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Article:

Title: At-sea distribution and habitat of breeding Japanese Murrelets Synthliboramphus wumizusume: implications for conservation management

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Abstract

The Japanese Murrelet (Synthliboramphus wumizusume) is a rare, globally Vulnerable seabird, endemic to Japan and South Korea. However, little is known of its at-sea distribution, habitat or threats. We conducted several years of at-sea surveys around Japan to model Japanese

Murrelet density in relation to habitat parameters, and make spatial predictions to assess the adequacy of the current Japanese marine Important Bird and Biodiversity Area (IBA) network for the species. During a five-year period, 3485 km of at-sea surveys recorded 3161 Japanese Murrelets around four breeding locations. Maximum murrelet group size was 90 individuals with a mean group size of 2.9 ± 4.2 individuals. Models of Japanese Murrelet at-sea density around the two largest breeding locations predicted that almost all murrelets occur within 30 km of the breeding colony and most within 10 km. Murrelets were predicted closer to the colony in May than in April and closer to the colony at a neritic colony than at an offshore island colony. Additionally, murrelets breeding on an offshore island colony also commuted to mainland neritic habitat for foraging. The marine habitat used by Japanese Murrelets differed between each of the four surveyed colonies, however oceanographic variables offered little explanatory power in models. Models with colony, month and year generated four foraging radii (9 – 39 km wide) containing murrelet densities of > 0.5 birds/km^2. Using these radii the Japanese marine IBA network was found to capture between 95% and 25% of Japanese Murrelet at-sea habitat while breeding and appears appropriately configured to protect near-colony murrelet distributions. Given the range of marine habitats that breeding murrelets inhabit, our simple models offer an applicable method for predicting to unsampled colonies and generating ecologically-informed seaward extension radii. However, data on colony populations and further at-sea surveys are necessary to refine models and improve predictions.

Introduction

The Japanese Murrelet (Synthliboramphus wumizusume, hereafter murrelet) is a small seabird

endemic to Japan and South Korea and is listed on the IUCN Red List as globally Vulnerable (Birdlife International 2015). With a global population of 2,500-10,000 adults it is the one of the rarest alcids in the world (Carter et al. 2002, Birdlife International 2015). The species was designated as a Japanese 'national monument' in 1972 in recognition of its endemic status and need for protection (Hasegawa 1984) but continues to decline and, owing to its rarity, is poorly studied and understood.

Murrelet populations are declining due to terrestrial and marine threats. At monitored breeding sites, human disturbance and predation by introduced rats (Rattus rattus, R. norvegicus) and carrion and jungle crows (Corvus corone, C. macrorhynchus) are apparent threats (Carter et al. 2002, Ogi 2008, Croxall et al. 2012). By contrast, the marine threats faced by murrelets are less well known, particularly due to poor data on murrelet at-sea distribution. Accidental bycatch of seabirds at-sea in gillnet fisheries has been identified as a major source of mortality, with alcids the most frequently caught group and the Northwest Pacific one of the most high-risk areas (Žydelis et al. 2013). Indeed, the Japanese Murrelet was identified as the second most exposed seabird species to gillnet bycatch in a global assessment (Waugh et al. 2011). Murrelets are taken as bycatch in driftnets and gillnets while foraging near breeding colonies (DeGange et al. 1993, Carter et al. 2002, Ogi 2008), and also in large-scale squid driftnet fisheries while wintering Southeast of Hokkaido (Ogi et al. 1993, Piatt and Gould 1994). Piatt and Gould (1994) estimated that in 1990 and 1991, 1-10% of the adult murrelets population was killed in northwest Pacific drift-net squid fisheries, highlighting the level of threat. In addition to bycatch, murrelets are likely threatened by human industrial activities while breeding in Japanese waters, such as oiling and pollution (Camphuysen and Heubeck 2001) and wind farm development (Furness et al. 2013).

To counter such threats, marine conservation in Japan has received increasing attention in recent years. In 2008, the Basic Act on Ocean Policy (Kantei 2007) was adopted, followed by the publication of the Marine Biodiversity Conservation Strategy of Japan in 2011 (Ministry Of Environment Japan 2011). This governmental strategy clearly defined Marine Protected Areas (MPAs), and under the definition, legally qualified 8.3% of Japanese waters as MPAs. Japan now seeks to designate an additional 1.7% of its exclusive economic zone (EEZ) as MPAs to meet the Convention on Biological Diversity (CBD) Aichi Target 11 (i.e. to conserve ≥10% of biologically and ecologically important national marine areas by 2020 (CBD 2010).

However, the current network of MPAs has received criticism from conservationists and researchers for not adequately representing areas of high marine biodiversity and lacking appropriate management (NACS-J 2012). Since 2010, the Wild Bird Society of Japan (WBSJ) has used Birdlife International's Important Bird and Biodiversity Area (IBA) criteria to identify a network of sites for the conservation of seabirds and marine ecosystems in Japanese waters. Marine IBAs have been identified in waters around breeding colonies, using radii informed by seabird foraging ranges and distribution at-sea (Birdlife International 2010, Thaxter et al. 2012). Although marine IBAs can be delimited more precisely using methods such as seabird tracking, the seaward extension method is recommended as a simple but effective approach, especially when refined using seabird habitat and oceanographic preferences (Thaxter et al. 2012, Soanes et al. 2016).

To assess and mitigate at-sea threats for seabirds, baseline data on at-sea distribution and marine habitat preferences are essential (Lascelles et al. 2014). However, acquiring these data is challenging for seabirds such as murrelets, for which telemetry studies are difficult (Kissling et al. 2015). As such, we conducted ship-based surveys to model the influence of marine habitat

variables on the distribution of breeding murrelets while at-sea. We describe: 1) habitat variables that influence near-colony murrelet distributions; 2) habitat variables that influence foraging murrelet distributions; and 3) the marine habitats of murrelets from different colonies. We use constructed models to predict the extent of murrelet at-sea distribution throughout breeding, and assess the adequacy of the current Japanese marine IBA network to protect the murrelets.

Methods

Survey data collection

At-sea surveys for murrelets were conducted around active colonies in four areas: by the WBSJ at Northern Izu islands and Kojine; by Y. Nakamura at Biroujima; and by H. Sato and S. Mori at Oki (Fig.1). Surveys were carried out from 2008 to 2012 during the breeding season and predominantly in the incubation phase. All surveys remained in the vicinity of murrelet colonies (<50 km) and, with the exception of two surveys at Biroujima, were conducted in daylight hours (Table 1). Surveys were made from the bow of a boat, travelling at 20 km/hr, by 1-4 observers using binoculars. All diving, floating and flying murrelets were counted within 30m of the boat on both sides and a 90º arc to the bow. Whenever murrelets were encountered, the GPS position was recorded and with the exception of three surveys, the number of murrelets was counted (Table 1).

