PICES SCIENTIFIC REPORT
No. 50, 2016

NORTH PACIFIC MARINE SCIENCE ORGANIZATION

PICES

Spatial Ecology of Marine Top Predators
in the North Pacific:
Tools for Integrating across Datasets and
Identifying High Use Areas

PICES SCIENTIFIC REPORTS

This document should be cited as follows:

Watanuki, Y., Suryan, R.M., Sasaki, H., Yamamoto, T., Hazen, E.L., Renner, M., Santora, J.A., O'Hara, P.D. and Sydeman, W.J. (Eds.) 2016. Spatial Ecology of Marine Top Predators in the North Pacific: Tools for Integrating across Datasets and Identifying High Use Areas. PICES Sci. Rep. No. 50, 55 pp.

Spatial Ecology of Marine Top Predators in the North Pacific:
Tools for Integrating across Datasets and Identifying High Use Areas

Edited by
Yutaka Watanuki, Robert M. Suryan, Hiroko Sasaki, Takashi Yamamoto, Elliott L. Hazen,
Martin Renner, Jarrod A. Santora, Patrick D. O'Hara and William J. Sydeman

PICES

Table of Contents

Acknowledgements

Summary

There are many applications and uses of spatial distributional data on marine birds and mammals in the North Pacific, including the design of pelagic marine protected areas, assessments of ecosystem health, modeling top-down effects of marine predators on food web dynamics, and projected future distributions of rare or threatened populations and species under climate change. Distributional data come in many different flavors, including ship-based observations of density and remotely-sensed tracking and movement data. These data provide complementary perspectives on species distributions but should not be combined for a variety of reasons including different spatial and temporal scales and resolution. There are many high quality datasets on marine birds and mammals in the North Pacific available for analyses, including the North Pacific Pelagic Seabird Database and the Seabird Tracking Database. More information is becoming available all the time.

Because ship-based and tracking observations are not spatially and temporally comprehensive, species–habitat models (*i.e*., coupling of apparent spatial distributions with biophysical factors that predict species distributions) are necessary. There are many different and highly technical approaches to habitat modeling or species distribution modeling; composite model output may provide optimal information, but this depends on the goals of study.

1   Introduction

Marine birds and mammals (MBMs) are important marine top predators that consume substantial amounts of zooplankton and micronekton in the North Pacific (Hunt *et al*., 2000). These taxa are of considerable conservation and management interest, yet are vulnerable to changes in marine food web structure and function as well as a variety of anthropogenic impacts, from contaminants to competition from fisheries. Marine birds and mammals are resilient, in part because they are highly mobile. Importantly, this feature of their life history can be relatively easily observed and tracked to determine their spatial distribution and abundance. Owing to their conspicuousness, MBMs can be spontaneous sentinels of ecosystem change, a feature that makes them of critical importance to monitoring and assessing the "health" of the North Pacific.

MBMs are not distributed evenly across the seascape but tend to aggregate at various temporal and spatial scales due to physical forces, biochemical factors, prey distribution, and behavioral and social factors. The coupling (*i.e*., spatio-temporal associations) of their distributions at sea with biological and physical factors (hereafter referred to as biophysical factors) is a subject of great interest and importance (Coyle *et al*., 1992; Hunt *et al*., 1993, and many others). Habitat models are a specific form of spatial ecological modeling that couples observed locations of organisms with biophysical factors that co-occur in space and time. These models have been variously referred to as bioclimatic models, climate envelopes, ecological niche models (ENMs), species distribution models (SDMs), and resource selection functions (RSFs) (Elith and Leathwick, 2009).

MBMs are relatively large and conspicuous marine organisms, making data collection on their distribution and movement relatively easy to accomplish, and providing useful information for marine spatial planning and management (Hyrenback *et al*., 2000; Louzao *et al*., 2006; Worm *et al*., 2003; Hooker, 2008). Additionally, the identification of *biological hot spots* (*i.e*., regions where abundance and/or biodiversity are relatively high) based on distribution and movement patterns, and elucidating the underlying biophysical mechanisms that drive these hot spots, is critical for fisheries management and the conservation of MBMs.

Over the past several decades, a wide variety of research programs have collected ship-based observational and individual-based tracking data of MBMs throughout the North Pacific. Observational survey data are essentially bird counts, controlling for area covered, and these data are collected from ships or aircraft. Tracking involves monitoring the movement birds using devices or "tags" attached to individual birds which are deployed then recovered (data stored internally, using GPS or position of the sun), or they are devices that send out signals which can be used to derive position (radio telemetry), or signals that are picked up by satellite systems. Tracking data is typically composed of locations at specific times. Portions of these data have been compiled into large databases. The U.S. Geological

Survey's North Pacific Pelagic Seabird Database[1] contains over 350,000 ship-based survey transects and observations of 17 million birds and a quarter of a million marine mammals spanning 40 years (Fig. 1.1). The Birdlife International global Seabird Tracking Database[2] contains, for the North Pacific alone, 250,000 locations from 11 species spanning 15 years (Fig. 1.2). Many more survey and tracking datasets exist, however, and need to be integrated for more complete coverage of all PICES regions. Although comprehensive, these databases are not complete as there remains a large number datasets in the PICES region that have yet not been integrated into these two databases, and therefore, these data are largely unavailable to PICES marine scientists.
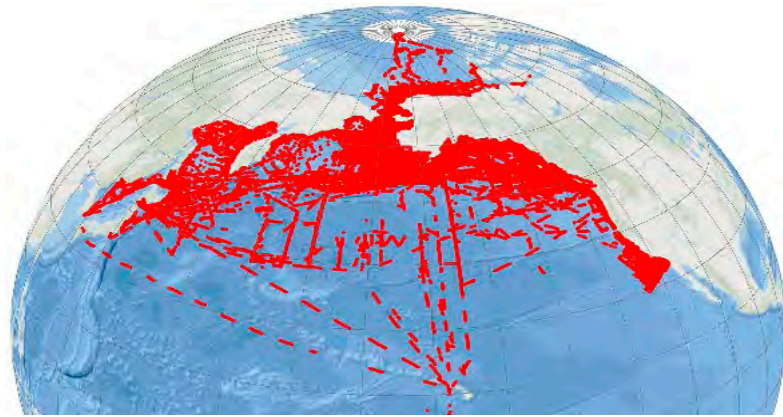
Fig. 1.1   The U.S. Geological Survey's North Pacific Pelagic Seabird Database contains over 350,000 vessel-based survey transects for birds and mammals spanning 40 years.
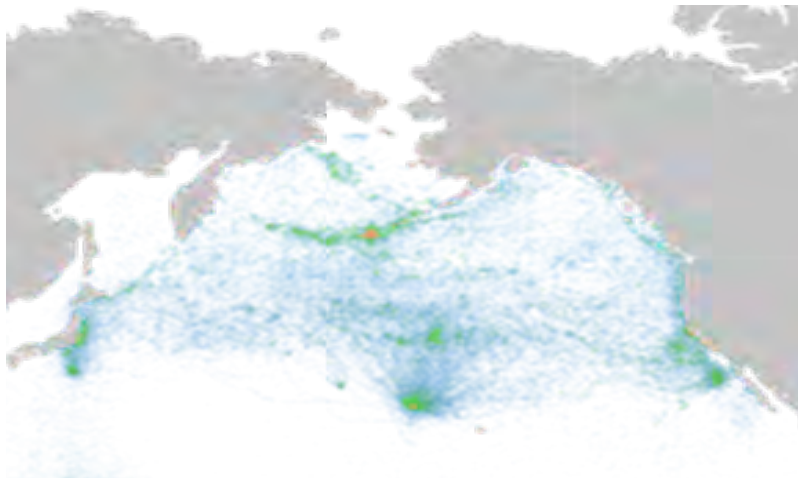
Fig. 1.2   The Birdlife International's Seabird Tracking Database contains 250,000 locations from 11 species of individually tracked seabirds spanning 15 years.

[1] http://alaska.usgs.gov/science/biology/nppsd/index.php

[2] http://www.seabirdtracking.org/

Over the last decade, the Advisory Panel on *Marine Birds and Mammals* (AP-MBM) has organized sessions and workshops on spatial ecology of marine birds and mammals. At the 2004 PICES Annual Meeting (Honolulu, USA), AP-MBM convened a Topic Session on "*Hot spots and their use by migratory species and top predators in the North Pacific*". Selected papers from the session were subsequently published in *Deep-Sea Research II* (Sydeman *et al.*, 2006). AP-MBM also convened a Topic Session on "*Mechanisms of physical-biological coupling forcing biological hotspots*" at PICES-2011 (Khabarovsk, Russia), and selected papers from the session were published in *Marine Ecology Progress Series* (Hazen *et al.*, 2013b).

