

Statistical integration of tracking and vessel survey data to incorporate life history differences in habitat models

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Abstract. Habitat use is often examined at a species or population level, but patterns likely differ within a species, as a function of the sex, breeding colony, and current breeding status of individuals. Hence, within-species differences should be considered in habitat models when analyzing and predicting species distributions, such as predicted responses to expected climate change scenarios. Also, species' distribution data obtained by different methods (vessel-survey and individual tracking) are often analyzed separately rather than integrated to improve predictions. Here, we eventually fit generalized additive models for Streaked Shearwaters *Calonectris leucomelas* using tracking data from two different breeding colonies in the Northwestern Pacific and visual observer data collected during a research cruise off the coast of western Japan. The tracking-based models showed differences among patterns of relative density distribution as a function of life history category (colony, sex, and breeding conditions). The integrated tracking-based and vessel-based bird count model incorporated ecological states rather than predicting a single surface for the entire species. This study highlights both the importance of including ecological and life history data and integrating multiple data types (tag-based tracking and vessel count) when examining species–environment relationships, ultimately advancing the capabilities of species distribution models.

Key words: *Calonectris leucomelas*; data integration; distribution; generalized additive model; habitat model; intraspecific difference; Japan; Northwestern Pacific; seabird; tracking; vessel survey.

INTRODUCTION

Animals often segregate their habitat use among sexes, age classes, colonies, current reproductive condition (i.e., breeding or nonbreeding), and stages of the life cycle (i.e., pre-breeding, breeding, post-breeding) within a species, due to biological differences, such as body size (Cristol et al. 1999, Lewis et al. 2005), energy or nutrient requirements (Ruckstuhl and Neuhaus 2005), breeding constraints (Bogdanova et al. 2011, Crawford et al. 2012, Catry et al. 2013a), and intraspecific competition (Cairns 1989, Grémillet et al. 2004). The niche width of a given species consists of preferences across individuals of different ecological states (i.e., sex, age, and reproduction), breeding populations, and life history stages (Bolnick et al. 2003). Hence, climate-related and other anthropogenic effects may have differential impacts within a species (Weimerskirch and Jouventin 1987, Frederiksen et al. 2005, Visser and Both 2005, Wei-

merskirch et al. 2012), but treating them implicitly as ecologically equivalent may obscure the actual ecological effects.

Species distribution data of marine vertebrates is traditionally obtained by direct sightings of non-marked individuals via shipboard, aerial, or other survey methodology. These methods provide useful information on overall distribution ranges of species and critical estimates of density and abundance, including diversity of different species in space and time (Ballance et al. 1997, Renner et al. 2013, Wong et al. 2014). However, as ecological information (e.g., sex, breeding colony, and current reproductive condition) of observed individuals cannot be detected during surveys, especially for species that do not exhibit sexual dimorphism including many seabird species, few studies have been able to examine distributions of a given species as a function of ecological or life history state (e.g., colony of origin, sex, maturity, and breeding condition). Furthermore, direct sightings are usually limited in terms of spatial and temporal coverage for highly mobile animals, and, therefore, there is a possibility that observed individuals could be a biased subset of the broader population (e.g.,

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from a specific colony). Alternatively, information on the spatiotemporal movement of individuals can be obtained in concert with ecological data using animal-borne tracking devices at a variety of spatial and temporal scales (reviews by Burger and Shaffer 2008, Rutz and Hays 2009). This technique enables us to examine differences in spatial distribution within species, such as among sexes, age classes, colonies, current reproductive condition, and stages of the life cycle (Phillips et al. 2004b, Gutowsky et al. 2014), as we can place tags on individuals of known ecological states within the colony. Meanwhile, tracking data can be relatively limited in scope due to the high cost of devices and attachment/recovery efforts.

Recently, increasing availability of species distribution data together with broadscale remote sensing data has resulted in a rapid growth of research using species distribution models (i.e., habitat modeling; Guisan and Zimmermann 2000, Manly et al. 2002, Franklin 2009, Peterson et al. 2011), and it has advanced quickly in the past fifteen years particularly for mobile marine predators (Redfern et al. 2006, Tremblay et al. 2009, Wakefield et al. 2009, Żydelis et al. 2011). Species distribution modeling has also been termed habitat modeling when trying to understand the factors that influence habitat choice, particularly for highly mobile species such as seabirds (Żydelis et al. 2011, Catry et al. 2013b, Yamamoto et al. 2015). Habitat modeling is a powerful tool because it can be used to estimate current distribution ranges of a species and relationships among occurrence or behavior and environmental covariates, and using species–environment relationships to predict responses to current and future environmental conditions (Elith and Leathwick 2009, Nur et al. 2011, Oppel et al. 2012, Hazen et al. 2013a, b), as significant effects of global climate change (e.g., range shifts) have already been observed for a variety of ecosystems (review by Walther et al. 2002, Parmesan and Yohe 2003, Burrows et al. 2011, Pinsky et al. 2013). Also, these models are now commonly applied to the designation of protected areas (Cañadas et al. 2005, Bailey and Thompson 2009, Hooker et al. 2011, Thiers et al. 2014). Although most protected areas (both terrestrial and marine) are static both temporally and spatially, management areas can be adopted to move with the dynamic seascape when based on species distribution estimates as a function of the underlying environmental variables that influence where species occur in space and time (Bailey and Thompson 2009, Hooker et al. 2011, Lewison et al. 2015). However, if within-species differences in foraging habitats exist, pooling data across individuals of different sexes, from different colonies, and at different reproductive conditions may introduce error in models of species distribution. Several studies have examined differences in habitat preference within species (i.e., depending on sex, colony, and current reproductive condition of individuals) and shown evidence of differences among distribution patterns (Huettmann and Diamond 2001,

Conde et al. 2010, Huettmann et al. 2011). These highlight the importance of considering ecological differences in species' environmental preferences to construct a robust species-wide model, essential for projecting the effects of climate change and effective spatial planning (Grémillet and Boulinier 2009, Hooker et al. 2011).