Marine habitat data

All data handling and statistical analyses were performed in the statistical software environment program R, version 3.1 (R Core Team 2014), mapping was conducted using QGIS 2.0.1 – Dufour (QGIS Development Team 2013). To model murrelet observations in relation

to marine habitat, we used a number of physical and environmental variables potentially correlated with seabird distribution and abundance (Appendix S1) (Louzao et al. 2009, Oppel et al. 2012). Static variables bathymetric depth (BATHY), seabed slope (SLOPE) and minimum distance to land (D_LAND) were extracted or calculated from the GEBCO 30 arc-second global bathymetry and topography grid (GEBCO 2014). As central-place foragers, the marine habitat accessed by breeding seabirds is heavily influenced by distance from the breeding colony (Grecian et al. 2012, Oppel et al. 2017). We compiled a list of all known murrelet breeding localities in Japan (Appendix S2) and calculated a 'minimum distance to colony' layer (D_COL) in order to quantify the constraints of central place foraging. Unfortunately, population estimates are unavailable for almost all colonies (but see Carter et al. 2002) and thus the impact of intra-specific competition (Lewis et al. 2001, Wakefield et al. 2017) could not be modelled.

Oceanographic variables sea surface temperature (SST) and chlorophyll-a concentration (CHLA) were created from MODIS Aqua and Terra level 2 satellite image products, downloaded via the OceanColor data portal (http://oceancolor.gsfc.nasa.gov). MODIS level 2 Local Area Coverage (L2_LAC) images are available every 1-2 days with an approximate spatial resolution of 1 km, but require quality-control processing to remove suspect pixels (Oceancolor 2015). We used ESA BEAM software (BEAM 2014) to georeference and apply quality-control flags to MODIS L2 imagery, processing images to level 3 quality, while maintaining the ~1km spatial resolution. Standard level 3 imagery has 17 L2 quality-control flags applied to mask pixels, however we included two types of flagged data: HILT (Observed radiance very high or saturated) and STRAYLIGHT (Straylight contamination is likely) because omitting these would have masked out too many pixels in near-shore areas where murrelet surveys took place. We created composite images by averaging temporally

consecutive data together, to account for cloud covered pixels in L2_LAC imagery and previous observations that seabird distribution is rarely related to concurrent conditions in SST and CHLA (Louzao et al. 2009, Oppel et al. 2012). Composite CHLA and SST images were created for each unique survey, by averaging all processed images falling within the period of the survey and the 3 months preceding. A three month composite window was used following Lavers et al. (2014) to characterise the broad oceanographic conditions of the murrelet incubation period, and to account for the time needed for energy to flow from remotely-sensed primary productivity to higher trophic levels, which constitute seabird prey (Wakefield et al. 2009). Gradient variables (G_CHL and G_SST) were created from the corresponding CHLA and SST composites, using the 3x3 pixel moving window to identify areas of rapid change between neighbouring pixels. All created environmental variables were stored as layers with 1 km cell size using package 'raster' (Hijmans et al. 2014).

Survey data processing and extraction

Although standardised survey protocols have at times been adhered to around Biroujima and Northern Izu island colonies, combined multi-year datasets represent a number of survey methodologies. To standardise across surveys, we aggregated the murrelet observation data into a spatial grid at 1km scale (matching the resolution of the environmental variables). For each survey, grid cells overlaying observations of one or more murrelets were attributed with the sum value and grid cells on the survey route where no murrelets were detected were assigned 'absent'. As survey routes frequently overlapped (occupied the same grid cells) over the multiple years of sampling, murrelets could conceivably be present and absent in the same cell but at different times, allowing for more accurate extraction of temporally dynamic oceanographic variables. With the murrelet data attributed to the 1km spatial grid we then extracted data from each of the habitat variables based on the corresponding timestamp. The

marine habitat of murrelets from each of the four sampled colonies was summarised from SST, CHLA, BATHY and D_LAND values in pixels where one or more murrelets were encountered.

The majority of surveys (n=11) in our dataset included count data, however for some surveys (n=3) only presence-absence data were available (Table 1). Count data was selected for modelling as the ability to estimate density is useful for understanding and inference in conservation management (Nielsen et al. 2005). Removing presence-absence data also removed the two Biroujima night surveys. Single surveys of colonies were dropped from modelling due to lack of observations (Kojine) or presences and absences only (Oki). The remaining colonies, Biroujima, and the Northern Izu islands, were well surveyed and were modelled separately due to their geographic differences (Fig.1). At-sea observations distant from the colony more accurately reflect preferred habitat for foraging compared to those made near-colony, which are complicated by behaviours unrelated to habitat quality such as transiting to and from the colony and rafting (Wilson et al. 2009, Grecian et al. 2012). Most murrelet observations in our data were made within 20 km of the colony (Fig. 1). However, surveys from the Northern Izu Island colonies recorded a second cluster of observations at distances of 20-50 km from the colony (Appendix S3). Using the >20 km distance from colony threshold, we took a subset of the Northern Izu Island dataset to represent counts of murrelets that were free of near-colony behaviours and more likely to accurately represent preferred foraging habitat.

Statistical modelling

Before constructing models, predictor variables were tested for multicollinearity. We calculated a Pearson's correlation score for all possible pairs of variables, using a value of 0.5

and above to identify significantly correlated variables (Dormann et al. 2007). CHLA was significantly correlated with G_CHL and D_COL was significantly correlated with D_LAND, correlated variables were not used together in the same model. Three density models were implemented: 'Biro colony', using the full Biroujima dataset; 'Izu colony', using the full Northern Izu Islands dataset; and 'Izu foraging', using a subset of the Northern Izu Islands dataset for observations >20km from the colony. Murrelet counts were fitted as a response using a generalized linear mixed model (GLMM) framework, in package 'lme4' (Bates et al. 2015). Survey was used as the random intercept to account for differences between surveys, such as weather or observation team (Zuur et al. 2009). We calculated the area of each 1 km grid cell covered by each survey (between 0.001 and 1 km^2) and included this as an offset term to account for differences in survey effort between cells. The Izu foraging model was modelled using a Poisson error distribution but the Izu and Biro colony models were overdispersed due to zero-inflation and modelled using a negative binomial error distribution (Zuur et al 2009). The Izu and Biro colony model terms were selected using forward selection, starting with D_COL, then Month and Year (including interaction terms) and then adding additional environmental variables in turn. The Izu foraging model was built using backward and forward selection, as all variables were assumed to have equal potential influence further from the colony. The support for addition (or removal) of model terms was based on likelihood ratio tests (χ^2) and confidence intervals (Bolker et al. 2009). We checked model residuals for spatial autocorrelation by calculating Moran's I values over distances: 1-100km in the package 'ncf' (Bjornstad 2015), but found no evidence of significant spatial autocorrelation. Goodness-of-fit was assessed for GLMMs split into marginal (var. explained by fixed effects) and conditional (var. explained by fixed + random effects) pseudo R^2 components (Nakagawa and Schielzeth 2013), in package 'piecewiseSEM' (Lefcheck 2016). Predictive performance was assessed using Pearson's and Spearman's rank correlation coefficients between observed and model-

predicted murrelet counts (Potts and Elith 2006). Predictive performance was calculated for each model predicting upon its training dataset, and additionally for Biro and Izu colony models, predictive performance was assessed for each model predicting to the other colony.