To further incorporate MBMs into the objectives of PICES' integrative science program, FUTURE (**F**orecasting and **U**nderstanding **T**rends, **U**ncertainty and **R**esponses of North Pacific Marine **E**cosystems)[3], AP-MBM proposed to concentrate efforts on MBM spatial ecology and conservation as a priority topic for 2012–2014 activities; three goals or primary objectives were proposed. These goals can also be linked to other components of PICES (Fig. 1.3). The primary objectives are to: 1) synthesize distribution data on MBMs and their temporal change in the North Pacific based on ship-based surveys and remote tracking, 2) examine the biophysical factors associated with the distribution and abundance of MBMs and their ecological/economic (fisheries) hot spots, and 3) provide information on important ecological areas throughout the North Pacific to increase understanding of MBM spatial ecology and to provide information on the sustainable use of marine resources within the organization. Recent AP-MBM activities were focused mainly on the first and second objectives. There are extensive datasets for marine bird and mammal distribution in the North Pacific, especially from recent decades, with increased ship-based bird and mammal surveys and the proliferation of individual-based electronic tracking studies. These two methodologies, however, provide different aspects of animal distribution and while complementary, are not easily integrated.
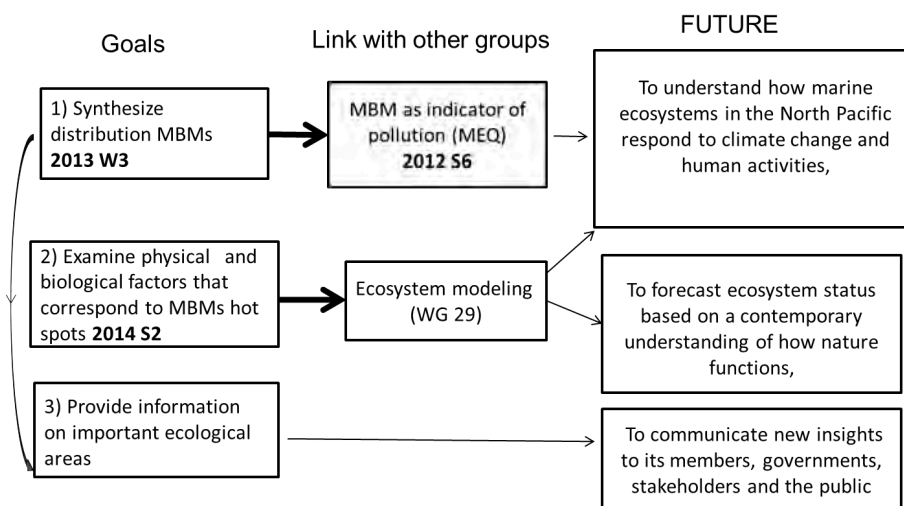
Fig. 1.3   Goals of AP-MBM's Spatial Ecology project (2012–2014), with links to FUTURE and other groups.

---

[3] (1) understand how marine ecosystems in the North Pacific respond to climate change and human activities, (2) forecast ecosystem status based on a contemporary understanding of how nature functions, and (3) communicate new insights to its members, governments, stakeholders and the public.

Here, we review methodologies and identify the most promising approaches for integrating ship- and individual-based species distribution data. We also discuss how habitat modeling can be a powerful tool to facilitate the integration of datasets and to examine the factors affecting the distribution of MBMs. Although AP-MBM did not fully accomplish objective 3, the results provide a foundation by which these objectives can be addressed in the future. To achieve the three objectives described above, AP-MBM organized and convened a series of topic sessions and a workshop on spatial ecology of marine birds and mammals between 2012 and 2014 (see Appendix). At PICES-2012 (Hiroshima, Japan), AP-MBM organized and convened a BIO/MEQ Topic Session (S6) entitled "*Environmental contaminants in marine ecosystems: Seabirds and marine mammals as sentinels of ecosystem health*". In this session AP-MBM tried to identify spatial patterns and geographic areas of concern for pollutants or other stressors using bio-indicator species, and explored mechanisms of transport and fate of contaminants in marine ecosystems. The AP also discussed health risks for certain predators and human consumers. At PICES-2013 (Nanaimo, Canada), AP-MBM held a BIO Workshop (W3) on "*Marine bird and mammal spatial ecology*" in which 29 participants representing data holders, analysts and data users attended. Topics discussed were: 1) existing datasets and gaps, 2) applications, and 3) data integration. A primary goal of the workshop was to assess techniques to compile and integrate ship-based marine bird and mammal surveys with individual tracking datasets and to determine how best to model species distribution and habitat use. Furthermore, AP-MBM convened a BIO Topic Session (S2), entitled "*Strengths and limitations of habitat modeling: Techniques, data sources, and predictive capabilities*" at PICES-2014 (Yeosu, Korea). A wide variety of taxa were represented in the presentations, including deep-sea sponges and corals, zooplankton, krill, squids, seabirds and marine mammals. A primary objective of the session was to examine factors causing biases, identify the direction of biases, discuss techniques for mitigating or accounting for biases, and create a best practices guide for using habitat modeling approaches to predict the distribution of marine organisms in dynamic marine environments.

In Section 2, the outcomes of the workshop held at PICES-2013 are summarized, and we discuss challenges and limitations that are particular for ship-based survey and tracking data using two case studies as illustration. In Section 3, we introduce habitat modeling and discuss the strengths and weaknesses of this approach, and review the types of data that most marine habitat models are based on.

2   Integrating Tracking and Ship-based Survey Data

2.1   Introduction

Individual tracking and ship-based surveys provide valuable insight into the distribution of free-ranging MBMs. These two data types provide different but complementary perspectives on questions regarding spatial ecology (Camphuysen *et al*., 2012). The benefit of using individual tracking data most relevant to spatial ecology is that they are unrestricted by study area boundary, season, time of day, or weather conditions. With individual tracking one can also determine how movements vary with age and sex of the individuals being tracked (Table 2.1). The benefits of ship-based surveys, on the other hand, include collecting data with larger sample sizes, on multiple species from a single sampling platform (enabling community analyses based on these data), data on individuals of all life stages, including non-breeding birds, and simultaneous *in situ* sampling of biophysical variables (often concurrent with MBM observations), permitting fine-scale habitat analyses (Table 2.1).

Table 2.1   Comparison of individual tracking *vs*. ship-based surveys for determining the distribution of birds and mammals at sea.

Variable	Individual tracking	Ship-based survey
Species included	Restricted	Unrestricted, communities
Sample size of individuals	Often low	Generally high
Colony, sex, or bird identification	Known, but possibly biased selection	Unknown, unbiased selection
Age and stage (non-breeders, breeders, pre-breeders, failed breeders, juveniles, *etc*.)	Often limited to age or stage	All ages and stages
Sampling range and period	Unrestricted by study area boundary, season, or time of day	Restricted to where and when vessel travels, and daylight
Sampling conditions	Unlimited	Limited
Presence *vs*. absence	Presence only	Presence and absence
Distance from colony	Known	Unknown
Habitat sampling	Remote, low resolution, few bio-physical variables measured	*In situ*, high resolution, simultaneous, many bio-physical variables measured

There are many opportunities for tracking and ship-based survey data to be integrated. However, to date there are few published examples, and most have focused on seabirds. The combination of tracking and ship-based survey data can initially provide a more robust estimate of at-sea distributions of single species (Priddel *et al*., 2014; Perrow *et al*., 2015) or communities (Ballard *et al*., 2012). Likewise, tracking studies combined with fisheries bycatch data allow for a similar combination of tracking and *in situ* observational data (Hyrenbach and Dotson 2003; Zydelis *et al*., 2011). In some cases, tracking data and ship-based survey data have been used in synergy to identify marine hot spots (Hyrenbach *et al*., 2006; Hughes *et al*., 2015; Bennison and Jessopp, 2015; Yamamoto *et al*., 2015) or to test the accuracy of distribution models based on the other types of data such as projecting foraging range from the colonies (Grecian *et al*., 2012).

Given these complementary strengths, it is clear how advantageous it would be to integrate the two data types to provide a more holistic view of animal distribution. There are, however, important limitations within each data type that complicate efforts to combine these inherently different data categories.

2.2   *Biases*

Being fundamentally different, tracking data and ship-based survey data types also require different assumptions, face different constraints, and present different analytical challenges (Camphuysen *et al*., 2012). Models can be biased differently depending on whether they are based on ship-based observational survey or tracking of individual animals. With some exceptions (*e.g*., Block *et al*., 2011), individual tracking data are often limited to relatively small sample sizes of individuals. However, these few individuals can produce tens to hundreds of thousands of locations each. Additionally these individuals are generally not randomly selected for tagging, and neither is the distribution of the start of tracks and subsequent locations. A colony effect where at-sea densities of individuals are exaggerated due to transit to or from an onshore attraction (*e.g*., seabird colonies, pinniped rookeries or haul-outs) is not only a common bias with tracking data, but can also impact ship-based survey data. Likewise, non-representative sampling of a population or a region is an important concern for both data types. Fortunately, plausible analytical methods exist to accommodate some of these biases (*e.g*., Renner *et al*., 2013; Whitehead and Jonsen, 2013). Ultimately, these potential biases need to be identified and addressed in the respective models before attempts can be made to quantitatively combine distribution surfaces produced by models based on survey and tracking data.

2.3   *Case studies*

The effect of different tagging locations *vs*. ship-based surveys

In the California Current System (CCS) off North America, multiple studies have been conducted using different approaches to determine the distribution and abundance of black-footed albatrosses (*Phoebastria albatrus*). During an initial satellite tracking study, birds were tagged at their breeding colony on Tern Island in the northwestern Hawaiian Islands (outside the U.S. exclusive economic zone; EEZ) and 12 birds were tracked. They entered and moved throughout the central and northern CCS (Fernández *et al*., 2001; Hyrenbach *et al*., 2006; Kappes *et al*., 2010). In a second satellite tracking study, 36 albatrosses were captured and tagged at Cordell Bank in the central CCS (inside the EEZ) and were tracked throughout the CCS (Guy *et al*., 2013, Hyrenbach and Hester, unpubl. data; Fig 2.1). Comparison of