Although the types of data obtained differ among vessel-based sightings (Eulerian) and tracking data (Lagrangian; Nathan et al. 2008), these two approaches can be complementary and their distribution relative to environmental features should remain more or less the same for the same life history stages. However, previous habitat modeling efforts treat them separately rather than combined (Grémillet and Boulinier 2009, Louzao et al. 2009, Hooker et al. 2011, Thiers et al. 2014). Although vessel survey data can provide a quantitative estimate of species densities, direct observations are usually limited in space and time due to high costs of ship time, constraining estimation of species distribution within the limited survey area, which often is insufficient to understand population level changes. Species distribution models could be extrapolated beyond surveyed areas with caution, assuming species–environment relationships will remain constant, which often is not the case (Elith and Leathwick 2009). On the other hand, individual tracking data can provide a more robust metric of species' habitat use (i.e., home range). Thus, the combination of these two distinct data sets may enable us to estimate species abundances within the defined range, resulting in a stronger and more parsimonious model to explain patterns and changes in species distribution than either approach alone.

We developed models of habitat use incorporating sex, breeding colony, and current reproductive condition as covariates from tracking data. Then, we fit hierarchical models using tracking and vessel data to integrate these two types of data including within-species ecological differences. In practice, the models were fit in the following order: (1) the spatial kernel density values from tracking data were partitioned by sex, colony, and breeding status and were modeled as a function of vessel-based bird observations, and (2) the tracking data-based kernel density estimates for each sex and each colony were predicted as a function of environmental variables, including an interaction variable with survey-based density estimates, with predictions normalized by vessel-based abundance estimates.

METHODS

Study site and species

Fieldwork was carried out at breeding colonies of Streaked Shearwaters (*Calonectris leucomelas*, TSN (taxonomic species number): 203449) on Sangan Island (39°18' N, 141°58' E; Iwate, Japan) in September 2006 and August–September 2007 and on Mikura Island (33°52' N, 139°14' E; Izu Islands, Japan) in October

2006, August 2007, and October 2008 (Fig. 1a). Streaked Shearwaters breed on islands in east and southeast Asia from April to early November (Oka 2004). During the breeding period, Streaked Shearwaters surface-feed on forage fish (mainly Japanese anchovy *Engraulis japonicus*; Matsumoto et al. 2012) returning often to the colony, known as central-place foraging. Previously, Yamamoto et al. (2011) examined the foraging areas of Streaked Shearwaters from spring to summer at these two different breeding colonies (Sangan and Mikura Islands, ~650 km apart) in the Northwestern Pacific and found colony, sex-related, and condition-dependent (breeding or nonbreeding) differences in their habitat use. Vessel survey observations of this species have been conducted in this region (Minami et al. 2000, Ito 2002, Ito and Watanuki 2008). However, previous studies were unable to distinguish the sex, colony of origin, and current breeding condition of observed birds. Given the different limitations of both tracking data and survey data, integrating data collected from two different methods (tracking and vessel survey) provides us with a prime opportunity to examine ecological covariates (sex, breeding colony, and reproductive status) in model fitting and prediction, ultimately resulting in a novel approach to model across life history stages.

Bird tracking

We fitted Mk4 geolocation-immersion loggers (British Antarctic Survey, Cambridge, UK; hereafter loggers or geolocators, $25 \times 18 \times 7$ mm, 4.5 g) to the tarsus of Streaked Shearwaters using a plastic ring (see Fig. 1 in Takahashi et al. 2008) at each breeding colony to track bird movement. Geolocators measure light levels at 60-s intervals and record the maximum value during each 10-min period. Light data were processed following the procedures in Yamamoto et al. (2010). Sunset and sunrise times were estimated using thresholds in the light curves. Then, day length was used to estimate latitude and the relative timing of local noon and midnight were used to estimate longitude, providing two position estimates per day. To improve the light-level based location estimates, daily mean of longitudes and daily median of water temperature records from the loggers were compared with remotely sensed sea surface temperature data (8-d composite, 9-km resolution, measured by Aqua-MODIS, downloaded from the Ocean Color Web; Teo et al. 2004; *available online*).⁶ Then, these daily positions were filtered using a speed threshold of 35 km/h sustained over a 48-h period (Takahashi et al. 2008), and unrealistic locations were excluded and interpolated linearly using the remaining neighboring locations. Simultaneous deployment of geolocators with satellite transmitters in a temperate region has shown a mean location error of 202 km (Shaffer et al. 2005).

Bird positions during the pre-laying and incubation periods (from April to July 2007) for 21 breeding birds (9 males and 12 females) and 9 nonbreeding birds from Sangan Island, in addition to 8 breeding birds (4 males and 4 females) from Mikura Island were reanalyzed from Yamamoto et al. (2011; Fig. 1b; see Yamamoto et al. 2011 for the detail of the logger deployment/recovery procedure). We determined the sex of all birds based on their vocalizations (Arima and Sugawa 2004, Arima et al. 2014) and their breeding status either by direct observation of eggs or chicks at the time of recapture or by examining repeated periods of darkness from the geolocator data which has previously been correlated with breeding activity (Yamamoto et al. 2011, 2012).

Due to the relative inaccuracy of geolocation estimation (more than one hundred kilometers; Teo et al. 2004, Shaffer et al. 2005), we created distributions of the tracked shearwaters for each month (April–July 2007) by generating kernel density maps using the ESRI ArcGIS Spatial Analyst tool with a search radius of 200 km (BirdLife International 2004, Phillips et al. 2004a) and a cell size of 9 km. The kernel density maps were calculated based on each breeding colony (Sangan and Mikura Islands), each sex (males and females from each colony, Sangan male, Sangan female, Mikura male, and Mikura female), and nonbreeders (from Sangan Island), resulting in seven different groups (hereafter category). Although tracking data is presence-only data, this analysis enables us to calculate a continuous density probability gradient (including near 0 values) spatially for use in our models. Bird density close to a breeding colony is stochastically high due to geometric spreading as birds commute to and from the island (i.e., colony effect; Ashmole and Ashmole 1967, Kinder et al. 1983, Decker and Hunt 1996, Renner et al. 2013), especially for central-place foragers, such as Streaked Shearwaters. The high density around the colony may not be a function of oceanic variables but merely a function of distance from the colony (Grémillet and Boulinier 2009). Therefore, we subtracted concentrically predicted density values from the tracking-based kernel density estimates to extract the shearwater–marine environment relationship, following the formula (Tanaka et al. 2008, Kurasawa et al. 2011):

$$D_{\text{total}} = \sum_{i=1}^n D_i = \sum_{i=1}^n k \times \frac{1}{x_i}$$

We would expect that at-sea density of shearwaters at any given cell (i) should be related to the distance from the colony. D_{total} is the sum of density from all cells, D_i is the expected density at a cell i , x_i is the distance between the colony and a given cell, and k is the coefficient determined by D_{total} and the number of cells. Then, we calculated the anomaly (fixed kernel density) by subtracting the distance-based density from the kernel density at each cells. To standardize the fixed kernel density values among the months (April–July

