).

Foraging trip durations and colony attendance patterns

From April to June, females from SA undertook foraging trips that were significantly longer than those undertaken by males (likelihood ratio test, all p < 0.01) (Fig. 5a−d). Similarly, females from MK showed longer foraging trips than males from April to June (all p < 0.05) (Fig. 5e−h). In July, foraging trip duration was similar for both sexes, although males of SA took significantly longer trips than females (p < 0.05).

In June, all females from both colonies performed one long foraging trip (15.5 ± 2.3 d at SA, and 17.0 ± 2.9 d at MK; Fig. 5c,g). This behaviour is presumably related to the pre-laying exodus, during which females are thought to accumulate resources required to produce an egg (Warham 1990). In contrast, the longest foraging trips for males from both colonies in June were shorter (5.6 ± 2.7 d at SA, and 6.8 ± 4.5 d at MK)

Table 2. *Calonectris leucomelas*. Percentages of overlap in core foraging areas (50% kernel density distribution) between sexes and colonies from April to July 2007 at Sangan (SA) and Mikura (MK) islands. Corresponding results are provided in parentheses. Overlaps in foraging areas of >30% are shown in **bold**

	April	May	June	July
SA male (female)	**73.7** (**83.5**)	0 (0)	**31.6** (**32.2**)	**82.4** (**36.4**)
MK male (female)	**62.1** (9.0)	**52.3** (29.6)	**39.9** (25.5)	**34.7** (**36.3**)
SA male (MK male)	0 (0)	0 (0)	0 (0)	7.6 (4.4)
SA male (MK female)	22.8 (10.0)	0 (0)	0 (0)	5.0 (3.0)
SA female (MK male)	0 (0)	27.4 (**52.3**)	0 (0)	10.5 (13.8)
SA female (MK female)	26.6 (10.2)	**35.2** (10.9)	0 (0)	8.6 (11.8)

than those of females. At SA, females started their longest foraging trips on 8 June ± 3.5 d (range from 1 to 14 June), and at MK on 4 June ± 3.0 d (range from 1 to 8 June). The SA females returned to the colony on 22 June ± 2.5 d (range from 18 to 27 June), and the MK females on 20 June ± 1.5 d (range from 18 to 21 June).

Shearwaters from both colonies showed different attendance patterns depending upon gender. Between April and June, males returned frequently to the breeding colony, while females returned to the colony much less frequently. In July, however, both sexes returned to the colony equally (Table 4).

Between April and June, both sexes were often present at the colony for a single night (at SA: males 1.4 ± 1.0 d, and females 1.6 ± 1.1 d; at MK: males 1.4 ± 1.0 d, and females 1.9 ± 1.3 d), while birds stayed continuously in the burrows for approx. 1 wk in July (at SA: males 6.7 ± 2.5 nights, and females 6.0 ± 3.3 nights; at MK: males 7.3 ± 3.7 nights, and females 6.7 ± 3.9 nights), presumably for incubation routines. The long attendance immediately after the long absence of females at the colony in late June indicates that, at SA, they probably laid their single egg on 23 June ± 2.6 d (range from 18 to 28 June), and at MK, on 21 June ± 1.3 d (range from 19 to 22 June).