these two tracking studies show different patterns of albatross distribution with the bias of tagging location evident for birds tagged within the CCS (*cf*., Fig. 2.1A and 2.1B). Most albatrosses tagged in the central CCS (the second study) remained within it for a while and then left; the remaining few moved north through the CCS. In contrast, albatrosses that were tagged outside of the CCS (the first study) entered it at different locations but primarily used continental shelf break habitat in the central and northern CCS (Fig. 2.1B). Overall, the distribution of birds tagged outside of the CCS (Fig. 2.1B) showed more similarity to the distribution determined by ship-based surveys (Fig. 2.1C). This example highlights differential habitat use based on tagging locations that need to be accounted for either through sampling design with deployment strategies or quantitatively in the analyses (Whitehead and Jonsen, 2013).
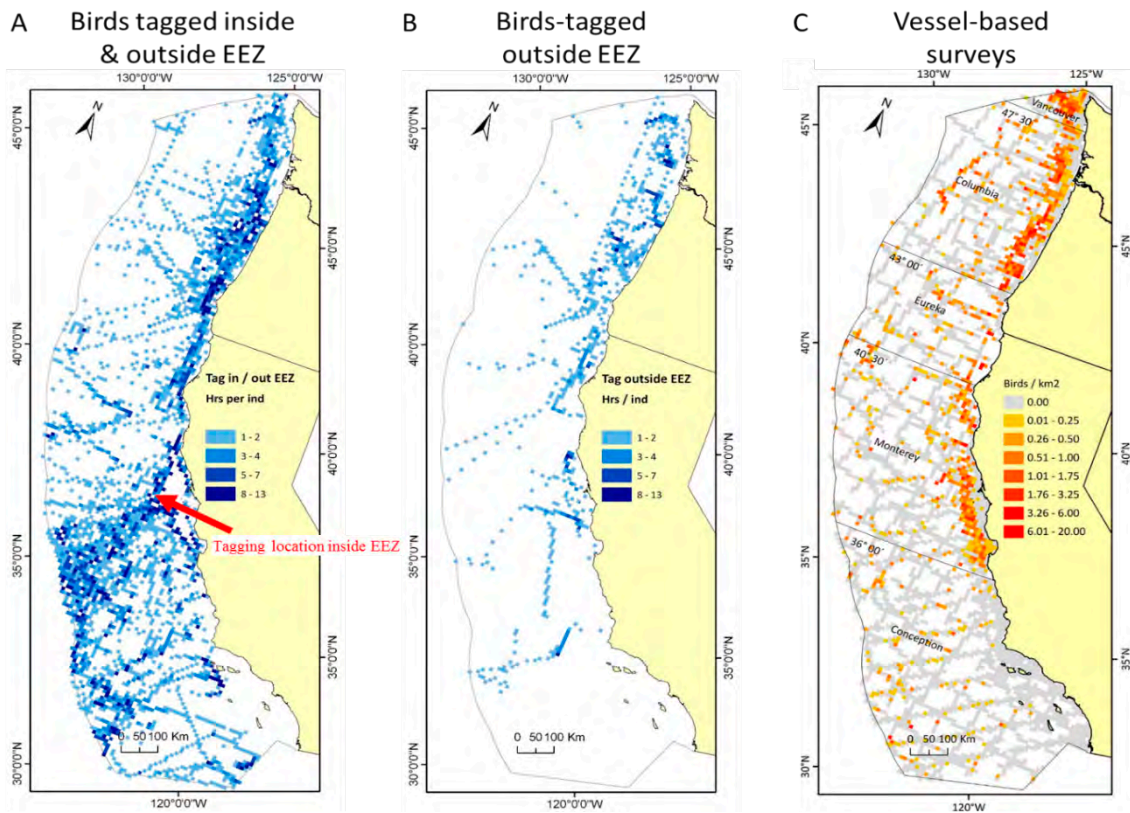
Fig. 2.1   Distribution data from satellite tracking of individuals and ship-based surveys for black-footed albatrosses in the California Current System (CCS: grey line indicates the exclusive economic zone, EEZ, 200 nm limit off the U.S. west coast). (A) Distribution from satellite tracking of individual albatrosses tagged both inside and outside outside of the CCS, compared to (B) albatrosses tagged only outside the CCS, and (C) albatrosses sighted from ship-based surveys. Data from Guy *et al*. (2013).

Spatial extent of tracking *vs*. ship-based surveys

Eighty-seven sooty shearwaters (*Puffinus griseus*) were tracked over 6 years (Adams *et al*., 2012) and compared to sooty shearwaters observed during 22 years of ship-based surveys in the central CCS (Santora *et al*., 2011). Density distribution surfaces were created using a Brownian bridge movement

model (weighted by the number of uplinks per cell and bird) to show a spatial intensity of satellite-tracked individuals (Fig. 2.2A) and a kernel density from ship-based surveys (Fig. 2.2B). Where the spatial extent of the two approaches overlapped, there was reasonable agreement in core areas of high use. Discrepancies between the two data types resulted from non-contiguous sampling of the ship transects (*i.e*., gaps between survey lines). Tagged birds showed higher concentrations nearshore where larger survey vessels were unable to survey because of shallow water depth. Additionally, there was a much larger overall spatial extent from unrestricted movements of individually tracked birds compared to fixed vessel transects.
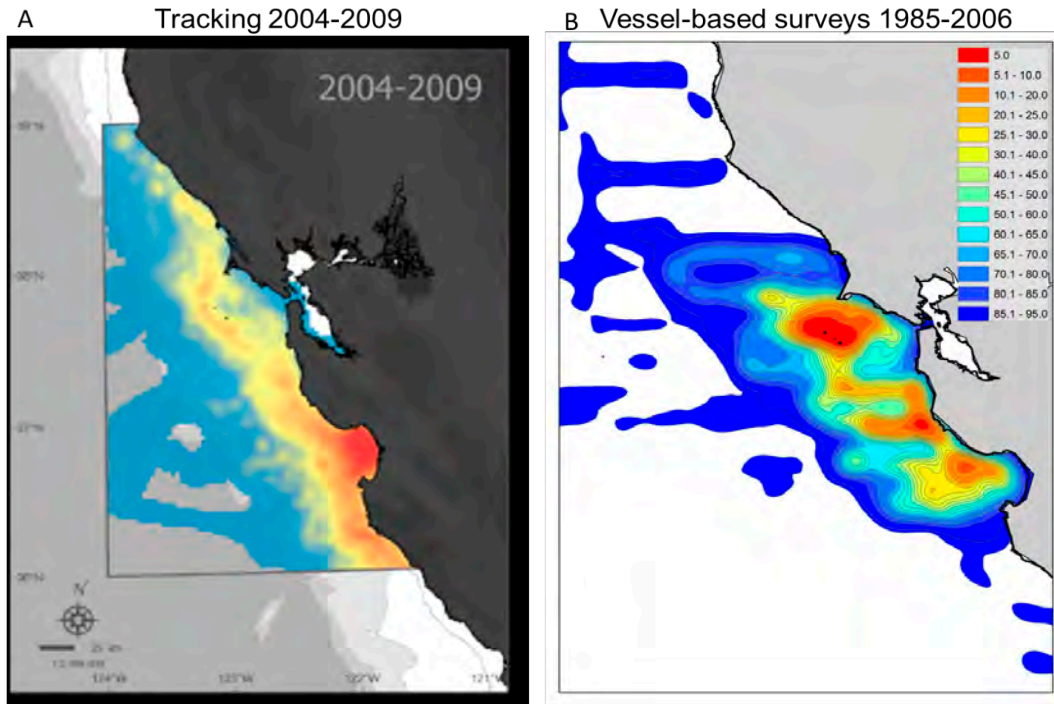
Fig. 2.2 Density distribution surfaces of sooty shearwaters from (A) tracking and (B) vessel-based surveys in the central California Current System. (A) "Spatial intensity" from a Brownian bridge movement model (weighted by the number of uplinks per cell and bird) from 6 years of satellite tracking data from 87 individuals. (B) Kernel density distribution from 22 years of vessel-based surveys. Both datasets were collected primarily during spring and summer of each year. Data from J. Santora, J. Adams, B. Henry and W. Sydeman.

Similarly in the Bering Sea, tracking data from black-legged kittiwakes (*Rissa tridactyla*; 73 individuals, over 200,000 locations) during the breeding season on the Pribilof Islands (Paredes *et al*., 2014) can be compared to 30 years of ship-based surveys around this colony (over 100,000 records; North Pacific Pelagic Seabird Database). Comparison of these datasets highlights typical biases in both approaches. The tracking data are biased by 1) location of the colony where birds are tagged since breeding birds are conducting foraging trips to and from the colony (Fig 2.3A) and by 2) breeding stages of birds since chick-rearing birds should make more trips than incubating and non-breeding birds. Ship-based surveys, on the other hand, include all age classes and breeding and non-breeding individuals and thus provide a more uniform sampling of the entire region (Fig 2.3B). A fundamental shortcoming of fixed transect surveys, however, is also highlighted in this comparison because in some years breeding birds are found