⁶ <http://oceancolor.gsfc.nasa.gov>

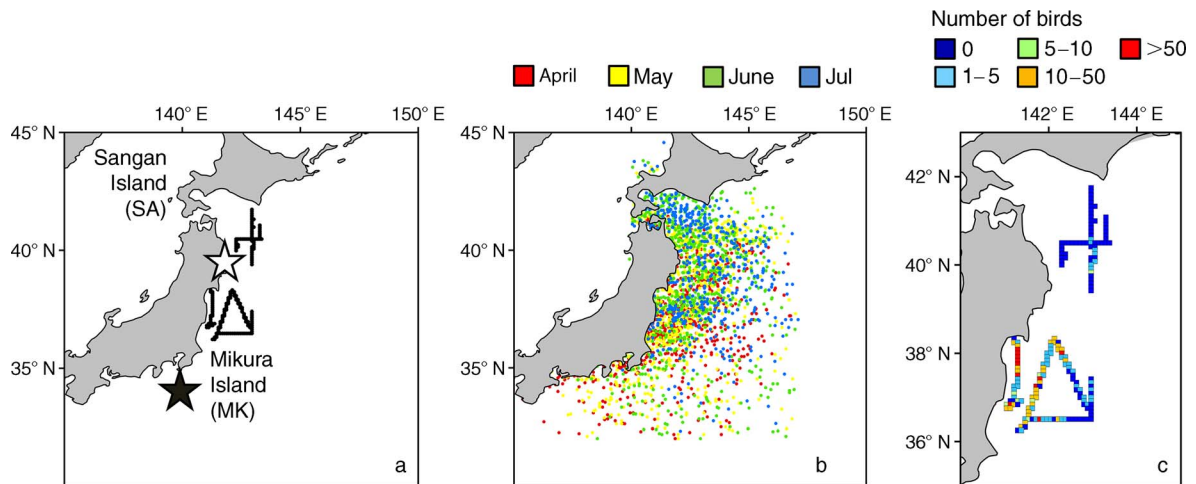


FIG. 1. (a) Study colonies of Streaked Shearwaters (*Calonectris leucomelas*) of Sangan and Mikura Islands, Japan, and vessel-survey transect lines are shown with (b) bird positions derived from light records in geolocators (from April to July 2007) and (c) the number of birds (abundance) observed by the vessel survey within 9-km grid cells (May 2009).

2007), we normalized the relative density within a given month, ranging from 0 (minimum value) to 1 (maximum value), so that data from different months can be pooled together for habitat models (see *Methods: Data integration*).

Vessel survey observation

The study was conducted during the research cruise of RV Tansai-maru (Atmosphere and Ocean Research Institute, Japan Agency for Marine-Earth Science and Technology) off the coast of western Japan (36°30'–41°43' N, 141°00'–143°22' E) between 1 and 6 May 2009 (Fig. 1a). We recorded the number of birds within a 300-m arc (from the bow to 90° off the either side with best visibility) continuously during daytime resulting in 62.5 observation hours, and birds following the ship were recorded when they firstly entered into the arc, but ignored thereafter (Tasker et al. 1984). As Streaked Shearwaters feed at the surface and rarely make dives (96% of dives are shallower than 3 m, and dives last only for 2–6 s; Matsumoto et al. 2012), we were unlikely to miss birds due to sub-surface foraging. We aggregated the number of birds (included both flying and sitting) into 9-km grid cells and recalculated the abundance (number of birds) of Streaked Shearwaters at this scale (Fig. 1c). We checked the independence of spatial data using a Moran's *I* coefficient for each grid cell (9 km) in all directions. Moran's *I* values range from -1 (negative autocorrelation) to $+1$ (positive autocorrelation; Sokal et al. 1998). Our analyses resulted in a Moran's *I* value of 0.32 ($P < 0.01$) for the abundance data set, indicating a significant spatial structure to the data.

Habitat modeling

We considered seven possible environmental variables relating to shearwater distribution (similar to variables used in Kappes et al. 2010, Nur et al. 2011, Żydelis et al.

2011, Oppel et al. 2012) in the window between 30–45° N and 135–150° E (Appendix A): bathymetry (DEP; coastal or pelagic water), monthly composite Aqua-MODIS sea surface temperatures (SST; thermal regime) and chlorophyll *a* concentration (CHL; proxy for primary productivity), monthly composite sea surface height anomalies (SSHA; proxy for mesoscale activity), bottom slope (SLOPE; upwelling probability), distance to the nearest shoreline (DIS; coastal or offshore), and distance to the nearest breeding colony (>1000 breeders; Oka 2004) for shearwaters of unknown origin (i.e., for the vessel-based model) or to the colony of origin for tracking data (COLONY; birds' travelling distance). Also, we included an interaction term between COLONY and SST (COLONY \times SST), because SSTs may differ in habitat to the north and south of the colony. DEP, SST, CHL, and SSHA data were obtained from the National Oceanic and Atmospheric Administration's CoastWatch database (*available online*).⁷ SLOPE, DIS, and COLONY were calculated using tools in ArcGIS. We examined the correlation coefficient of the explanatory variables for collinearity, and DIS was excluded from further analyses (strong collinearity between COLONY and DIS; Pearson's $r = 0.79$ for 9-km grid cells). All other correlation coefficients were <0.56 . We extracted oceanographic variables in each grid cell for corresponding months (April, May, June, and July 2007 for the tracking data, and May 2009 for the vessel data). For the tracking data, the normalized monthly data sets (April–July) were pooled into a single data set to fit and refine the model across seasons (Louzao et al. 2009), as pooled data may be more representative of habitat use for a given species compared to monthly data alone.