Spatial prediction

To assess the adequacy of the current Japanese marine IBA network for breeding murrelets, we used Biro and Izu colony models to predict murrelet at-sea density around all known murrelet colonies (see Appendix S2). We applied a minimum density threshold of 0.5 birds/km^2 to model predictions, thereby limiting their extent to areas appropriate for conservation management while protecting core murrelet at-sea densities. For each marine IBA that included a murrelet breeding colony, we calculated the proportion of model-predicted murrelet at-sea distribution that was captured within the marine IBA.

Results

Survey results

A total of 3161 murrelets were recorded in 1221 at-sea encounters from a total of 3485 km of surveys undertaken between 2008 and 2012. Murrelets were encountered singularly and in groups of up to 90 individuals with a mean group size of 2.9 ± 4.2 individuals. The Northern Izu islands were the most intensely surveyed location with a total of 2283 km of surveys; when gridded at 1 km, murrelets were observed in 17% of surveyed cells. 634 km of surveys were undertaken at Biroujima, with 21% of surveyed cells containing murrelets. 361 km of surveys were undertaken at Oki with 6% of surveyed cells containing murrelets. 205 km of surveys were undertaken at Kojine with 3% of surveyed cells containing murrelets. Mean density of murrelets at-sea was highest around Biroujima colony (1.86 murrelet/km^2), followed by Northern Izu colonies (1.16 murrelet/km^2) and Kojine (0.06 murrelet/km^2). Average group size

of murrelets was highest at Northern Izu Islands with 3.1 ± 4.7 individuals per group, followed by Biroujima with 2.2 ± 1.6 individuals per group and Kojine with 1.6 ± 0.84 individuals per group.

Marine habitat at different Japanese Murrelet colonies

The marine habitat in which murrelets were observed, differed significantly between the four surveyed colonies by SST ($F_3 = 285.2$, $p = <0.001$), CHLA ($F_3 = 862.7$, $p = <0.001$); BATHY ($F_3 = 538.6$, $p = <0.001$) and D_LAND ($F_3 = 368.8$, $p = <0.001$; Table 2).

Variables influencing Japanese Murrelet at-sea density

The at-sea density of murrelets at Biroujima significantly increased closer to the colony ($\chi^2_1 = 108.8$, $p = <0.001$), at 1 km of the colony mean murrelet at-sea densities ranged from 1.75 to 7 birds/km^2 (Figure 2). Their density was dependent on year ($\chi^2_2 = 26.4$, $p = <0.001$; 2008 being significantly higher than 2009 and 2012), but did not differ between March and April ($\chi^2_1 = 2.7$, $p = 0.1$). No other environmental variables significantly influenced murrelet density at Biroujima (Table 3). The D_COL and YEAR fixed terms accounted for all variation within the survey random term, giving an identical marginal and conditional R^2 of 0.37.

The at-sea density of murrelets at Northern Izu colonies also increased closer to the colony, at 1 km of the colony mean murrelet at-sea densities ranged from 3.49 to 6.74 birds/km^2 (Figure 2). However, in contrast to Biroujima, where the distribution of murrelet density in relation to colony distance was static over time, the distance at which murrelets were distributed from Northern Izu colonies changed by month ($\chi^2_2 = 94$, $p = <0.001$): murrelets were distributed closer to the Northern Izu colonies in May than in April (Figures 2 & 3). However, there were no significant differences in overall murrelet density between April and May ($\chi^2_1 = 2.6$, $p =$

0.11), or between 2010 and 2011 (χ^2_1= 1.7, p = 0.20). The Izu colony model had a marginal R^2 of 0.42 and conditional R^2 of 0.56, indicating that some of the variance in murrelet density was due to survey differences. Additional environmental variables SLOPE (density was higher over shallower seabed slopes; χ^2_1= 9.9, p = 0.002) and G_SST (density higher at more homogeneous SST gradients; χ^2_1= 4.8, p = 0.028) also significantly influenced murrelet density at Northern Izu colonies. However, inclusion of these variables added very little to model explanatory power (marginal R^2 of 0.44 and conditional R^2 of 0.59), so, in the interest of transferability of models to un-surveyed colonies, they were dropped from model predictions.

The at-sea density of murrelets foraging at distances > 20km from Northern Izu colonies was not influenced by distance to colony (χ^2_1= 0.56, p = 0.451), month (χ^2_1= 0.14, p = 0.708) or year (χ^2_1= 0.67, p = 0.415). The density of foraging murrelets was significantly influenced by distance to land (χ^2_1= 17.1, p = <0.001), the model predicted that for every 10 km further offshore, murrelet density increased by 0.2 birds/km^2. The density of foraging murrelets was also slightly influenced by CHLA (χ^2_1= 4.1, p = 0.044), the model predicted that for every 1 mg m^{-3} increase in the chlorophyll-a concentration, murrelet density increased by 0.025 birds/km^2. The Izu density model had a marginal R^2 of 0.05 and conditional R^2 of 0.24, indicating that almost all of the variance in murrelet density was due to survey differences.

Prediction of density models

The Biro colony model was better than the Izu colony model for predicting murrelet density back onto the sampled colony (Table 3). The Izu colony model was able to predict murrelet density at the Biroujima colony better than the Biro colony model could predict murrelet density at Northern Izu colonies (Table 3). The Izu foraging model was the poorest performing model when predicting to the training dataset and was not used for predicting to independent

test data (Table 3). Applying the minimum density threshold of 0.5 birds/km^2 to predictions from colony models generated radii of 9 km distance from Biroujima colony in 2009/2012 (hereafter, Model A) and 18 km in 2008 (Model B), and radii of 27 km from Northern Izu colonies in May (Model C) and 39 km in April (Model D; Figure 3).