to extend their foraging range well beyond the continental shelf break, where very few ship transects occur, and especially at night (Paredes *et al.*, 2012),. For a more standardized comparison between data types, kernel densities of tracking data can be scaled to breeding colony size and compared to surface distributions from ship-based surveys (Fig. 2.3C, D). Surface distributions from both data types show high use areas near the colonies and the continental shelf break to the south, but also show differences in higher use of off-shelf for tracking (Fig. 2.3C) and inner shelf for ship-based surveys (Fig. 2.3D); highlighting how well the two data types complement each other.
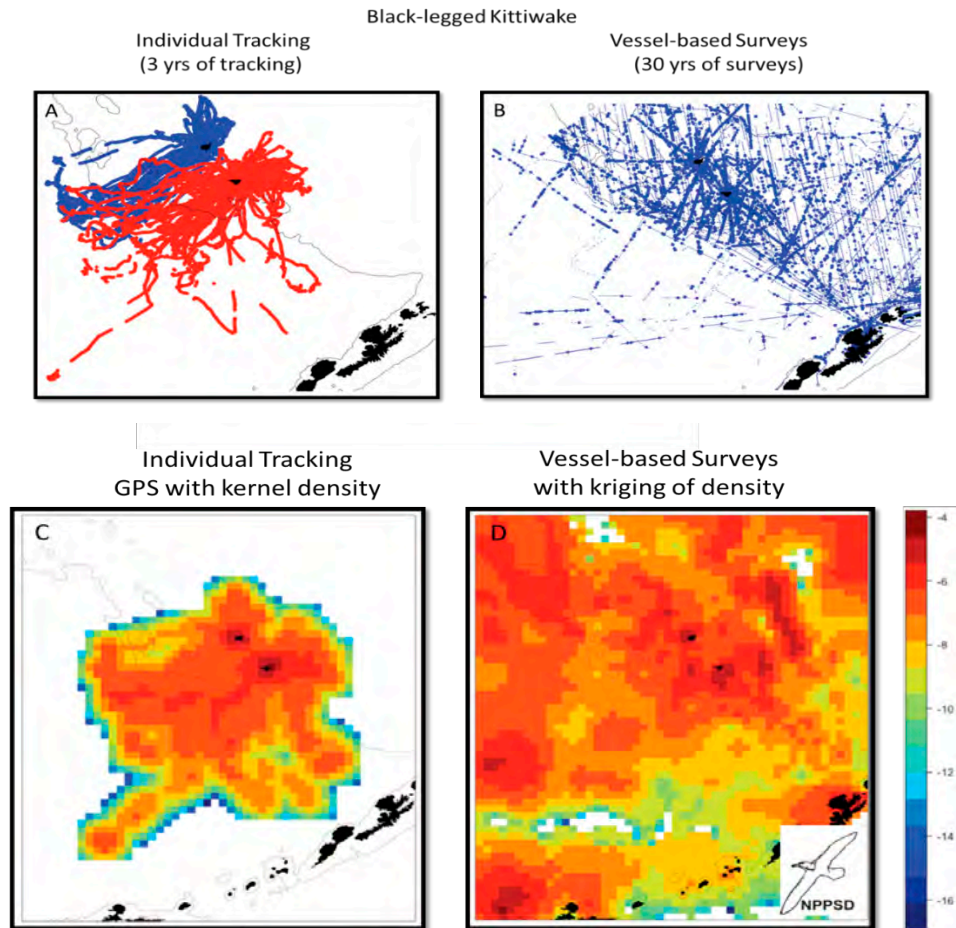
Fig. 2.3   Distribution of black-legged kittiwakes around the Pribilof Islands (St. Paul and St. George) in the southeastern Bering Sea from individual tracking and vessel-based surveys. (A) Individual tracking data from 73 kittiwakes and 200,342 GPS locations during three breeding seasons on the Pribilof Islands. (B) Distribution of kittiwakes from 30 years of vessel-based surveys around the Pribilof Islands. (C) Kernel density distribution of kittiwakes from tracking data, scaled by breeding population size at each colony. (D) Surface density of kittiwakes from vessel-based surveys created *via* kriging. Data from M. Renner, G. Drew, K. Kuletz. G. Hunt, R. Paredes and J. Piatt.

Significant environmental factors derived from tracking *vs*. ship-based surveys

Short-tailed shearwaters (*Puffinus tenuirostris*) were tracked using geolocators in the Bering, Chukchi, and Beaufort seas (19–27 birds per year for 2 years; Fig. 2.4A, B, E, F). In the subsequent two years, ship-based surveys were conducted through this same region in July and September (Fig. 2.4C, G) where 16,000–18,000 short-tailed shearwaters were observed each year. To find important environmental factors explaining the density of short-tailed shearwaters, Generalized Linear Models (GLM) were created using remotely-sensed explanatory environmental variables of sea floor depth, bottom slope, sea surface temperature (SST) and chlorophyll *a* (Chl-*a*). Environmental factors associated with the bird density, based on tracking data and ship-based surveys, were then compared qualitatively (statistical significance level and the sign of the parameter estimates) within and between seasons (July or September).

A TRACKS 2010 (Kernel density)

B TRACKS 2011 (kernel density)

C VESSEL 2013 (Oshoro) (density)

D

Method	Period	Depth	Slope	SST	CHLa
TRACK	2010JUL	-*		-*	+*
TRACK	2011JUL	-*		-*	
BOAT	2013JUL	+*	+*		

E TRACKS 2010 (Kernel density)

F TRACKS 2011 (Kernel density)

G VESSEL 2012 (Mirai) (density)

H

Method	Period	Depth	Slope	SST	CHLa
TRACK	2010SEP		-*	-*	+*
TRACK	2011SEP	+*	-*	-*	-*
BOAT	2012SEP		-*	+	+*
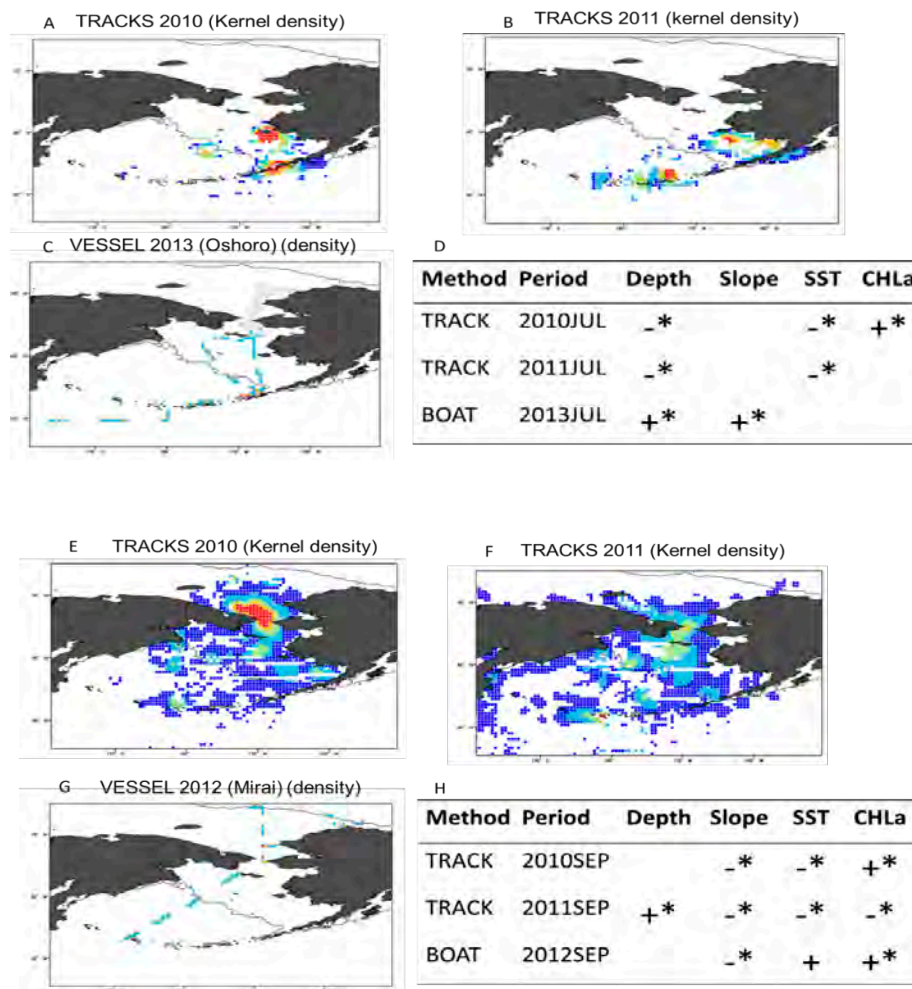
Fig. 2.4 Kernel density surfaces (50 × 50 km) and habitat modeling (GLM) results of short-tailed shearwater distribution from individual tracking (geolocation) and ship-based surveys in the Bering Sea during July (A–C) and September (E–F), 2010–2013. Sign of the parameter estimate and its significance level (*: < 0.05) are shown. Habitat model output for July (D) and September (H) show more similarities between data collection methods than between time periods. Data from Y. Watanuki, B. Nishizawa, Y. Yamamoto, E. Labunski, K. Kuletz, C. Meathrel and R.A. Phillips.

Despite some differences in the significance of explanatory variables between tracking and ship-based models (for example, positive relationship between density and depth based on ship-based survey data collected but negative relationship based on tracking data collected, in July), relationships between densities and explanatory variables generally showed more similarity between types of data within seasons rather than between seasons (for example, positive relationship between density and bottom slope in July, and negative in September; Fig. 2.4D, H).

Therefore, this basic modeling comparison of a relatively small dataset shows promise in a likely preferred direction for integration of initially creating habitat use models independently, then combining models to produce a unified distribution surface.

2.4   *Data integration*

Many studies have used both ship-based and individual tracking data where species and spatial coverage overlap, and although data are typically modeled independently, there have been various levels of integration of model output (Table 2.2). Tools such as OBIS–SEAMAP provide a dynamic way to visualize multiple datasets and thus provide the initial steps towards integrating modeling efforts (Fujioka *et al*., 2014) or a combined tracking and survey model.

Table 2.2   Examples of studies using both individual tracking and ship-based survey data to model species distribution. Two of the studies, Louzao *et al*. (2009) and Thiers *et al*. (2014), produced separate "side-by-side" models for tracking and survey, not integrated surfaces. The two other studies combined outputs to produce a distribution showing where kernel densities from tracking differed from modeled distribution from surveys (Benoit-Bird *et al*., 2013).

| Study | Spatial resolution | Input model | | Output |
		Tracking	Survey	
Louzao *et al*., 2009	5 × 5 nm	Binomial response: cells containing at least 1 feeding event (GLMMs)	Binary presence/ absence variable (GLMs)	2 side-by-side models
Thiers *et al*., 2014	0.25°	Logistic regressions (GLMMs)	Logistic regressions (GLMMs)	2 side-by-side models
Benoit-Bird *et al*., 2013a, b	100 m	Kernel density	Multiple Linear Regression (GLM) – predicted distribution	Difference surface: Predicted density from survey – kernel density
Yamamoto *et al*., 2015	9 × 9 km	At-sea density of groups weighted by colony location (GAMs)	Abundance (GAMs)	Combined model which incorporates ecological states (groups) (GAM response curves)

GLMM = Generalized Linear Mixed Model; GAM = Generalized Additive Model

In some cases, investigators have taken the approach of building distinct models based on the two datasets and then interpreting the resulting model outputs separately (Hyrenbach *et al*., 2006; Louzao *et al*., 2009; Thiers *et al*., 2014). For instance, Louzao *et al*. (2009) used ship-based survey data to identify large-scale habitat and then tracking data to identify small-scale feeding habitat of Cory's shearwater (*Calonectris diomedea*). Both datasets were modeled separately, and a comparison of the model results showed differences in the scale of habitat use and highlighted different spatial areas. Similarly, Thiers *et al*. (2014) built separate predictive spatial models based on tracking and ship-based survey of frigatebird distributions using Generalized Linear Mixed Models (GLMMs) and suggested that the differences in the resulting distributions reflect breeders and non-breeders. These studies, however, produced separate "side-by-side" predictive models and did not quantitatively integrate individual tracking and ship-based survey model outputs to produce a single density surface (Table 2.2).