⁷ <http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowerWW360.jsp>

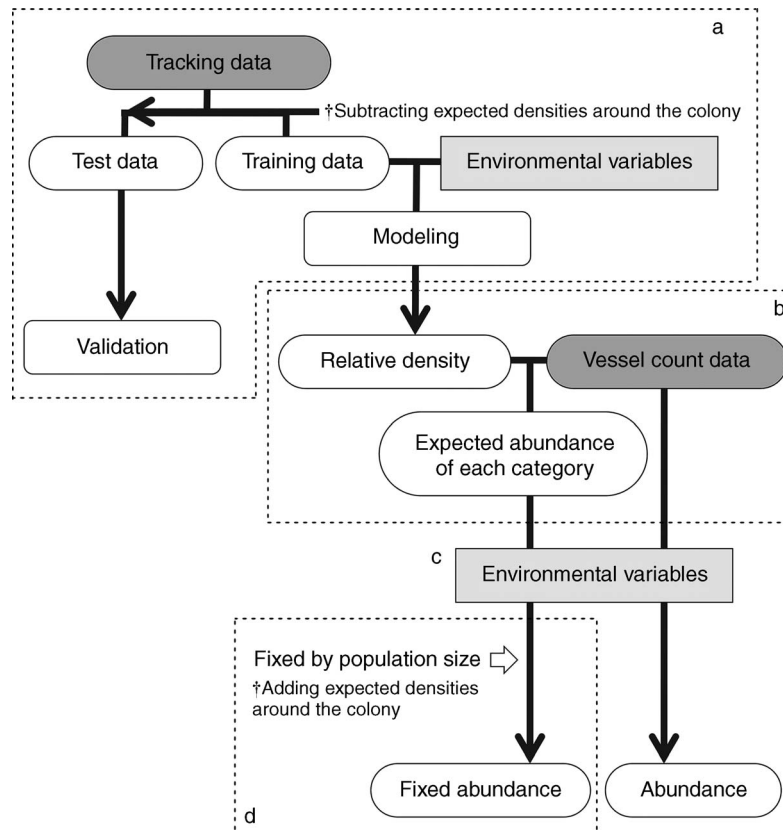


FIG. 2. A schematic showing the multistage modeling framework used to incorporate vessel survey and tracking data: (a) prediction of Streaked Shearwater distributions using the tracking-based models, (b) extracting the density values for each category corresponding to vessel survey observations and fitting a GAM to quantify the likely contribution of each category to vessel-based observed densities, (c) predicting the abundance of each ecological category with environmental variables as predictors and relative density as an interaction term for all variables, and (d) adding the concentrically predicted density around the colony and multiplying the estimated abundance of each category by the population ratio to account for the colony effect.

The performance of species distribution models may differ among modeling techniques used (e.g., Yen et al. 2004, Oppel et al. 2012, Renner et al. 2013). In order to assess the predictive capacity of the various modeling techniques in estimating shearwater distribution, we compared shearwater tracking models from 2007 using four different modeling techniques: generalized linear model (GLM), generalized additive model (GAM), random forest, and an ensemble of all models (ensemble model). In this study, we ultimately chose GAMs (Guisan et al. 2002) to identify the characteristics of shearwater oceanographic habitat (see Appendix B for the summary of the model comparison).

Habitat modeling and exploratory statistics were performed in R (version 2.10.1, R Development Core Team 2007) using packages mgcv, MASS, MuMIn, and PresenceAbsence.

Data integration

The flowchart for our hierarchical modeling procedure is presented in Fig. 2. We predicted the shearwater distributions in May 2009 using the previously described

tracking-based model (predicted using GAM) with environmental variables of May 2009 for Sangan Island (including males, females, and nonbreeders), Sangan males, Sangan females, Mikura Island (including males and females), Mikura males, Mikura females, and nonbreeders (these seven ecological states hereafter, referred to as category; Table 1), avoiding a potential confounding effect of difference across years (Figs. 2a and 3). Of these, Sangan males, Sangan females, Mikura males, Mikura females, and nonbreeders were used in models to partition vessel-based observation data. We extracted the density values for each of the five categories corresponding to vessel survey observations and fit a GAM to quantify the likely contribution of each category to vessel-based observed densities with bird abundance as the response variable and the density values of each category as explanatory variables using a negative binomial distribution and log link function because of its high dispersion (Figs. 2b and 4). Then, the number of birds observed in each grid cell was multiplied by the tracking-based density value in each category to avoid a negative relation between the density