Behaviour of non-breeding birds

In April, core foraging areas (50% of kernel density) of non-breeding birds (4 males and 5 females) from SA overlapped with those of breeding males from SA by 67.5%, and with those of breeding females from SA by 63.7%; in May, by 50.9 and 4.6%, respectively; in June, by 35.1 and 33.9%, respectively; and in July, by 60.8 and 71.9%, respectively. In April, core foraging areas of non-breeding birds (2 males) from MK overlapped with those of breeding males from MK by 40.9% and with those of breeding females from MK by 52.4%; in May, by 71.4 and 60.7%, respectively; in June, by 41.2 and 23.3%, respectively; and in July by 16.2 and 27.1%, respectively.
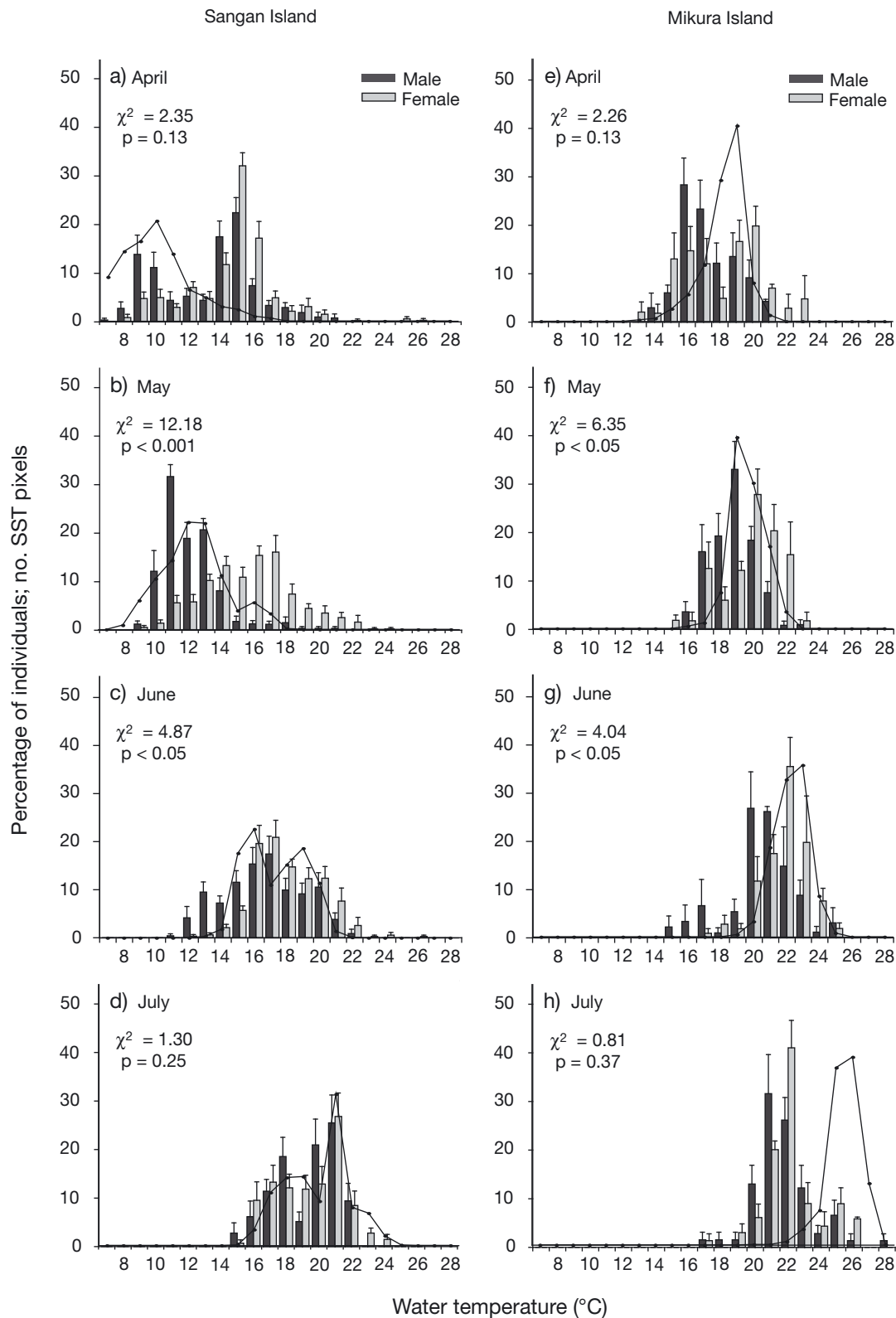
Fig. 4. *Calonectris leucomelas.* Daily averaged water temperatures that individuals experienced during foraging trips; (a–d) birds from Sangan Island, and (e–h) birds from Mikura Island in April (a,e), May (b,f), June (c,g), and July (d,h) 2007. Data are presented as mean ± SE, calculated using individual bird data. Number of sea surface temperature (SST) pixels within the potential daily foraging range of birds (within 250 km from the colony) obtained from satellite data are also shown as line graphs

Table 3. *Calonectris leucomelas*. Chlorophyll *a* concentration (mean ± SD) within the core foraging area (50% kernel density distribution) at Sangan and Mikura islands from April to July 2007. Significant differences were tested using ANOVA

| Month | Sangan Island | | df | *F* | p | Mikura Island | | df | *F* | p |
	Male	Female				Male	Female			
April	0.92 ± 0.42	1.02 ± 0.52	1,879	11.26	<0.01	1.30 ± 1.79	0.64 ± 0.68	1,1052	52.82	<0.01
May	1.25 ± 0.33	1.49 ± 0.45	1,749	68.96	<0.01	0.71 ± 0.52	0.63 ± 0.74	1,1607	6.55	<0.05
June	0.55 ± 0.25	0.53 ± 0.16	1,1297	3.06	0.08	0.50 ± 0.44	0.25 ± 0.15	1,1341	225.95	<0.01
July	0.39 ± 0.17	0.36 ± 0.14	1,1367	15.96	<0.01	0.24 ± 0.10	0.23 ± 0.07	1,1289	3.82	0.05