Benoit-Bird *et al*. (2013a) provide examples where density surfaces based on tracking and survey data were merged. In their study, ship-based survey data for fur seals (*Callorhinus ursinus*), thick-billed murres (*Uria lomvia*), and black-legged kittiwakes were modeled using multiple linear regression models with the distribution and density of prey measured with acoustics and hydrographic data collected concurrently to create predicted density surfaces for each species. Density surfaces based on individual global positioning system (GPS) tracking data were created using Kernel Density Estimators for each species. Then the density surfaces based on tracking data were subtracted from the predicted density surfaces created by the ship-based survey data regression models to produce a single "difference" layer showing where densities of tracked birds were different from those predicted from the ship-based model. This comparison also highlights the strong colony/rookery effect of breeding birds and fur seals from colony/rookery-based tracking studies. Another approach to quantitatively integrating the two data types is to use detailed information from one data source to inform the other. For example, Yamamoto *et al.* (2015) used tracking data to model the relative density of groups (*e.g*., sex, colony, and breeders *vs*. non-breeders) in the form of Generalized Additive Model (GAM) response curves to weight habitat models from ship-based surveys where group identity was cryptic. This technique is described in detail in Section 3.

2.5   Conclusions

Animal distribution determined by ship-based surveys and individual tracking provide different analytical challenges, but ultimately can be highly complementary. At this point, there is limited possibility for integrating ship-based survey and tracking data prior to modeling efforts because of inherent constraints and biases that vary between the two types of data collection. Combining output density surfaces is promising. However, creating a combined density surface requires more complex data-specific treatments prior to integration. After data-specific treatments are applied, there are considerably more options for quantitative integration of the two data types. For example, information on area use by tracked individuals of different age, sex, or breeding status can be used to inform age- or stage-specific predictive surfaces from ship-based surveys. To produce a combined density distribution surface, habitat use models should be first created independently for individual tracking and ship-based surveys, then combined through ensemble or other model averaging approaches to create a single predicted distribution layer from the two datasets. With the continued use of ships of opportunity for conducting at-sea bird and mammal surveys along with miniaturization and economical production of tracking devices, spatial data for these organisms are accumulating at a rapid pace. While extensive analyses of distribution, abundance, and habitat use from ship-based surveys and individual tracking have been published independently, integration of these large-scale, complementary datasets will be a major step in developing a more complete understanding of bottom-up processes from local to ocean basin scales.

3   Strengths and Limitations of Habitat Modeling

3.1   *Introduction*

Models for exploring spatial pattern

Habitat modeling is a tool used to explore the statistical relationships between the distribution of organisms (presence/absence or the number of organisms in unit area; "response variable") and biophysical characteristics of their environments ("explanatory variables") (*e.g*., Guisan and Zimmermann, 2000; Redfern *et al*., 2006). Innate characteristics (age, sex, *etc*.) of organisms can be explanatory variables. There are two other general approaches for exploring and predicting the spatio-temporal distributions of marine organisms: ecosystem modeling and individual-based models. *Ecosystem modeling* involves the parameterization of physical, chemical and biological processes (feeding, growth and reproduction rates) and their interactions in ecosystems, and calculates the densities of producers and primary and secondary consumers at small spatial scales (grid cells usually greater than 4×4 km) over the ocean (*e.g*., Franks, 2002; Kishi *et al*., 2007). Ecosystem modeling requires information regarding trophic relationships and time series data on density and distribution of organisms to parameterize and evaluate the model performance (Fulton, 2010). *Individual-based modeling*, on the other hand, assumes some simple rules to describe the movement of individual organisms (*e.g*., speed and direction), and estimates the positions of a large number of individuals under given or modelled biophysical conditions (Dorman *et al*., 2011). This approach requires knowledge about the rules describing the movement of individuals, which is often unclear for most species. The latter two approaches can be computationally intensive and require significant knowledge about animal behavior, physiology and/or trophic relationships. The ecosystem modeling and individual-based model approaches have been rarely applied to MBMs because of the considerable requirements of ecological information, including life history, foraging and prey data. Furthermore, physiological requirements such as the direct and indirect response to temperature, often used as factors for deciding recruitment and movement of poiko-thermic zooplankton and fish, are uncertain for MBMs.

Habitat modeling makes use of integrating multiple empirical datasets and is a simple and useful approach for predicting species habitat preference and response to environmental variability without requiring significant ecological data on organisms and their prey (Fig. 3.1). The spatial distribution of organisms is easier to record than measuring the consumption/production efficiency, growth rate, reproduction and movement rules. Habitat modeling is less computational to construct using desktop computers and can be a good starting point to understand the effects of environmental biophysical factors. However, habitat modeling is a non-deterministic statistical approach based on statistical correlations and spatio-temporal associations, so it is difficult to draw conclusions about the mechanisms driving the distribution.
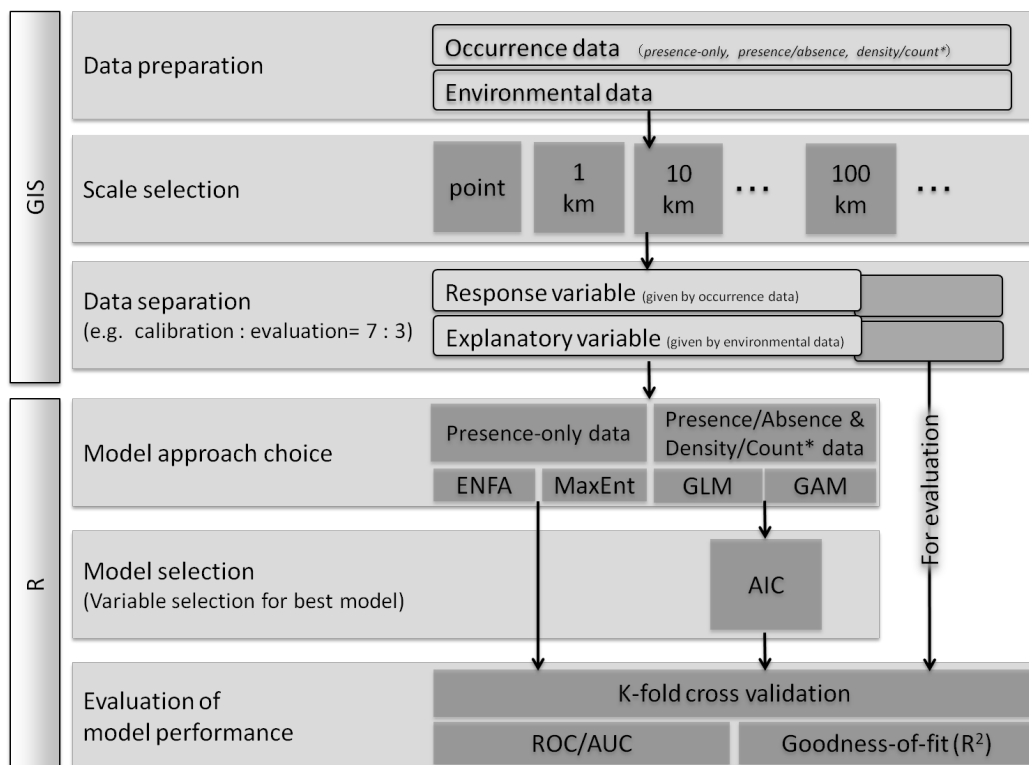
Fig. 3.1 Scheme of the habitat model. R and GIS indicated by the statistical software R and GIS (Geographic Information System) software (*e.g.*, ArcGIS ESRI and Q-gis), respectively. The details of occurrence and environmental data are described in type of response and environmental variables. Scale selection indicates the decision of spatial and temporal scales (here only showing spatial scale). Model approach choice indicates the decision of model approaches depending on the type of response variables (see Section 3.3 for type of response variables). Model selection indicates the decision of variables in the best models. After model selection, evaluation of model performance is conducted (see model selection and evaluation in Section 3.5). AIC = Akaike Information Criterion, ROC = Receiver Operating Characteristic, AUC = Area Under the ROC Curve. See Table 3.3 for other acronym definitions.

Applications and pitfalls of habitat modeling

Habitat modeling is a powerful tool to make inference and predictions on the distribution of marine organisms. Applications include, but are not limited to: 1) finding key factors affecting the distribution of marine organisms (*e.g.*, Guisan and Zimmermann, 2000; Redfern *et al.*, 2006), 2) predicting optimal fishing grounds for efficient and sustainable fisheries (*e.g.*, Santos, 2000; Klemas, 2013), 3) evaluating the impacts of human activities on individual species or communities (Renner *et al.*, 2013; Bombosch *et al.*, 2014) for marine spatial planning (Humphries and Huettmann, 2014) or for species conservation (Chivers *et al.*, 2013), and 4) identifying or projecting shifts in distribution or future potential habitat in the face of climate change (Hazen *et al.*, 2013a; Chust *et al.*, 2014).