Assessment of marine IBA network

All 22 known murrelet breeding colonies (within Japanese waters) were included in the Japanese marine IBA network (Figure 4). 13 marine IBAs overlapped with the 22 murrelet colonies, each created using seaward extensions (though not always centred on a murrelet colony) of between 8 and 120 km. Around the 22 murrelet colonies, the four radii predicted a total area of at-sea habitat where murrelet densities > 0.05 birds/km^2 of between 4,188 km^2 (Model A) and 56,134 km^2 (Model D; Table 4). Under the most conservative radius of 9 km from the colony (Model A), the 13 marine IBAs captured 95% of murrelet at-sea habitat, by contrast under the most liberal radius of 39 km from the colony (Model D) marine IBA capture of potential habitat fell to 25% (Table 4).

Discussion

At-sea distribution and habitat of breeding Japanese Murrelets

The at-sea density of murrelets in the vicinity of breeding colonies was mostly explained by the distance to the colony, with a contribution from temporal effects. This is consistent with the general dominance of distance to colony in governing habitat use by central-place foraging seabirds (Oppel et al. 2017, Wakefield et al. 2017). Our study period (Mar-May) covers the later part of pre-laying, the entirety of incubation and the early part of provisioning (Ono 1996).

Throughout this time murrelets are constrained to the colony and higher densities in the vicinity of the colony are expected (Grecian et al. 2012). There was no evidence that total murrelet at-sea density differed by month: April no higher than March at Biroujima and May no higher than April at Northern Izu colonies. However, month did interact with distance to colony, showing a shift in at-sea density from more offshore in April to more colony-centred in May. No such change was observed between March and April. Murrelet breeding phenology could explain our results; eggs are laid in March and incubated until hatching in late April and May, at which point parents and their semi-precocial chicks move to the sea (Ono 1996). A more colony-centric at-sea distribution in May relative to April could come from observations of adult murrelets accompanying semi-precocial chicks at-sea. Such family groups are limited in their ability to disperse from the colony by chick flightlessness (Sealy et al. 2015). Murrelet density did not vary by year at Northern Izu colonies but was significantly higher at Biroujima in 2008 relative to 2009 and 2012. The 2008 Biroujima prediction is likely the most representative estimate of murrelet at-sea density near this colony given that this was the best sampled year. Furthermore, April murrelet densities predicted for Biroujima in 2008 are higher than those for the Northern Izu islands in, which is consistent with colony data for Biroujima being the largest single breeding colony for the species with a population of ~3000 individuals (Iida 2008, Birdlife International Tokyo and Wild Bird Society of Japan 2017), compared to the smaller Northern Izu colonies (combined estimated population of 1000 individuals; Carter et al. 2002). Finally, 2009 was an El Niño year, which impacted Japanese seabirds (Mizutani et al. 2013) and could explain reduced murrelet at-sea density. Further study will be able to elucidate whether inter-annual variance in near-colony at-sea density is an artefact of sampling differences or in response to environmental heterogeneity.

The more colony-centric distribution of murrelets around the Biroujima colony compared to

the Northern Izu colonies could be related to differences in competition pressure and at-sea habitat between the two locations (Paiva et al. 2010b, Oppel et al. 2015). Intra-specific competition pressure should be higher surrounding the denser populated Biroujima colony than the Northern Izu colonies, but greater foraging distances (sensu Ashmole 1963) were not observed. The likely explanation for this disparity is that higher competition pressure at Biroujima was offset by greater background resource availability from the productive neritic habitat we describe. By contrast, the cooler, deeper, less productive, pelagic habitat experienced by murrelets from offshore Northern Izu island colonies, could limit local resource availability and necessitate greater foraging ranges (Paiva et al. 2010b).

Our exploration of at-sea habitat used by breeding Japanese Murrelets found large differences between colonies. Kojine, at the centre of the Izu island chain is a remote offshore island surrounded by deep, oligotrophic water; whereas Oki, situated in the shallow Sea of Japan, is surrounded by waters ~4 °C cooler than the other colonies on Japan's East coast that are warmed by the Kuroshio Current. Such different marine habitats are likely to promote different foraging strategies (Paiva et al. 2010a), including different at-sea distributions between populations (Paiva et al. 2010b). The potential for such local adaptation of foraging strategy in the Japanese Murrelet is problematic for applying at-sea distribution findings from studied to unstudied colonies. Additionally, as population estimates are unavailable for most Japanese Murrelet colonies, we could only link at-sea distributions to marine habitat with considerable uncertainty from unknown intra-specific competition pressure. Future study is required to incorporate these data into models and improve accuracy.

Despite differences in marine habitat between colonies, oceanographic variables explained very little about murrelet density. This could be due to satellite data limitations, such as

oceanographic features, which aggregate murrelets for foraging, occurring at spatio-temporal scales beyond the resolution of our data. Alternatively sampling limitations, such as murrelets foraging in excess of 50 km from colonies and thus beyond the scope of our surveys, as seen in congeners (Shoji et al. 2012), may have obscured relationships between foraging and oceanographic variables. The Izu foraging model, designed to capture foraging habitat, was also unable to contribute much evidence for important oceanographic characteristics of the habitat. Considering the Izu foraging model pragmatically, we observe that all the murrelets distributed > 20 km from Northern Izu colonies were found northwest of the islands over the mainland shelf. As no other colonies are nearby, we can assume these birds are from Northern Izu colonies and chose neritic habitat (< 200m depth) for foraging. Murrelets are thought to forage throughout the water column, feeding on small pelagic fishes and euphausiids (Piatt and Gould 1994) and may favour neritic habitats to prey upon benthic molluscs (Moyer 1957). However, as our surveys around the Northern Izu islands did not extend far into pelagic waters, we cannot discount the possibility that breeding murrelets also target pelagic habitat (e.g. large-scale anticyclonic eddies and warm-core rings; Piatt and Gould 1994) for foraging.

Overlap of current marine IBA network with predicted Japanese Murrelet at-sea density

Overall the current Japanese marine IBA network appears reasonably well configured to protect murrelets at-sea during breeding. The two marine IBAs capturing almost all murrelet habitat from different model predictions (>90%) were able to do so due to a large seaward extension radius for a different seabird species: Brown Booby Sula leucogaster (70 km), in the case of Danjo Islands IBA; and Black-tailed Gull Larus crassirostris (120 km), in the case of Fumishima Islet and Oki Islands IBA (Birdlife International Tokyo and Wild Bird Society of Japan, 2017). The Northern Izu Islands IBA and Torishima Island IBA have 20 km seaward extensions and perform reasonably well. The remaining marine IBAs were designated based

on seaward extension radii of 10 km or less, hence the steep decline in total marine IBA network coverage of murrelet at-sea habitat from 95% when murrelets are predicted within 9 km of colonies, to 52% when murrelets are predicted within 18 km of colonies. As such, the effectiveness of the marine IBA network to protect murrelets at a broad scale is dependent upon which model prediction is applied: the network performs well if murrelets are distributed within 9 km of colonies (Model A) but poorly if they are distributed within 39 km of colonies (Model D).