At SA, non-breeding males tended to return to the breeding colony less frequently (from 34.7 to 44.4% of the nighttime from April to July) than breeding males (ANOVA, April: $F_{1,11} = 9.60$, p < 0.05; May: $F_{1,11} = 14.80$, p < 0.01; June: $F_{1,11} = 4.15$, p = 0.07; and July: $F_{1,11} = 4.80$, p = 0.05; Table 4). Non-breeding females of SA returned to the colony at a similar frequency to breeding females in April, May, and July (from 45.8 to 60.6% of the nighttime), but returned more frequently (60.0% of the nighttime) in June (ANOVA, April: $F_{1,11} = 1.54$, p = 0.23; May: $F_{1,11} = 4.22$, p = 0.06; June: $F_{1,11} = 57.93$, p < 0.01; and July: $F_{1,11} = 0.11$, p = 0.74). In June, non-breeding females at SA showed only a relatively short absence from the colony (7.8 ± 4.3 d), unlike breeding females of the same colony, which showed a long pre-laying exodus (Fig. 5c,g). Similarly, at MK, non-breeding males tended to return to the breeding colony less frequently (from 37.1 to 60.0% of the nighttime from April to July), than breeding males (Table 4). We have no data for non-breeding females at MK.

Table 4. *Calonectris leucomelas*. Differences, by sex, in the percentage of nights that birds spent in the breeding colony at Sangan Island (9 males, 12 females) and Mikura Island (4 males, 4 females) from April to July 2007. Values are presented as mean percentage ±SD, calculated using individual bird data. Significant differences were tested using ANOVA

Breeding colony	Month	Male	Female	df	*F*	p
Sangan Island	April	58.5 ± 8.4	40.0 ± 11.8	1,19	15.86	<0.001
	May	69.5 ± 8.6	32.5 ± 6.4	1,19	114.33	<0.001
	June	68.5 ± 11.9	24.2 ± 6.5	1,19	99.46	<0.001
	July	55.9 ± 5.8	59.1 ± 8.3	1,19	1.05	0.32
Mikura Island	April	47.5 ± 5.0	35.0 ± 6.9	1,6	8.60	<0.05
	May	57.3 ± 16.5	31.5 ± 7.2	1,6	7.62	<0.05
	June	55.0 ± 12.9	25.8 ± 9.2	1,6	12.01	<0.05
	July	51.6 ± 4.6	52.4 ± 8.5	1,6	0.04	0.85

DISCUSSION

Seasonal changes in foraging area

Information on the diet of streaked shearwaters indicates that they predominantly feed on pelagic fish in the Northwestern Pacific; principally Japanese anchovy *Engraulis japonicas* (65.1% at SA and from 23.1 to 50.0% at MK, by percentage frequency of occurrence), with the rest of the diet including Pacific saury *Cololabis saira* (9.3% at SA and from 3.8 to 18.8% at MK), flying fish *Cypselurus hiraii* (4.7% at SA and from 6.3 to 18.2% at MK), and squid *Todarodes pacificus* (2.3% at SA and from 18.2 to 23.1% at MK) (K. Matsumoto unpubl. data). Although the prey species of streaked shearwaters during the pre-laying and incubation periods has not been reported, streaked

shearwaters are often observed aggregating over pelagic fish schools at sea (Nakamura 1974, Takahashi 2000, Ogi & Ryu 2001).