Habitat models, however, are never perfect, and can often over-fit the data or have poor predictive capabilities (even though they explain most of the deviance). Habitat modeling predicts the expected distribution of a population based on a limited amount of environmental data collected concurrently with ship-based surveys, remotely sensed data, or modeled oceanographic data to characterize the species' habitat requirements (Becker *et al.*, 2010; Alabia *et al.*, 2015). Difficulties with habitat models can arise from

numerous sources that are not accounted for in the model, such as biases in the underlying surveys (tracking *vs.* ship-based survey), the sampling time and regions, the lack of key explanatory variables, inappropriate spatial scales, inappropriate extrapolations, behavioral responses, and limits of the modeling algorithms (Elith and Graham, 2009). Thus evaluation of the strengths and weaknesses of habitat modeling approaches is increasingly important particularly for MBMs, as they live in highly dynamic environments.

In this section, we will review the factors that may introduce bias, limit effective inference, and/or reduce performance of habitat modeling, and discuss techniques for mitigating or accounting for these factors. More specifically, we will: 1) review types of response and explanatory variables, 2) clarify the assumptions (biological, statistical, and environmental) that limit the predictive power and bias the outcome of habitat modeling, and 3) discuss how we can mitigate against the biases of model selection by averaging several models (ensemble models).

3.2   Innate limitation: Biology of organisms

Response that may change across time and space

Habitat modeling assumes that species distribution patterns are the direct result of their preference for a specific combination of environmental conditions (Barry and Elith, 2006; Elith and Leathwick, 2009). However, species habitat may be restricted by geographical barriers, inter-specific competition, or the moving ability of a given species that are usually not taken into account in habitat modeling. Hence, "occupied distributional area" is only a subset of the full "potential geographic distributional area" of a species (Peterson *et al.*, 2011), harkening back to the concepts of realized *vs.* fundamental niches (Connell, 1961). Failure to occupy such potential areas may also arise from previous extirpation or vagaries of biogeographic history, or simply from the lack of population expansions. These factors should be considered as a stochastic element for the prediction of species distribution. Such phenomena are commonly referred to as contingent historical factors in biogeography (Patterson, 1999).

Habitat modeling relies heavily on environmental variables to predict species distribution, which makes them vulnerable to behavioral responses of organisms to variation in these environmental conditions particularly when these responses vary across regions, seasons and years. For example, this is particularly problematic for migratory species which may depart a summer area earlier than a habitat model may predict if it were based on local environmental conditions as explanatory variables alone. Over larger spatial and time scales, adaptive changes may take place, which are usually not taken into account. However, increasing evidence suggests that the organisms can respond to ongoing climate change, adapting to new environment by means of phenotypic plasticity without altering their genetic constitution, or by means of genetic changes through the process of evolution (*e.g.*, Bearhop *et al.*, 2005; Parmesan, 2006; Gienapp *et al.*, 2008; Visser, 2008; Weimerskirch *et al.*, 2012). Therefore, the potential adaptive responses (*i.e.*, flexibility of behavioral and physiological responses) of species also should be considered during evaluation of habitat modeling exercises.

Inherent factors: Age, sex, body condition and breeding status

Sex-, age-, and condition-related habitat differences have been reported extensively in many species of seabirds (*e.g*., Forero *et al*., 2005; Lewis *et al*., 2005), marine mammals (*e.g*., Breed *et al*., 2006; Crawford *et al*., 2012) and fish (*e.g*., Sims, 2005; Farley *et al*., 2007; Wearmouth and Sims, 2008). These differences in the habitat preference likely relate to physical and biological differences such as body size (Lewis *et al*., 2005; Weimerskirch *et al*., 2012), competitive exclusion (González-Solís *et al*., 2000; Forero *et al*., 2005), energy or nutrient requirements (Ruckstuhl and Neuhaus, 2005), and breeding constraints (Phillips *et al*., 2004; Yamamoto *et al*., 2011; Crawford *et al*., 2012; Catry *et al*., 2013). However, habitat models often do not include information on sex, age, and condition or breeding status. With fisheries information, only data for fishable age and sex classes of targeted species may be available. Individual tracking data may be biased as data typically come from individuals that are most easily tagged (*e.g*., incubating parents of seabirds, female adult sea turtles on nesting beaches) leading to potentially significant gaps in our understanding of a species' habitat use (Hazen *et al*., 2012). With ship-based surveys of seabirds and marine mammals, age, sex, and condition or breeding status of observed individuals is usually unknown.

In some cases age, sex and condition or breeding status can be determined. For example, age and sex of fish can be identified in fishery logbook or observer data. Also, information on the spatio-temporal movement of individuals can be obtained in concert with biological data (*i.e*., sex, age, and condition/breeding status) using recent animal-borne tracking techniques (see review by Burger and Shaffer, 2008; Rutz and Hays, 2009). Sex and age can be treated as fixed explanatory variables. If the identity of observed individuals is available, it can be treated as a random factor in the habitat model, where modeling algorithms allow. In this way, the integration of tracking and ship-based data could help resolve this issue (see below).

During the breeding season, seabirds and seals have to commute between their colony or rookery and foraging areas. The position of the colony is therefore a constraint to the distribution for these central place foragers (see Section 3.4). This constraint can be addressed by adding a colony-effect explanatory variable, comprised of the sum of the inverse distances from all colonies, scaled by the size of colonies (see Renner *et al*., 2013 for details). Complicating factors could exist in relation to changes in attendance patterns at the colony over the course of a breeding cycle. In seabirds, both adults typically attend the colony prior to egg laying, alternate brooding and foraging duties during incubation and early chick rearing, and then both spend most of their time at sea as the chick approaches maturity.

3.3   *Response variables*

Sampling techniques

Distribution data of marine species are collected using a variety of sampling techniques. Sampling techniques can be categorized into three types: 1) *ship-based* and *aerial line-transect surveys* (we discuss ship-based surveys only), 2) *fisheries-dependent* data (*i.e*., log data, observer data, satellite-based detections of fishing light distributions), and 3) *animal tracking* (Table 3.1). These techniques likely contain different biases such as the selection of the survey line and season, tagging location of tracked animals, traits of the sample animals, type of fishing activities, and biased sampling of the population.

Table 3.1 Example of response variables. Materials, sample collecting gear or observational methods, types of variables and presentation of data. Types of response variables are: Density/Count, Presence/Absence and Presence-only data. The limitations of each variable are also noted.

Type of gear (survey)	Data	Materials	Type of response variable	References	Note
Boat-sighting (line)	Occurrence	Whales and dolphins	Presence-only and Presence/Absence data	Kanaji et al., 2015	Information is limited on the survey line. Not applicable for animals under the water.
Boat-sighting (line)	Occurrence/ Absence	Dolphins	Presence/Absence-data	Isojunno et al., 2012	
Boat-sighting (line)	Number of animals	Albatrosses	Density/Count*	Nishizawa et al., 2015	
Long-line (log)	Position of fishing ground	Big eye tuna	Presence/Absence data	Syamusuddin et al., 2013	Cells where fish catch is greater than threshold is denoted as 1; others as 0; 0-cell may be treated as absent. All depends on where the fishing is operated.
Fishing (log)	CPUE	Skipjack tuna	Density/Count*	Mugo et al., 2010	
Fishing (log)	CPUE	Squid	Presence/Absence	Alabia et al., 2015	
Trawl net (log)	CPUE	Benthic invertebrates	Density/Count*	Rooper et al., 2014	Limit to the place where bottom-trawling is possible.
Trawl net (log)	Position of harvest and species diversity	Benthic invertebrates	Presence-only, Presence/Absence	Rooper et al., 2014	Cells where species are found is denoted as 1; others as 0; 0-cell may be treated as absent. All depends on where the survey is operated.
Trawl net (log)	Species diversity	Benthic invertebrates	Number of species data	Rooper et al., 2014	
Satellite (area)	Fishing light (night time lights)	Fishing vessel	Presence-only data	Zhang et al., 2013, Mugo et al., 2014	Snap-shot when satellite is available.
Plankton net (fixed point)	Abundance	Zooplankton	Density/Count*	Zarauz et al., 2007, Sasaki et al., unpublished	
Acoustic (line)	Abundance	Zooplankton	Density/Count*	Santora et al., 2012	
Tracking (area)	Position of animals	Sea birds and marine mammals	Density/Count*, Presence-only and Presence/Absence data	Suryan et al., 2006, Raymond et al., 2015	Animals are tracked by telemetry or biologging techniques. Information on place that animals do not use cannot be used.

* Density data indicate the number of animals per unit area or CPUE (catch per unit effort) or SPUE (sighting per unit effort). Effort includes the number of net tows, the number of hooks, filtered water volume, observation time, and the distance of each transect line. Count data are often used as dependent variables. For this case, the effort is treated as an offset term in habitat models.

1.   *The ship-based line transect surveys* are often used to study the distribution of marine mammals and seabirds (by sighting), fish (by acoustic survey and trawl samples), phytoplankton (by continuous sampler and automated analyzer) and zooplankton (by the Continuous Plankton Recorder or CPR: Batten *et al*., 2003). Thus data are limited within a survey area, along survey lines or within surveys swaths (*i.e*., area of coverage along survey lines). Given a fixed width of ship-transects (*e.g*., 300 m from the boat for seabird surveys), and estimates of detectability and flux (Tasker *et al*., 1984; Spear *et al*., 1992; Buckland *et al*., 2001), the number of animals observed can be converted into an estimate of density. The survey line can be systematically determined according to program objectives and surveys. However, surveys can also be based on ships of opportunity and clustered in space and seasonal coverage.

2.   *Fisheries logbook data and observer data* are used to study the distribution of commercial fishes and squids, benthic marine invertebrates, and bycatch of top predators. Catch Per Unit Effort (CPUE) is typically used as the response variable. In many cases, effort with zero catch goes undocumented. This is considered a challenge for researchers who study the distribution of these commercial species, as this undocumented effort makes it difficult to define a total study area represented by the catch data.