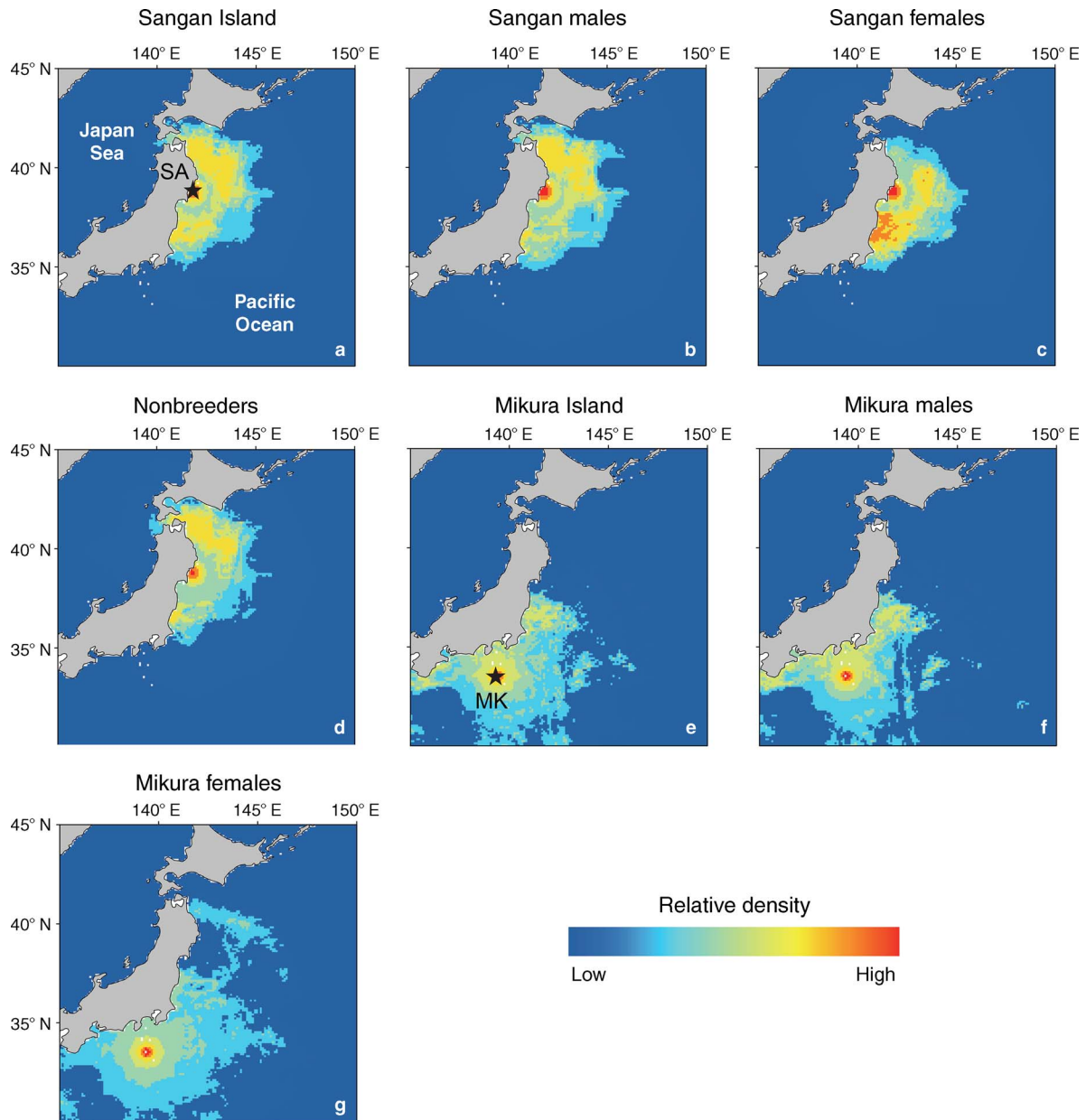


FIG. 3. The relative density and distribution of Streaked Shearwaters in May 2009 predicted using the tracking-based model: (a) Sangan Island (SA; males, females, and nonbreeders all included), (b) males, (c) females, and (d) nonbreeders from Sangan Island, (e) Mikura Island (MK; males and females all included), (f) males, and (g) females from Mikura Island.

and abundance (i.e., birds observed where tracking density was 0). Next, we predicted the abundance of each ecological category using GAMs with environmental variables as predictors and relative density as an interaction term for all variables (Table 2, Fig. 2c). To account for colony effects, we calculated the concentrically predicted density around the colony from estimated relative densities of birds in each category to reflect their use around the colony. Colony size should correlate with the number of sighted birds in a given area, as larger colonies should contribute a larger

percentage of shipboard observed birds. There are four other breeding colonies (>1000 breeders) between Sangan Island and Mikura Island or nearby (Oka 2004; Appendix A). Of those, three neighbor Sangan Island and one is close to Mikura Island, with ~135 000 birds breeding on Sangan Island and 820 000 birds breeding on Mikura Island, including the neighboring colonies (Oka 2004, Matsumoto et al. 2007, Biodiversity Center of Japan 2013). For other shearwater species (e.g., the Short-tailed Shearwater *Puffinus tenuirostris*; Wooller et al. 1990), researchers estimated that 15% of

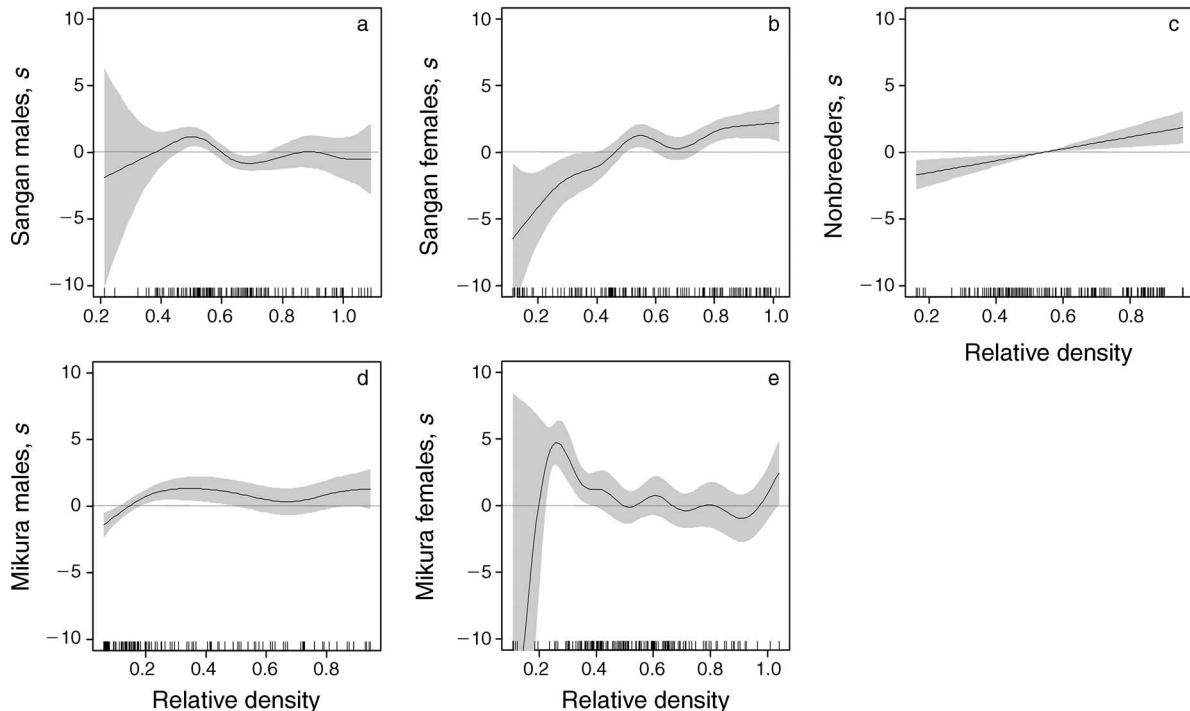


FIG. 4. GAM response curves for the model for (a) Sangam males, (b) Sangam females, (c) nonbreeders, (d) Mikura males, and (e) Mikura females, estimating the probability of contribution of each category to the vessel survey data. The black vertical bars below curves represent data of tracking-based fixed kernel density values of each category corresponding to the vessel survey points.