Streaked shearwaters from both colonies studied changed their major foraging areas, moving northward in association with seasonal changes in SST (Figs. 2 & 3). The northward seasonal movements appeared to match the seasonal development of oceanographic processes in the Kuroshio-Oyashio region. Zooplankton biomass is generally low in the warm Kuroshio water, except along the frontal or coastal regions, while primary productivity and zooplankton biomass are generally high in the cold Oyashio water (Odate 1994, Kasai et al. 2001, Sakurai 2007). For this reason, the Oyashio is the main feeding grounds for many pelagic fish species (Odate 1994, Sakurai 2007). However, the distribution of these pelagic fishes is directly affected by water temperature (Oozeki et al. 2007, Takasuka et al. 2008b). Water temperatures of the Kuroshio-Oyashio region increase from spring to summer by solar heating and by the seasonal decrease of cold water transport of the Oyashio current (Kawai 1972, Qiu 2001). Thus, pelagic fishes such as Japanese anchovy, Pacific saury, and Japanese sardine, in association with increasing SST, migrate northward in spring and summer to feed or spawn in the productive Kuroshio-Oyashio transition area (Odate 1994, Mihara 1998,
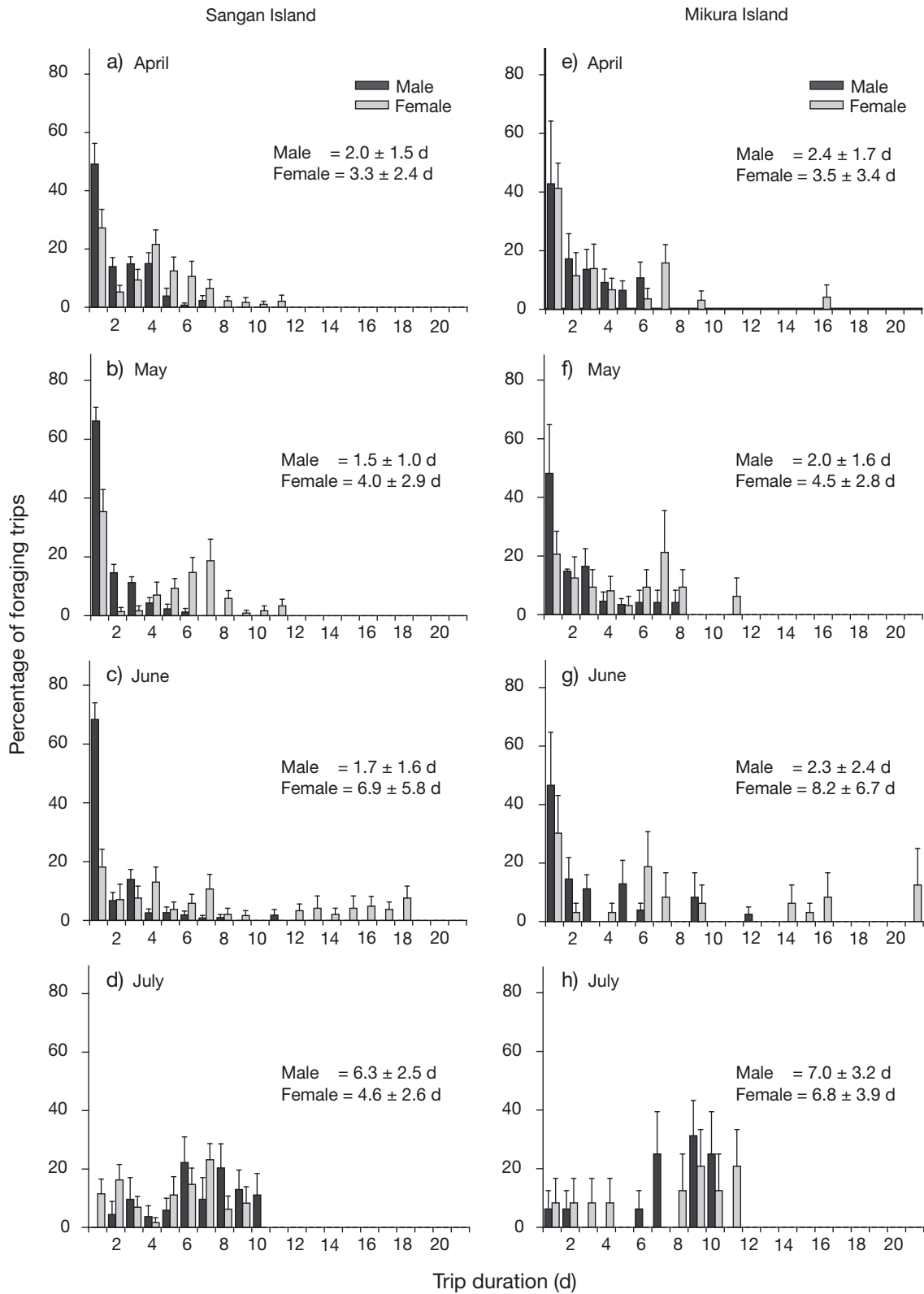
Fig. 5. *Calonectris leucomelas*. Sex-related differences in foraging trip duration undertaken by individual breeding streaked shearwaters from Sangan Island (a–d), and Mikura Island (e–h) from April (a,e), May (b,f), June (c,g), and July (d,h) 2007. Data are presented as mean ± SE, calculated using individual bird data. Grand mean ± SD is also shown

Sugisaki & Kurita 2004, Iwahashi et al. 2006, Sakurai 2007). Predators of these pelagic fishes, such as tunas and seabirds, are also known to migrate into this area in the summer (Shiomi & Ogi 1992, Nihira 1996, Kitagawa et al. 2004).