3.   *Animal tracking* based on a satellite-linked platform terminal transmitter (PTT) or global positioning system (GPS) data-logger attached to animals has been used often for studying the distribution and movement of a small portion of the population of large seabird species and marine mammals. Tracking data can be examined using mixed models on a track-by-track basis, or after aggregating data, *e.g*., into density per grid cell (Block *et al*., 2011; Yamamoto *et al*., 2015).

Spatial resolution varies among data collection techniques (Table 3.2). For line transect data, spatial and temporal resolution can be relatively fine (*e.g*., as fine as 300 m) and from seconds to 10 minutes. For point sampling, spatial resolution is usually 0.1–1°. Fishing log data is usually aggregated over $0.25° \sim 1° \times 1°$ cells and month by fisheries investigations where data collected during a month or so is summarized (Syamsuddin *et al*., 2013; Robinson *et al*., 2015). GPS tracking gives the finest spatio-temporal resolution (1 s, ~10 m) while spatial resolution of PTT-based tracking is broader (day, ~10 km). Geolocators determine positions based on the timing of sunset and sunrise, providing at most one fix per day with an error of ~100 km, depending on the season and location.

Data type

Data collected by each of the above techniques can be categorized as one of three types: *presence-only*, *presence/absence*, or *density/count data*.

1.   *Presence-only* data contain sighting information of any number of animals in a cell, but have no information of where a species was not detected or where no survey effort was made. Thus presence-only data have the least stringent requirements for data quality, and can be acquired from numerous sources including museum records, casual observations, and tracking data. For example, fishing-lights detected using satellite imagery as an index of squid distributions can be treated as presence-only data as this index of squid location would only be effective inside squid fishing grounds.

2.   *Presence/absence* data contain information where a species was not detected, which does not necessarily imply that it was actually absent. For example, cetaceans and seals make long dives so often that density cannot be estimated without making assumptions about time spent underwater. The likelihood of any detection also decreases with distance from the observer, so a recorded absence is somewhat dependent on the local density of the studied organism. Thus cetacean sightings data are sometimes treated as presence-

only or presence/absence data. Logically, tracking techniques provide only presence-only data, as the entire population is not sampled. However, techniques for creating pseudo-absences for tagging data (*i.e.*, random walk generation techniques, for example) may outperform presence-only approaches, but additional studies are needed to ensure this is the case (VanDerWal *et al.*, 2009; Wingfield *et al.*, 2011; Willis-Norton *et al.*, 2015).

3.   *Density/count* data is the number or biomass of animals caught or observed per unit effort, *i.e.*, CPUE. Effort includes the area of net tows for the otter bottom-trawl, the number of hooks for long-line (Mugo *et al.*, 2010; Howell and Kobayashi, 2006), time by the number of hooks for squid jigging, filtered water volume for plankton net sampling, transect line distance by swath width (as area) for marine bird and mammal surveys. In some cases, CPUE data are treated as presence-only or presence/absence data, such as for bigeye tuna long-line fishing log data (fish per 100 hooks was converted to presence/absence data; Syamsuddin *et al.*, 2013) and for squid jigging data (mass of catch was converted to presence-only data; Alabia *et al.*, 2015).

In habitat modeling, presence-only data and presence/absence data are assumed to follow a binomial distribution, while density data tend to follow a highly skewed non-Gaussian distribution such as Poisson, Tweedie or negative binomial (over-dispersed). These data can also be zero-inflated.

The quality of response variable will dictate what kind of predictions can be made. Presence-only data have the least stringent requirements regarding data quality, and accordingly the interpretation of the predicted distribution may be difficult. Presence/absence and presence-only models can provide a probability of occurrence, or a simple yes/no of reaching a pre-defined probability threshold. Models based on density data, on the other hand, provide a density surface that could allow estimates of regional population sizes, population trends over time, and distribution shifts within a species' range (*e.g.*, Renner *et al.*, 2013).

Data type and modeling approaches

Depending on the data type, four categories of model approaches are available (Hirzel *et al.*, 2002; Elith and Graham, 2009; Phillips *et al.*, 2006; Panigada *et al.*, 2008; Stockwell and Peters, 1999). 1) *Presence-only approach* uses environmental data at locations where animals are present. 2) *Presence/background approach* uses presence-only data and the environmental variables at the locations of species occurrence are compared to the entire survey area. 3) *Presence/absence approach* uses presence/absence data and assesses the potential ranges using differences in environments between the location of presence and absence (Breiman, 2001; Peterson *et al.*, 2011). We can make pseudo-absence data through random sampling of absence cells, then use the presence/absence approach for presence-only data (Wisz and Guisan, 2009). 4) *Density/count approach* uses density/count data to assess gradients and non-linear changes in species density across the environmental seascape. A problem associated with converting count to the density or CPUE is that information on sampling effort variability is lost and probability distributions may not accurately reflect true animal distributions as a result. To resolve this, sampling effort can be treated as an "offset" term in habitat models (Zuur *et al.*, 2009a).

3.4   Explanatory variables

Environmental variables

Environmental variables can be dynamic (vary with time) or fixed. Dynamic environmental variables may vary spatially, temporally, or both. Sea surface temperature (SST), salinity (SSS), height (SSH), and Chlorophyll *a* (Chl-*a*) are dynamic environmental variables that can be collected during ship-based surveys. As well, these variables can be derived from satellite remote sensing or from hydrodynamic and simulated oceanographic models (Table 3.2). Temporal and spatial variations of these environmental factors are used as an explanatory variable since variability across time (or predictability) and space can be an important proxy for mesoscale processes. As an example, spatial gradients in SST may indicate hydrographic features such as convergent fronts (Cayula and Cornillon, 1992, 1995, 1996), and marine organism are known to associate with fronts (Scales *et al*., 2014). The upwelling index can be calculated by strength and direction of the wind and alongshore wind stress (Bakun, 1973). The stratification index is calculated as a function of density, salinity and temperature (Ladd and Stabeno, 2012).

The resolution of these dynamic environmental variables depends on the sampling tools. For satellite-derived data, the finest spatial resolution is 500 m (*e.g*., SST and Chl-*a*) and ranges through 0.25° (slope of SSHa and geostrophic current) to 1° (SSS; Table 3.2). However, we can scale up (*i.e*., reduce spatial resolution) using GIS software (*e.g*., ArcGIS and SeaDAS) to ensure appropriate spatial resolution is used. Temporal scales of satellite data products range from daily to long-term climatology (*e.g*., SST and Chl-*a*, Table 3.2). Data collected during ship-based surveys, such as the density of prey, water turbidity, and salinity, have high spatial and temporal resolution but have the major drawback that predictions over the entire study area tend to be impractical, as data collection is constrained to survey lines. These explanatory variables can also be aggregated to potentially more suitable larger temporal and spatial scales (see Section 3.6).

Bathymetry or bottom substrates are examples of static environmental variables which can be derived from bathymetry or other features such as landmarks (seamounts, estuaries or coastlines) (Amante and Eakins, 2009). There are numerous examples of derived static environmental variables such as bottom slope, bottom rugosity (variability in depth or roughness), shelf-break location, distance from shelf-break, distance from seamount, distance from coast, or distance from estuary.

Prey

Prey is an important environmental factor affecting the distribution of predators, although it is relatively unexplored because prey distribution data are not easy to collect. Acoustic volume backscatter data can provide a metric of prey density which can be used for habitat modeling (Murase *et al*., 2002; Hazen *et al*., 2009; Hazen and Johnston, 2010; Benoit-Bird *et al*., 2011; Hazen *et al*., 2011). Murase *et al*. (2002) found a simple correlation between concentration of cetacean and large aggregation of euphausiids determined by acoustics. Several studies used acoustic volume backscatter data as input in habitat models and showed non-linear relationships between cetacean abundance and prey density (Friedlaender *et al*., 2009; Laidre *et al*., 2010). Also, volumetric backscatter often is less important than prey patch structure (*e.g*., density, patch size, patch separation distance) as predators rely on dense aggregations of prey for efficient foraging (Hazen *et al*., 2007; Benoit-Bird *et al*., 2013a,b). Even when prey data are available, the lack of broad spatial coverage severely limits the potential applications of models incorporating prey densities.

Table 3.2 Example of explanatory variables. Spatial and temporal resolution and survey methods are shown.

Variable	Description	Spatial resolution	Temporal resolution	Method	References
Bathymetry	Water depth and its gradient	500 and 1000 m, 30″, 1′, 2′ and 5′	NA	Measurement	Skov et al., 2008, Forney et al., 2012
Distance from some landmarks	e.g., Distance from seamounts and to nest	Same as bathymetry	NA	Calculate distance from some land marks	Becker and Beissinger, 2003, Nishizawa et al., 2015
Thermal front	Sea surface temperature gradient defined by Cayula and Cornilon (1992,1995,1996)	1, 4 and 9 km (satellite)	Daily, 3 and 8 days, monthly, seasonal and annual composite, and climatology (satellite)	Satellite	Etnoyer et al., 2006
Distance from oceanic front	e.g., Polar Front (defined by Favorite et al., 1976), Subarctic Front (Mizuno and White, 1983), and Kuroshio Extension Front (Kawai, 1969)	Same as thermal front	Daily, 3 and 8 days, monthly, seasonal and annual composite, and climatology (satellite)	Calculate distance from thermal front	Oppel et al., 2012, Murase et al., 2014
Chlorophyll a concentration	Mean Chl-a concentration and its persistency at the surface and at some depth observed	Sampling point (in situ) 1, 4 and 9 km (satellite)	Real time, daily, 3 and 8 days, monthly, seasonal and annual composite, and climatology (satellite)	Satellite, water sampling and bouy	Oppel et al., 2012, Sasaki et al., 2013
Sea temperature	Mean sea temperature at some depth (e.g., surface, 50 m and bottom)	Sampling point (in situ) 1, 4 and 9 km (satellite)	Real time, daily, 3 and 8 days, monthly, seasonal and annual composite, and climatology (satellite)	Satellite, water sampling and bouy	Becker et al., 2010, Kanaji et al., 2015, Alabia et al., 2015
Salinity	Mean sea salinity at some depth (e.g., surface, 50 m and bottom)	Sampling point (in situ) and 0.1° (model derived)	Real time and 5 days	Electronic probe and model-derived	Stoner et al., 2001, Alabia et al., 2015
Sea surface height anomaly	Anomaly of sea surface height	0.25°	Real time and 7 days	Satellite	Sasaki et al., 2013, Mugo et al., 2014
Geostrophic current	Geostrophic current	0.25°	Real time and 7 days	Satellite	Mugo et al., 2010

Table 3.2 Continued.