This highlights the importance of differences in at-sea murrelet distribution between colonies and the potential for error when predicting to unsampled colonies, especially in different oceanographic regions. Our results, although based only on two breeding locations, suggest that the at-sea murrelet density around a neritic colony cannot effectively predict the more pelagic distribution of an offshore island colony, and that the murrelet density around the offshore island colony, although more informative, cannot fully predict the more colony-centric distribution of the neritic colony. As a speculative recommendation the Izu model predictions could be applied to other offshore island murrelet colonies (Kojine, Torishima, Danjogunto hanagari and Takeshima/Dok) while the Biro model predictions applied to all the other colonies upon the Japanese continental shelf. However, this approach does not account for differences in colony sizes, which are known to impact the foraging range of seabirds via intra-specific competition pressure (Lewis et al. 2001, Oppel et al. 2015, Wakefield et al. 2017). To accurately predict murrelet at-sea distributions to unsampled colonies it is essential that: a) population estimates are obtained for all known Japanese Murrelet colonies (Appendix S2); and b) at-sea surveys are undertaken at colonies in different oceanographic regimes.

Potential at-sea threats identified by model predictions

Our results indicate that murrelets breeding on neritic colonies do not range far, and that murrelets from offshore islands commute to the mainland shelf to forage. This neritic distribution puts murrelets at greater threat from interaction with anthropogenic marine activities. Murrelets are sensitive to marine pollution and have been killed in oil spills, alongside large numbers of other alcids (Sato 1999). In addition to occasional large oil spills, the effects of numerous chronic oil spills from shipping poses a significant threat to seabird population stability (Camphuysen and Heubeck 2001, Wiese and Robertson 2004). The proximity of murrelet colonies to major ports and shipping lanes (e.g. Northern Izu colonies to Tokyo Bay), likely exposes breeding murrelets to the persistent threat of oiling while foraging (Carter et al. 2002). A neritic distribution also exposes breeding murrelets to a higher risk of disturbance and displacement impacts from offshore wind farms (Busch et al. 2013, Furness et al. 2013), pertinent in Japan given their expansion is promoted in the wake of the 2011 Fukushima nuclear disaster (Busch et al. 2013). Finally, a neritic distribution also exposes breeding murrelets to higher gillnet bycatch as most nets are set within 20 nautical miles of the coast (Waugh et al. 2011). As murrelets forage throughout the water column (Moyer 1957, Piatt and Gould 1994) they potentially interact with both coastal driftnets (targeting tuna and salmon), and bottom-anchored gillnets (targeting flatfish and greenling) in Japanese coastal waters (Ogi and Shiomi 1991). Given that Japan reports one of highest annual gillnet catches (Waugh et al. 2011), we re-iterate here the need for monitoring of seabird bycatch in small-scale gillnet fisheries within the Japanese EEZ (Piatt and Gould 1994, Carter et al. 2002, Ogi 2008, Žydelis et al. 2013).

Acknowledgements

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Tables

Table 1. Summary of at-sea survey data for Japanese Murrelets collected during this study

Location	Year	Month	Day(s)	Survey area (km^2)	Mean density (murrelet/km^2)
Biroujima	2008	March	16-29	83	2.17
Biroujima	2008	April	26-27	56	2.73
Biroujima	2009	March	07	60	2.00
Biroujima *†	2009	March	21	31	
Biroujima *†	2009	April	19	58	
Northern Izu islands	2010	April	06	450	0.97
Northern Izu islands	2010	April	20	441	0.65
Northern Izu islands	2010	May	11-12	241	2.09
Northern Izu islands	2011	April	06	823	0.42
Northern Izu islands	2011	April	21	794	0.51
Oki †	2011	April	25-28	185	
Northern Izu islands	2011	May	09	294	2.31
Kojine	2012	March	20-22	266	0.06
Biroujima	2012	April	14-16	330	0.52

Night survey data (*), presence-absence data only (†)

Table 2. Oceanographic characteristics of Japanese Murrelet encounter locations around each surveyed colony. SST = sea surface temperature, CHLA = chlorophyll-a concentration, BATHY = bathymetric depth, D_LAND = distance to land

Colony	No. of Japanese Murrelet encounters	SST (°C)	CHLA (mg m^{-3})	BATHY (m)	D_LAND (km)
Izu	867	16.48 ± 0.61	0.58 ± 1.05	260.42 ± 186.25	6.92 ± 3.2
Biroujima	330	17.25 ± 0.78	3.62 ± 2.89	33.81 ± 59.89	1.79 ± 2.32
Kojine	10	17.78 ± 0.77	0.18 ± 0.04	224.7 ± 147.06	5.49 ± 3.21
Oki	14	12.69 ± 0.06	0.44 ± 0.06	67.93 ± 22.63	3.34 ± 2

Table 3. Selected variables and predictive ability of density models. r is the Pearson's correlation coefficient and p the Spearman'r rank correlation coefficient between predicted and observed densities, (train) is predicting upon data used in each model's construction, (test) is predicting upon independent data from the other colony (Biroujima to Izu and vice versa), : denotes an interaction term, all models included a sampling effort offset term. CHLA = chlorophyll-a concentration, D_COL = distance to colony, D_LAND = distance to land

Model	Variables	r (train)	p (train)	r (test)	p (test)
Biroujima colony (negative binomial GLM)	D_COL + Year	0.46	0.48	0.12	0.15
Izu colony (negative binomial GLMM)	D_COL : Month + (1 | Survey)	0.30	0.23	0.25	0.36
Izu foraging (poisson GLMM)	D_LAND + CHLA + (1 | Survey)	0.25	0.22	-	-

Table 4. Japanese marine Important Bird and Biodiversity Areas (mIBAs) that include Japanese Murrelet colonies. Four radii are provided by density models: Model A, from Biroujima in 2009/2012; Model B, from Biroujima in 2008; Model C, from Northen Izu colonies in May and; Model D, from Northern Izu colonies in April. The extent of each radii (given in brackets under model name) is defined as the distance from the colony at which density is predicted to fall below 0.5 birds/km^2. For each colony and the area of sea the radii cover and % of this area captured within each mIBA are reported