Although streaked shearwaters broadly showed the northward shift of their foraging areas, the pattern of seasonal changes differed between the colonies depending upon the location of accessible productive areas. Shearwaters from SA changed their foraging areas along the coastal areas of the Kuroshio-Oyashio transition (Fig. 2), while shearwaters from MK changed their foraging areas along the Kuroshio and Kuroshio Extension (Fig. 3). In coastal areas of the Kuroshio-Oyashio transition, Kuroshio, Oyashio, and Tsugaru Warm Current interact and enhance primary productivity (Hanawa & Mitsudera 1987, Kasai et al. 2002, Suryan et al. 2006), supporting high fish abundance (Hayasi 1966, Nakata et al. 2000, Takasuka et al. 2008a). The eastward-flowing Kuroshio and Kuroshio Extension regions, on the other hand, where shearwaters from MK feed, support major spawning and nursery grounds for various pelagic fishes, such as anchovy and sardine (Aoki & Miyashita 2000, Kasai et al. 2002, Komatsu et al. 2002, Sassa et al. 2004, Takahashi & Watanabe 2004). Frontal cyclonic eddies in this region enhance primary and secondary productivity (Kimura et al. 1997, 2000, Qiu 2001), supporting a range of predators, including, tunas, turtles, and seabirds (Kitagawa et al. 2004, Takasuka et al. 2004, Polovina et al. 2006, Suryan et al. 2006, Shaffer et al. 2006).

Core foraging areas overlapped only slightly between the colonies (Table 2), and these overlapping areas were located in the coastal water (Figs. 2 & 3). Colony-specific foraging habitat has been reported in a variety of seabird species (Weimerskirch et al. 1988, Wanless & Harris 1993, Grémillet et al. 2004). Seabirds from neighbouring colonies tend to feed in non-overlapping zones to minimise intra-specific competition for food resources, with the zone of feeding habitat typically closer to a focal colony than any of the neighbouring colonies in the hinterland (Cairns 1989). Females of MK often used offshore areas along the Kuroshio and Kuroshio Extension, where productivity is locally enhanced by frontal cyclonic eddies in low-productivity Kuroshio water, and where many predators congregate to feed (Kimura et al. 1997, 2000, Kitagawa et al. 2004, Polovina et al. 2006). Waters of the Kuroshio and Kuroshio Extension are much closer to MK than to SA (Fig. 1), hence females of MK are able to reach and forage in these regions in addition to coastal areas during their pre-laying period. As MK contains the largest breeding colony (from 17.5 to 35 million birds) of this species (Oka 2004), the broad range of foraging areas for females from MK may possibly relate to the avoidance of intra-specific resource competition (Lewis et al. 2001).

In the Northwestern Pacific, other shearwater species (such as short-tailed *Puffinus griseus* and sooty shearwaters *P. tenuirostris*) also occur during the boreal summer whilst over-wintering (Warham 1996, Shaffer et al. 2006). Short-tailed shearwaters feed mainly on euphausiids (Ogi et al. 1980), and sooty shearwaters predominantly feed on pelagic fish, such as Japanese sardine and Pacific saury (Shiomi & Ogi 1992). In spring, short-tailed shearwaters migrate north to northern Oyashio areas; sooty shearwaters also migrate northwards, congregating over waters of 9 to 13°C (Ogi 1984, Shiomi & Ogi 1992, Ito 2002). These northward migrations have also been considered to coincide with the distribution and availability of prey (Shiomi & Ogi 1992, Warham 1996, Ito 2002).

Sex-related differences

Our results showed that foraging trip duration, foraging areas, and attendance patterns differed between sexes at both colonies from April to June (pre-laying period) but not in July (incubation period).