mature birds skip a breeding season in any given year, so we assumed a similar proportion of Streaked Shearwaters may skip breeding. Therefore, we multiplied the estimated abundance of each category by the population ratio (Sangan males and females by 0.16, nonbreeders by 0.06, Mikura male and females by 1) to obtain a fixed abundance estimated from the vessel-survey data (Fig. 2d). Also, using the raw vessel-survey data (not partitioned by each category), we predicted observed shearwater abundance as a function of environmental variables (Table 2, Fig. 2).

RESULTS

Tracking-based habitat models

The tracking-based models showed differences in relative use (density) as a function of life history category (Fig. 3). Sangan birds (all categories) were concentrated both north and south from the colony (Fig. 3a), while males and nonbreeders were more abundant in the northern study area (Fig. 3b, d) and females were more abundant in the south (Fig. 3c). Mikura birds (all categories) had greater densities north of the colony along the coast (Fig. 3e), while males were abundant along the coast (Fig. 3f) and females were further offshore (Fig. 3g).

Integration of tracking and vessel-based data

The GAM response curves of vessel observed birds as a function of relative density of tracking data parti-

tioned by category are presented in Fig. 4. High abundance grid cells from the vessel data were estimated to consist of Sangan females, Mikura males, and Mikura females (Fig. 4b, d, e). For each category, we fitted models (Table 2) and predicted the category-specific abundance estimates (Fig. 5a–e).

As the Mikura colony is much larger, the predicted abundance was higher for males and females from Mikura Island compared to Sangan Island (Fig. 5a–e). Thus, Mikura males and females contributed the most to observed individuals in the vessel survey. Furthermore, the predicted bird abundance in each category was summed to obtain an estimate of total abundance, which was multiplied by the vessel survey data (Fig. 5f). In the integrated model, the abundance of Streaked Shearwaters was relatively high along the coast between Sangan and Mikura Islands and also offshore areas east of Sangan Island (Fig. 5f). In contrast, shearwater abundance predicted by the vessel-only model extrapolated to the seas in northern Japan was high along the coast around Japan, including the Pacific Ocean and also Sea of Japan beyond the survey area (Fig. 5g).

DISCUSSION

Previous studies have examined the differences in habitat use among sexes, age classes, breeding colonies, and current reproductive conditions (e.g., Cairns 1989, Cristol et al. 1999, Grémillet et al. 2004, Ruckstuhl and Neuhaus 2005, Crawford et al. 2012). However, studies

TABLE 1. Model selection table showing selected models (<2 Δ AIC; Burnham and Anderson 2010) with environmental variables and results for the validation for Streaked Shearwaters (*Calonectris leucomelas*) in Japan.

Category and model	AUC	COR	Calibration	Bias	AIC	w_i
Sangan Island						
Density ~ DEP + log(CHL) + SSHA + SST + COLONY	0.96	0.83	1.003605	-0.000725	5 868.85	1.00
Sangan male						
Density ~ DEP + log(CHL) + SLOPE + SSHA + SST + COLONY + COLONY \times SST	0.87	0.70	1.022290	-0.001586	5 741.29	0.52
Density ~ DEP + log(CHL) + SLOPE + SSHA + SST + COLONY \times SST	0.87	0.70	1.022409	-0.001602	5 741.47	0.47
Sangan female						
Density ~ DEP + log(CHL) + SLOPE + SSHA + SST + COLONY \times SST	0.95	0.81	1.011002	-0.001892	5 343.46	0.50
Density ~ DEP + log(CHL) + SLOPE + SSHA + SST + COLONY + COLONY \times SST	0.95	0.81	1.011002	-0.001892	5 343.46	0.50
Nonbreeder						
Density ~ DEP + log(CHL) + SSHA + SST + COLONY	0.92	0.78	1.015496	-0.001974	5 592.70	1.00
Mikura Island						
Density ~ DEP + log(CHL) + SLOPE + SSHA + SST + COLONY \times SST	0.82	0.48	0.980464	-0.000787	9 598.29	1.00
Mikura male						
Density ~ DEP + log(CHL) + SLOPE + SSHA + SST + COLONY \times SST	0.83	0.53	1.020622	0.000368	7 717.75	1.00
Mikura female						
Density ~ DEP + log(CHL) + SLOPE + SSHA + SST + COLONY + COLONY \times SST	0.84	0.43	0.998698	0.000128	12 720.60	1.00

Notes: The best model for each category is indicated in bold; model terms are Density, fixed kernel density; DEP, bathymetry; log(CHL), log-transformed chlorophyll *a* concentration (primary productivity); SSHA, sea surface height anomalies; SST, sea surface temperature; SLOPE, bottom slope (upwelling probability); COLONY, distance to nearest breeding colony for shearwaters of unknown origin (vessel-based model) or to colony of origin (for tracking data). Statistical terms are AUC, area under the receiver-operated characteristic curve; COR, point biserial correlation coefficient between observed and predicted values; calibration, slope of regression of observed vs. predicted values; bias, intercept of regression of observed vs. predicted values; AIC, Akaike's information criterion (see Appendix B for details); w_i , Akaike weight.

rarely incorporate ecological and life history differences into a habitat-modeling framework (Huettmann and Diamond 2001, Conde et al. 2010, Huettmann et al. 2011). Our study showed that the predicted density distribution patterns of a single species, the Streaked Shearwater, differed among sexes, originating colonies, and breeders and nonbreeders. Furthermore, when pooling data from males and females together (i.e., colony specific models), estimated foraging habitats were less clearly defined (Fig. 3). This certainly highlights the need to study multiple ecological states (i.e., sex and breeding condition), life history stages, and populations in a given species, since climate-related and other anthropogenic effects on a given species may be underestimated when all conspecific individuals are treated as ecologically equivalent (Hazen et al. 2013b). By using combined models of tracking data and independent shipboard survey data, we can make more inference about species habitat use than from either data set alone.