Marine IBA site	No. of murrelet colonies	mIBA area (km^2)	Model A (9 km)		Model B (18 km)		Model C (27 km)		Model D (39 km)	
			Area (km^2)	% within mIBA	Area (km^2)	% within mIBA	Area (km^2)	% within mIBA	Area (km^2)	% within mIBA
Danjo Islands	1	14663	235	100	960	100	2175	100	4551	100
Fumishima Islet and Oki Islands	1	27323	197	100	853	100	1967	100	4417	90
Northern Izu Islands	8	4757	1443	100	4122	100	7093	67	11622	41
Torishima Island	1	1174	231	100	955	100	2150	55	4482	26
Tsukuejima Islets	1	254	208	100	779	33	1546	16	2745	9
Eboshijima Islet	1	306	246	100	964	32	1868	16	3498	9
Kanmurijima and Kutsujima Islets	1	310	249	93	939	33	1836	17	3304	9
Kii Nagashima Islets	1	184	161	90	510	36	1020	18	2005	9
Seinan Islands	2	284	251	78	898	32	1795	16	3530	8
Nanatsujima Islets	2	319	315	94	1149	28	2313	14	4223	8
Okinoshima Koyajima Islands	1	308	247	100	993	31	2230	14	4670	7
Biroujima Islet	1	154	188	82	646	24	1322	12	2541	6
Hachijojima	1	266	217	100	911	29	2131	12	4546	6

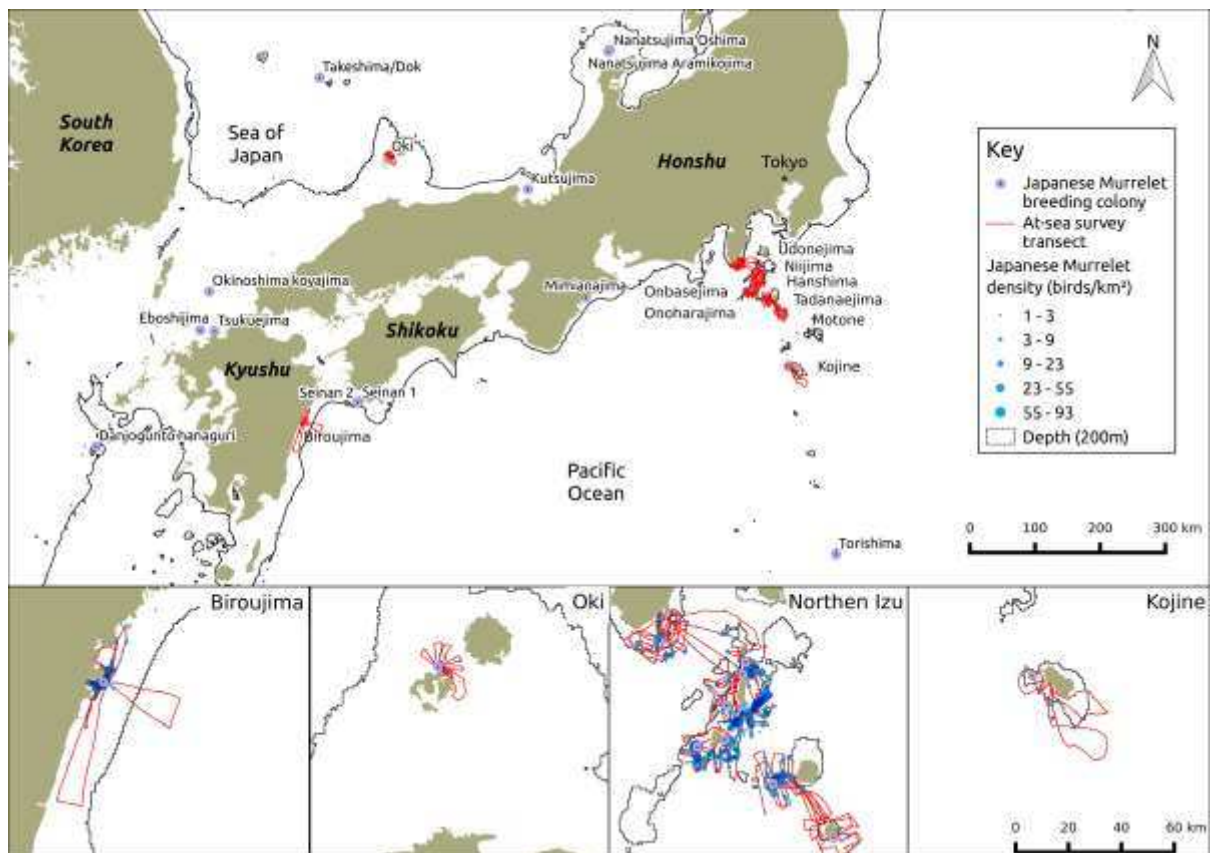|									
Island									
Total marine IBA network	22	50302	4188	95	14679	52	29446	35	56134	25

Figures

1

Figure 1. Japanese Murrelet breeding colony locations in Japan and at-sea survey data undertaken around colonies at Kojine, Northern Izu islands, Biroujima and Oki. Overlapping density counts appear darker blue. See Appendix S1 for colony details
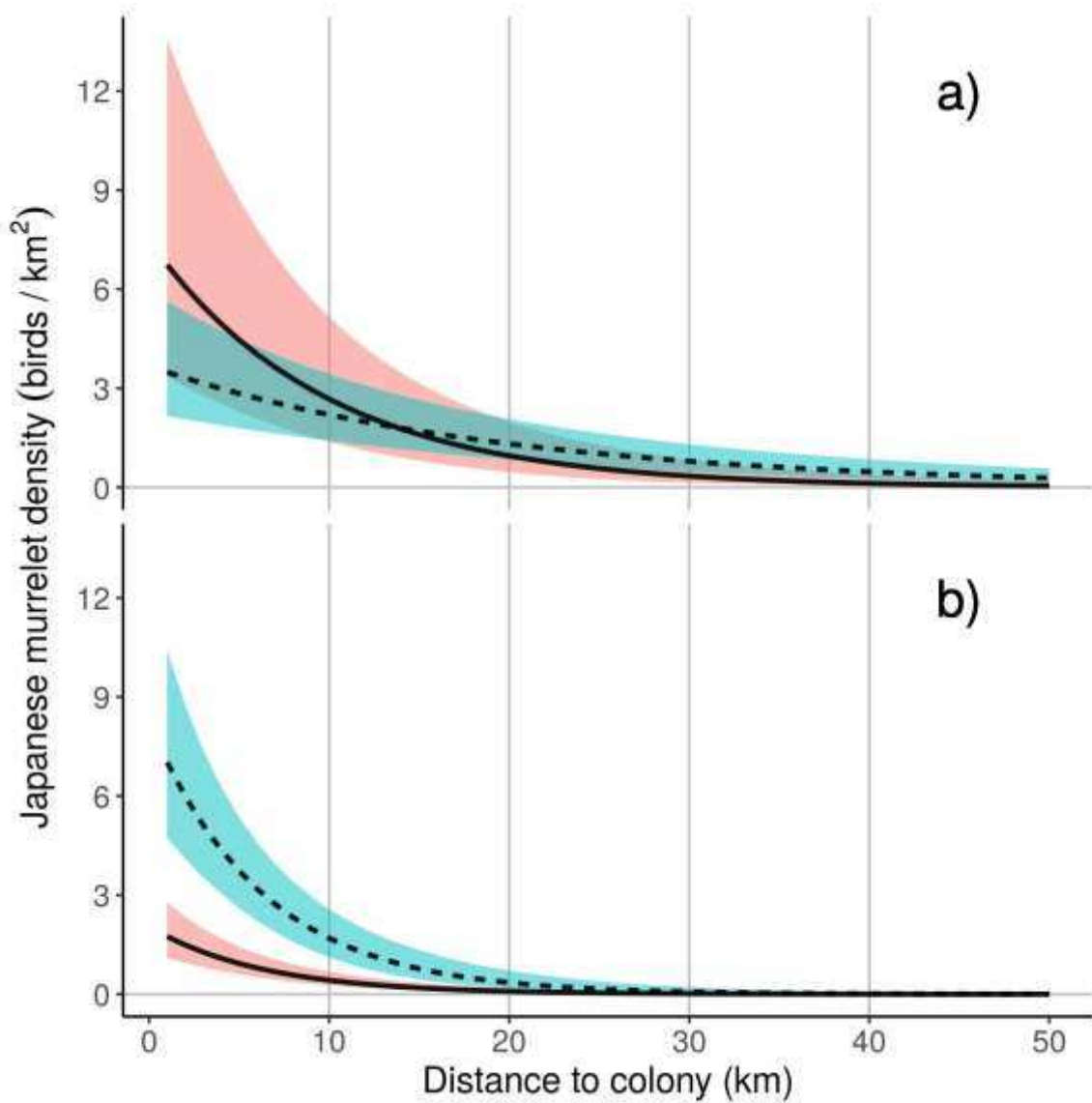
Figure 2. Predicted Japanese Murrelet density (line) and 95% confidence interval (shade) against colony