Male streaked shearwaters had shorter foraging trips than females during the pre-laying period, but not during the incubation period (Fig. 5). During the pre-laying period, time available for foraging may be limited for males by the need to attend the breeding colony (Table 4), which may limit the potential foraging distance from the colony. In contrast, more foraging time should be available for females at this time. In this respect, we might expect females to forage in more productive areas than males during the pre-laying period. In both colonies, however, foraging areas for females did not always coincide with areas of higher chl a concentration (Table 3). This could be explained, in part, by the time lags between increased primary productivity and associated increase in the availability of shearwater prey (Odate 1994, Suryan et al. 2006, Grémillet et al. 2008). Furthermore, the distribution of pelagic fishes that shearwaters mainly feed on is affected directly by SST (Oozeki et al. 2007, Takasuka et al. 2008a,b). For example, Japanese anchovy appear to prefer particular ranges of SST (from 12 to 18°C for feeding, and from 20 to 22°C for spawning; Tsuruta & Takahashi 1997, Mihara 1998, Takasuka et al. 2008b). In fact, female streaked shearwaters from both colonies appeared to favour relatively narrow ranges of SST through several months, as compared to males (Fig. 4). This may suggest that female streaked shearwaters feed on those migratory fish, distributed in particular SST zones, in the Northwestern Pacific.

In June, all females as well as some males undertook longer foraging trips (Fig. 5). We consider these trips to be related to the pre-laying exodus. The pre-laying exodus is seen among most Procellariiformes, and is thought to occur so that females can gather the necessary resources needed to produce an egg (Warham 1990). In fact, in June, non-breeding females showed shorter absences from the colony than breeding females. The periods that streaked shearwaters were absent were similar to that of the closely related Cory's shearwater (females: 19 d, males: 8 d; Jouanin et al. 2001).

Sex-related differences in foraging areas are commonly observed among flying seabirds, and have been attributed to the differences in flight morphology or to differing reproductive roles between the sexes (González-Solís et al. 2000, Shaffer et al. 2001, Lewis et al. 2002, Phillips et al. 2004b). Although male streaked shearwaters are 1.2 times heavier and have larger bodies than females (Arima & Sugawa 2004, Ochi et al. 2010), foraging areas differed between the sexes only during pre-laying and not during incubation. Thus, we suggest that the sex-related preference for foraging areas is related to the difference in reproductive roles, rather than the difference in body size, as nest attendance patterns also differed accordingly between sexes.

Males returned to the breeding colony more frequently than females during the pre-laying period (Table 4), possibly to prevent burrows from being occupied by other prospecting birds (Burger 1981, Hatch 1987). Aggressive territorial defence is observed in streaked shearwaters at the colony from March to May, although the sex of birds conducting the defence was undetermined (Yoshida 1981). Males may also be engaged in extra-pair copulations, or, conversely, in guarding a mate from being copulated with other prospectors (Hatch 1987). Extra-pair paternity rate in streaked shearwaters breeding on SA was about 30% (K. Watanabe unpubl data), and frequent extra-pair copulation attempts occur between mid May and mid June at the breeding colony (Yoshida 1981).

Non-breeding males returned to the colony less frequently than breeding males. Therefore, the foraging ranges of non-breeding birds may not be constrained by breeding duties as much as the ranges of breeders. However, the foraging areas of non-breeding birds unexpectedly overlapped with those of breeding males rather than those of breeding females. We have no clear explanation for those patterns, but it may relate to the fact that we were not able to distinguish whether non-breeding birds did not attempt to breed in the study year, or just failed in the early breeding stage. A previous study has also shown that non-breeding birds do not always behave differently from breeding birds

(marbled murrelets *Brachyramphus marmoratus*; Hébert & Golightly 2008). Although the foraging behaviour of non-breeding birds has been much less reported than that of breeding birds, populations do include a certain proportion of non-breeding birds (Warham 1990). Thus it is important to examine the foraging behaviour of non-breeding birds in relation to oceanographic features for understanding the ecology of a given species.

CONCLUSION

Streaked shearwaters changed their foraging areas, moving northwards from April to July as SST increased seasonally in the Northwestern Pacific. The northward shift of foraging areas appeared to match the general northward movement of pelagic fish from spring to summer reported in this region. However, the patterns of change in foraging areas differed between the colonies as well as between the sexes. Shearwaters from SA foraged along the coastal areas of the Kuroshio-Oyashio transition, while shearwaters from MK foraged in areas along the Kuroshio and Kuroshio Extension. From April to June (pre-laying period), males took shorter foraging trips and foraged in areas closer to the colony than females did, possibly because males needed to return to the breeding colony more frequently to defend their nests or mates. Thus, the environmental responses of streaked shearwaters would be limited by colony location and sex-specific breeding constraints. These results imply that the effects of climate-related changes in the Northwestern Pacific (Chiba et al. 2006) may have a differential impact on shearwaters from different colonies and of different sexes.

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