By combining vessel-based sighting data with tracking-based models, we were able to estimate the abundance of individuals partitioned across categories. Using the GAM-estimated abundance of birds in each category, we could predict their distributional range and

density separately, which may be more accurate than treating them as a whole. Individuals observed during a vessel survey may be dominated by a single sex, life history stage, or colony of origin based on transect locations and survey timing, possibly resulting in the misestimation of species habitat. Extrapolating model results to outside of the study may predict the species habitat beyond their actual home range (Elith and Leathwick 2009) resulting in an overestimation of potential habitat. For example, in our vessel-based model (Fig. 5g), the estimated prediction showed a relatively high abundance in the Sea of Japan, although we have no data supporting their distribution and abundance there in this study.

As tracking data provide a method to delineate species' habitat (i.e., home range) and vessel survey data provide a quantitative estimate of population abundance, including multiple life history categories (i.e., sex, colony, and breeding condition) in a modeling framework may provide a more comprehensive picture, including identifying differential habitat use and environmental preferences within a species. In addition, using tracking-based models to examine habitat limits can be used in combination with model hindcasts and future prediction scenarios to estimate past and future

TABLE 2. Final selected models for the combined model of vessel survey and tracking data (models $<2 \Delta AIC$ are shown).

Category and model	COR	Calibration	Bias	AIC	Weight
Vessel only data, no consideration of the categories					
Abundance \sim DEP + log(CHL) + SLOPE + SSHA + SST + COLONY + COLONY \times SST	0.32	0.558250	5.274440	793.32	0.48
Abundance \sim DEP + log(CHL) + SLOPE + SSHA + SST + COLONY \times SST	0.32	0.558250	5.274440	793.96	0.34
Sangan male					
Abundance \sim DEP \times Density + log(CHL) \times Density + SLOPE \times Density + SST \times Density	0.49	1.486000	-0.468600	484.80	0.33
Abundance \sim DEP \times Density + log(CHL) \times Density + SLOPE \times Density + SSHA \times Density + SST \times Density	0.49	1.468000	-0.441800	485.89	0.19
Sangan female					
Abundance \sim DEP \times Density + log(CHL) \times Density + SLOPE \times Density + SST \times Density + COLONY \times Density	0.59	1.509520	-1.191130	578.27	0.32
Abundance \sim DEP \times Density + log(CHL) \times Density + SLOPE \times Density + SSHA \times Density + COLONY \times Density	0.53	1.302440	-0.553010	579.58	0.17
Abundance \sim DEP \times Density + log(CHL) \times Density + SLOPE \times Density + SSHA \times Density + SST \times Density + COLONY \times Density	0.52	1.290430	-0.512730	579.58	0.17
Abundance \sim DEP \times Density + log(CHL) \times Density + SSHA \times Density + SST \times Density + COLONY \times Density	0.52	1.253430	-0.360800	580.22	0.12
Nonbreeder					
Abundance \sim DEP \times Density + log(CHL) \times Density + SLOPE \times Density + SST \times Density + COLONY \times Density	0.44	1.261350	-0.091330	448.92	0.29
Abundance \sim DEP \times Density + log(CHL) \times Density + SST \times Density + COLONY \times Density	0.48	1.438800	-0.391600	449.40	0.23
Abundance \sim DEP \times Density + SLOPE \times Density + SST \times Density + COLONY \times Density	0.43	1.278000	-0.113300	450.07	0.16
Mikura male					
Abundance \sim DEP \times Density + log(CHL) \times Density + SLOPE \times Density + COLONY \times Density	0.41	1.184400	-0.173800	451.24	0.35
Abundance \sim DEP \times Density + log(CHL) \times Density + SLOPE \times Density + SST \times Density + COLONY \times Density	0.40	1.199300	-0.202900	452.05	0.23
Abundance \sim DEP \times Density + log(CHL) \times Density + SST \times Density + COLONY \times Density	0.38	1.100240	0.071260	452.60	0.18
Abundance \sim DEP \times Density + log(CHL) \times Density + COLONY \times Density	0.39	1.166500	-0.134100	452.90	0.15
Mikura female					
Abundance \sim DEP \times Density + log(CHL) \times Density + SLOPE \times Density + COLONY \times Density	0.48	1.485200	-0.928800	534.30	0.54
Abundance \sim DEP \times Density + log(CHL) \times Density + SLOPE \times Density + SST \times Density + COLONY \times Density	0.49	1.567800	-0.956300	536.17	0.21

Notes: The best model for each category is indicated in bold. Abbreviations and definitions are as in Table 1.

patterns in habitat use. This approach can be used to identify and quantify habitat for particularly sensitive life history stages based on predicted changes in habitat use within a species. In recent decades, tracking data is being collected for a wide range of animal species including terrestrial and marine taxa (BirdLife International 2004, Tremblay et al. 2009, Hebblewhite and Haydon 2010, Block et al. 2011) and more often is being used to assess risk to anthropogenic threats (Żydelis et al. 2011, Maxwell et al. 2013). The ability to combine these data sets with conventional surveys of species distribution (i.e., vessel, aerial, or terrestrial surveys) can be used to improve species-specific density estimates, interannual changes in habitat use, and estimation of biodiversity patterns.