distance at a) the Northern Izu Islands in April (dotted line, blue shade) and May (solid line, pink shade);

and b) Biroujima in 2008 (dotted line, blue shade) and 2009/2012 (solid line, pink shade)
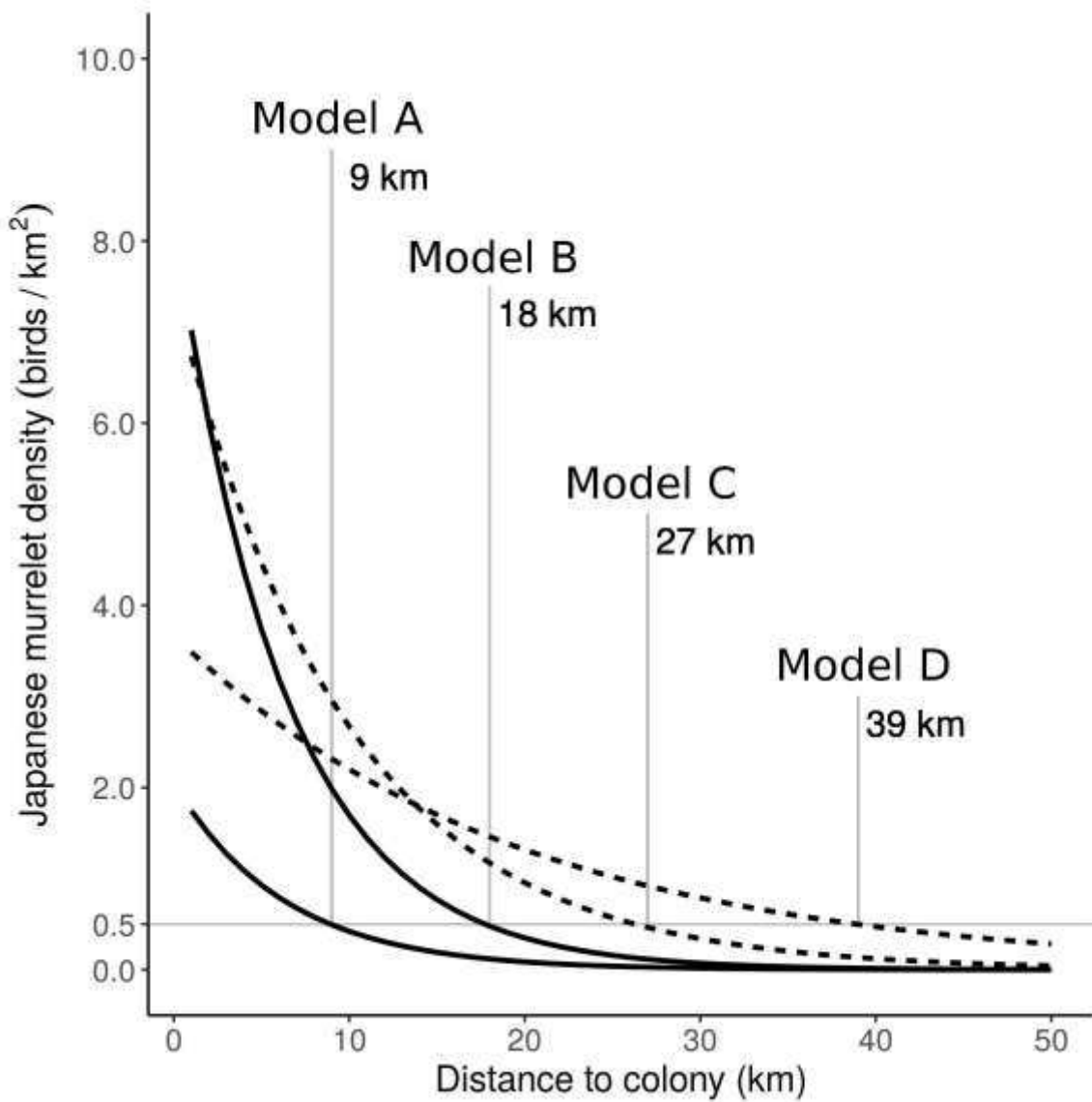
Figure 3. Predicted Japanese Murrelet density against colony distance from the Biroujima colony model (solid line), in 2009/2012 (Model A) and 2008 (Model B); and from the Izu colony model (dotted line), in May (Model C) and April (Model D). The colony distance is given at which density is predicted to fall below 0.5 birds/km^2 for each model prediction
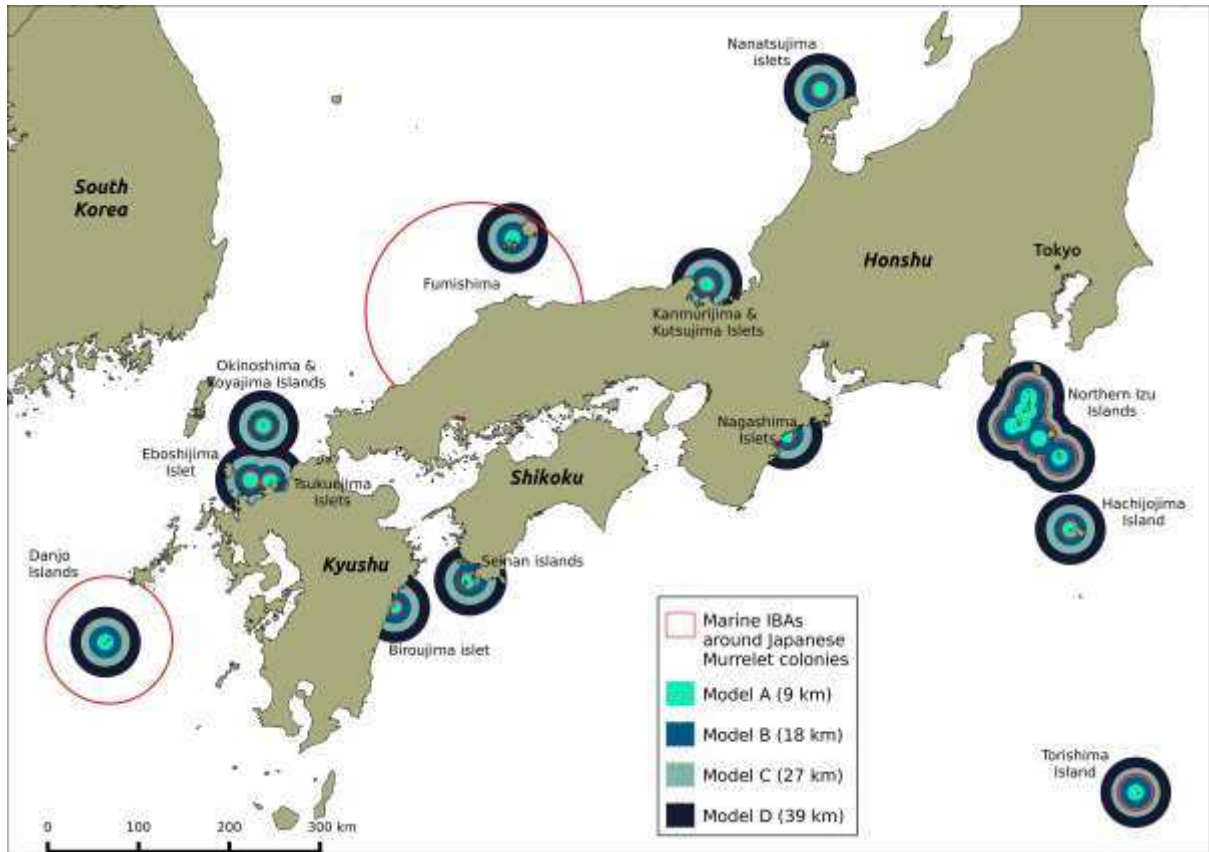
Figure 4. Four radii from model predictions applied to Japanese Murrelet colony locations, and overlap with current Japanese marine IBA network. Each radii is defined as the maximum distance around Japanese Murrelet colonies at which murrelet density is predicted to be above 0.5 birds/km^2. Radii are generated from predictions for: Biroujima in 2009/2012 (Model A); Biroujima in 2008 (Model B); Northen Izu colonies in May (Model C); and Northern Izu colonies in April (Model D)

Supplement

Table S1. Details of oceanographic variables used in modelling

Variable code	Variable	Type	Source	Layers created
SST	Sea Surface Temperature	Dynamic oceanographic	MODIS Aqua Terra; http://oceancolor.gsfc.nasa.gov/	5 (one per year: 2008-2012)
CHLA	Chlorophyll-a Concentration	Dynamic oceanographic	MODIS Aqua Terra; http://oceancolor.gsfc.nasa.gov/	14 (one per survey)
G_SST	SST gradient	Dynamic oceanographic - derived	MODIS Aqua Terra; http://oceancolor.gsfc.nasa.gov/	5 (one per year: 2008-2012)
G_CHLA	Chlorophyll-a gradient	Dynamic oceanographic – derived	MODIS Aqua Terra; http://oceancolor.gsfc.nasa.gov/	14 (one per survey)
Bathy	Bathymetry	Static	GEBCO; http://www.gebco.net/	1
Slope	Seabed slope angle	Static - derived	GEBCO; http://www.gebco.net/	1
D_Land	Distance to land	Static - derived	GEBCO; http://www.gebco.net/	1
D_Col	Distance to colony	Static - derived	Survey data	1

Table S2. Names and locations of all known Japanese Murrelet colonies within Japan, coordinates not disclosed for Seinan colonies for conservation purposes

Location (Island/Islet)	Latitude	Longitude	Region
Nanatsujima Oshima	37.61028791	136.9002056	Chubu
Nanatsujima Aramikojima	37.58873089	136.876688	Chubu
Kutsujima	35.70024392	135.4452896	Chubu
Udonejima	34.47189184	139.294281	Northern Izu
Niijima	34.43069985	139.2795181	Northern Izu
Hanshima	34.32571722	139.2772865	Northern Izu
Tadanaejima	34.20768528	139.1914558	Northern Izu
Onbasejima	34.18695586	139.0754986	Northern Izu
Onoharajima (Sanbondake)	34.048056	139.383889	Northern Izu
Motone	33.851028	139.62001	Northern Izu
Kojine	33.12993056	139.6986361	Central Izu
Torishima	30.48344429	140.2885437	Southern Izu
Mimianajima	34.18393831	136.3799429	Kansai
Okinoshima koyajima	34.23146103	130.1111698	Kyushu
Eboshijima	33.68963859	129.9828529	Kyushu
Biroujima	32.46472948	131.7308807	Kyushu
Danjogunto hanaguri	32.01127832	128.3615112	Kyushu
Tsukuejima	33.68333333	130.2166667	Kyushu
Oki	36.154	133.073	Oki
Seinan 1	-	-	Shikoku
Seinan 2	-	-	Chuugoku
Takeshima /Dok	37.239167	131.868611	Japan/South Korea (disputed)

Figure S3. Bimodal distribution of Japanese Murrelet density (birds/km^2) in relation to distance from colony (D_COL, km) around Northern Izu colonies. A clear break in murrelet observations is observed at 20km distance from colonies in both March (pink) and May (blue)

1
2