Collection of additional tracking and vessel-based observation data independently will often improve fit

and predictive capacity for models of species' distributions, however our study highlights the importance of combining multiple data sets and considering intraspecific differences in movement and behavior in habitat modeling. Also, for the first time to our knowledge, we have developed a novel method to integrate data collected from these two different methods (tracking and vessel survey) offering a valuable approach towards habitat modeling techniques of disparate data sets. Over the past decades, significant ecosystem effects of global climate change have been observed, particularly evidenced by observed shifts in species home ranges (review by Walther et al. 2002, Parmesan and Yohe 2003, Burrows et al. 2011, Pinsky et al. 2013). In addition, many species of marine vertebrates have declining population numbers due to the increase in human pressures, such as fisheries bycatch (Lewison et al.

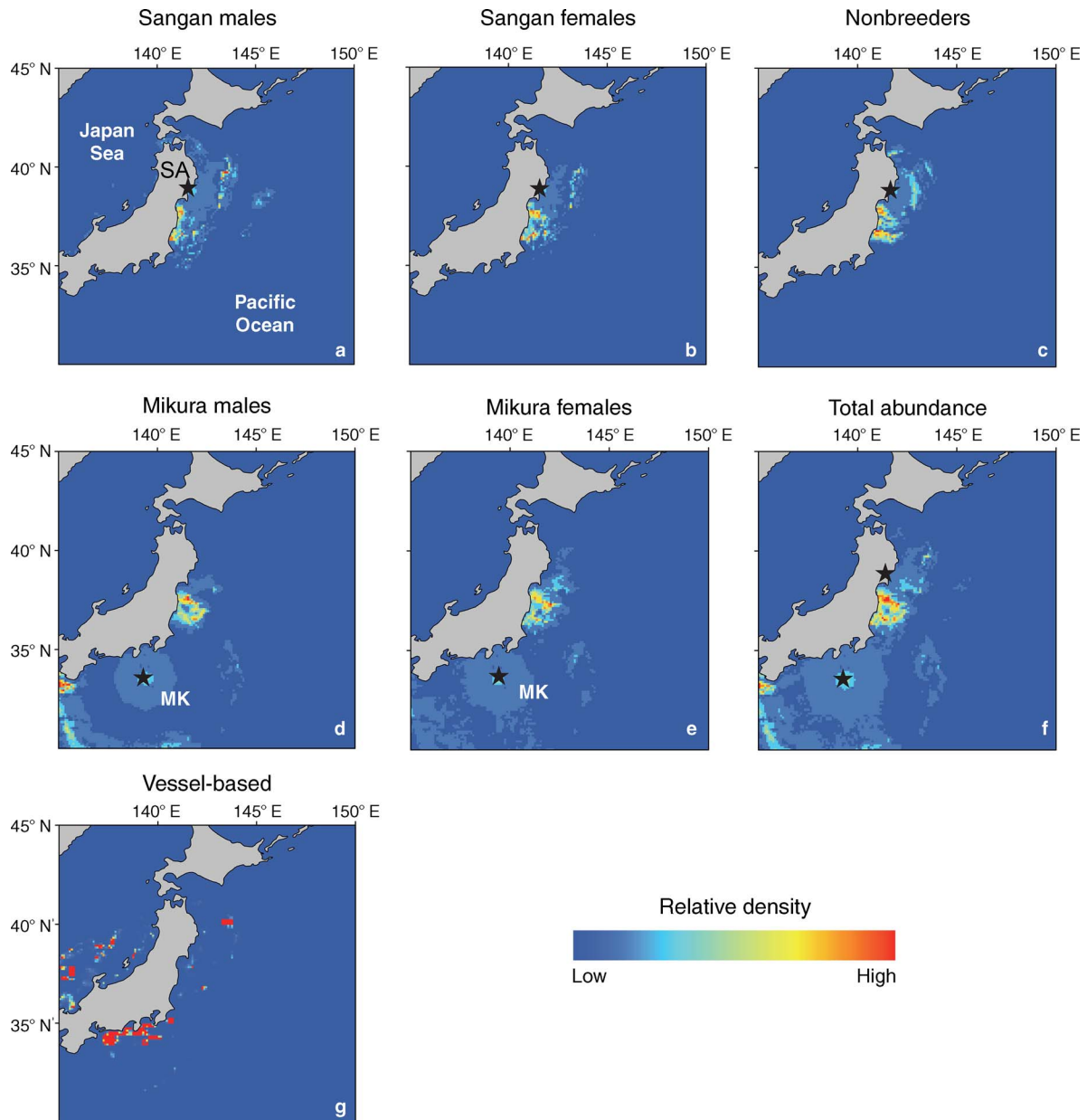


FIG. 5. Abundance and distribution of Streaked Shearwaters predicted using the estimated abundance for each category as a function of environmental variables with the tracking-based model framework for (a) males, (b) females, (c) and nonbreeders from Sangan Island (SA), (d) males and (e) females from Mikura Island (MK), (f) the total abundance across all categories, and (g) predicted abundance from vessel survey data as a function of environmental variables only.

2004, Oro et al. 2004, Anderson et al. 2011). Hence, the designation and enforcement of conservation areas for critical life history stages (e.g., EBSA, MPA, and IBA; Game et al. 2009, Arcos et al. 2012, Gregr et al. 2012, BirdLife International 2013) remains an urgent task. In this respect, the integration of multiple data types may be useful to adjust the vessel-based survey transects to monitor particularly sensitive life history stages and marine environments where conditions are changing seasonally and interannually (Tremblay et al. 2009).

Many statistical modeling techniques have been developed to predict species occurrence and abundance (Yen et al. 2004, Huettmann and Diamond 2006, Louzao et al. 2009, Tremblay et al. 2009, Nur et al. 2011), although there is still debate on how modeling methods differ in their ability to predict species distributions and which approaches yield the most reliable predictions (Yen et al. 2004, Opperl et al. 2012). These studies have not focused on the within-species differences in habitat use and have not examined multiple colonies to examine whether

niche width differs among life history and ecological categories examined here (Bolnick et al. 2003). Hence, we may suggest the importance of examining and incorporating when possible within-species habitat preferences to constructing more robust models to predict species distributions more holistically.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/15-0142.1.sm>

Data Availability

Data associated with this paper have been deposited in BirdLife:

http://seabirdtracking.org/mapper/?dataset_id=945

http://seabirdtracking.org/mapper/?dataset_id=946