Variable	Description	Spatial resolution	Temporal resolution	Method	References
EKE	Eddy Kinetic Energy calculated by geostrophic current	0.25°	Real time and 7 days	Satellite	Mugo et al., 2010, Santora et al., 2012
Duration from sunrise	Minutes from local time of sunrise	Sampling point (*in situ*)	Minutes	Calculated or table	Isojunno et al., 2011
Tide flow	Rate of change of tidal height	Sampling point (*in situ*)	Minutes	Calculate the rate from duration between high and low tide	Isojunno et al., 2011
Mixed layer depth	Depth of mixed layer	0.5°	Monthly	Models	Arrizabalaga et al., 2014, Su et al., 2011
Sediment type	Sediment classes in the survey area obtained from the British Geological Survey	Sampling point (*in situ*)	NA	Geological Survey	Macleod et al., 2004
Stratification	Surface to bottom temperature difference. Depth of maximum density gradient	Sampling point (*in situ*)	Real time	CTD vertical profiles	Zarauz et al., 2007, Sasaki et al., unpublished

NA = not applicable, CTD = conductivity, temperature, depth

Spatial CPUE and fishing log data can be also used as explanatory variables although these are often collected at a resolution that is too low to be useful (Torres *et al*., 2008). Indeed, dedicated field sampling may be the only way to collect sufficiently high-resolution information on prey. However, it is often difficult to sample the entire study area. An alternative technique is to use the modeled spatial pattern of density of prey species that is derived from individual-based models or ecosystem models. To use modeled prey density surfaces, the model predictions should be evaluated using reference data. Further, collinearity (some variables are highly correlated) between the predicted density of prey species and other explanatory variables (*i.e*., variables that were likely used to model prey species) must be checked and accounted for in the final habitat model (see below).

Competitor/predator

The presence of other species (competitors/predators) can be an important environmental factor affecting species distribution (Franklin, 2010), but is usually not included in the habitat models (Wisz *et al*., 2013) simply because of a lack of data. If there is information on biotic interactions between species (*e.g.*, predator–prey, competition, and facilitation), presence/absence or density of the other species can be an explanatory factor. One approach is to integrate pairwise dependencies using surrogates for biotic interaction gradients and another is to hybridize models with dynamic models (*e.g*., Sebastian-Gonzelaz *et al*., 2010). However, as mentioned in Wisz *et al*. (2013), biotic interactions are not constant in time and space, and species interact across complex networks.

Innate factors

As described in Section 3.2, many innate factors influence habitat utilization. For this reason, age, sex, and condition and breeding status should be used as explanatory variables in habitat models. Location of the colonies constrains the choice of feeding area in breeding seabirds. Therefore, distance to the colony should be included as an explanatory variable.

Collinearity

Environmental variables (SST, SSH, *etc*.) are often correlated each other. If so, it is necessary to check for collinearity (highly correlated variables) and eliminate explanatory variables, as necessary, or combine several variables into a single index using Principal Component Analysis (PCA, see Section 3.7). Approaches to test and account for collinearity are discussed in detail in Zuur *et al*. (2007).

3.5   *Selection of the models*

Groups of models

The choice of the model depends largely on the type of response variables. Above, we have summarized the different types of response data. We will briefly discuss suitable models and model selection for practical usage (see Oppel *et al*. (2012); Praca *et al*. (2009); Austin (2007); Araújo and New (2007); Araújo and Guisan (2006) for details). We also will discuss the biases introduced by the scale of analyses, year and regions, and validation techniques.

Habitat models are categorized into four groups, depending on statistical model types: profile methods, regression methods, machine learning methods, and geographic methods (Busby, 1986, 1991; Hastie and

Tibshirani, 1990; Guisan and Zimmerman, 2000; Breiman, 2001; Hirzel *et al*., 2002; Wood, 2006; Hijmans and Elith, 2013; Bombosch *et al*., 2014; Hijmans *et al*., 2014). Murase (oral presentation in S2 at PICES-2014)[4] summarized the applicable models for marine organisms (Table 3.3).

Table 3.3   Types of habitat modelling approaches and groups of models, revised from Franklin (2009) and Murase *et al*. (2014) in PICES-2014 presentation S2.

Group	Approaches			
	Presence/Absence	**Presence/Background**	**Presence-only**	**Density/Count data**
Profile		Ecological Niche Factor Analysis (ENFA)	Bioclimatic Analysis and Prediction System (BIOCLIM) DOMAIN (Extended Domain algorithm to Habitat Modeling)	
Regression	Generalized Linear Model (GLM) Generalized Additive Model (GAM)			Generalized Linear Model (GLM) Generalized Additive Model (GAM)
Machine learning	Decision Tree (DT) Boosted Regression Tree (BRT) Random Forest (RF) Artificial Neural Network (ANN) Support Vector Machine (SNM)	Maximum Entropy Model (MaxEnt)		Decision Tree (DT) Boosted Regression Tree (BRT) Random Forest (RF)

Model selection and evaluation

The best-performing model (or models) is (are) selected using a number of suitable algorithms. There are numerous techniques to select models. To choose the best performing model, predictive performance is often used (Peterson, 2005; Peterson *et al*., 2011). Although frequently used today, step-wise model selection should not be guided by statistical tests of significance, as this has been widely discredited, producing spurious results (*e.g*., Mundry and Nunn, 2009). Alternatively, selecting suitable potential models that fit hypotheses to be tested *a priori* is a better approach.

---

[4] http://pices.int/publications/presentations/PICES-2014/2014-S2/S2-1405-Murase.pdf

There are several statistics that can be used to measure model and/or predictive performance and these include simple correlation, Root Mean Squared Error (RMSE), Akaike Information Criterion (AIC), Area Under the ROC (Receiver Operating Characteristic) Curve (AUC), Leave-One-Out Cross-Validation (LOOCV) or K-fold Cross-Validation (k-fold CV), and the True Skill Statistic (TSS) (Johnson and Omland, 2004; Allouche *et al*., 2006; Elith and Graham, 2009; Elith *et al*., 2010; James *et al*., 2013). To evaluate the predictive performance, first, the model is constructed by using a subset of data ("training"). Then evaluation ("calibration" or "test") of the selected model is carried out by using the remaining data that were not used for training (Huberty, 1994; Guisan and Zimmerman, 2000; Franklin, 2010). For presence-only models, the goal is to test if the model predicts positive value (localities of presence for species) better than a random prediction. For presence/absence models, the AUC (Redfern *et al*., 2006) of ROC plot represents an overall measure of the model performance. AUC ranges from 0 to 1, and 0.5 corresponds to the expected performance of random classifier. If there is no single model supported by the data, model averaging can be used (Johnson and Omland, 2004).

Ensemble prediction

Modeling techniques vary in terms of robustness and performance (*e.g*., Yen *et al*., 2004; Oppel *et al*., 2012; Renner *et al*., 2013), and to address this, ensemble modeling techniques have been developed. Ensemble models are composed of more than one habitat model, and ensemble predictions are calculated as weighted averages of predictions from each constituent model, with weights assigned to each modeling technique based on its discriminatory power as measured by the evaluation statistic (*e.g*., AUC). Predictions by the ensemble model are often more robust than predictions derived from a single model (Araújo and New, 2007; Marmion *et al*., 2009; Thuiller *et al*., 2009; Oppel *et al*., 2012). However, predictions can also suffer as results from good models may be diluted by results from poor models (Peterson *et al*., 2011). This could be solved by including only robust models, based on the evaluation statistics, or combination of model outputs *via* some objective weighting scheme such as weighting based on evaluation statistics (Marmion *et al*., 2009), or spatial weighting if one model has better performance in specific areas than others. A second risk is that mixing the results of different methods may create difficult problems of interpretation although it may be not matter much if one is interested primarily in predictive ability.

An example for streaked shearwaters (*Calonectris leucomelas*) is shown in Table 3.3. The models were based on the position data of tracked individuals using light-based geolocators and included four techniques, Generalized Linear Model (GLM), Generalized Additive Model (GAM), Random Forest (RF), and ensemble model (Yamamoto *et al*., 2015). AUC (*i.e*., assessing the performance of models) and Cross-Validation techniques were used to rank the models (Potts and Elith, 2006; Oppel *et al*., 2012). Furthermore, the Pearson correlation coefficient, and the slope and intercept of a linear regression of the observed *vs.* predicted values were used to evaluate the bias and consistency of model predictions. The slope and the intercept of this regression indicate the calibration and the bias of the model, respectively (Phillips and Elith, 2010).

In the above analysis, the RF had the highest AUC and highest correlation in the prediction followed by ensemble model, but showed larger calibration error and bias. The machine learning methods, including RF, usually provide excellent discrimination between areas of presence and absence. However, when used on spatially independent data, these methods likely suffer proportionally more (*e.g*., larger biases) from over-fitting than parametric models such as GLM and GAM. GLM was not applicable in this case, probably because the responses of streaked shearwater to environmental variables are non-linear (*i.e*., they appear to exhibit a preference for particular ranges of SST; Yamamoto *et al*., 2011).

3.6   Scales and seasonal and regional variations

Choice of scale

Spatial resolution of response variables may be from 100 to 1,000 m (density or presence/absence of seabirds and whales based on tracking and ship-based survey) and $1° \times 1°$ (density or CPUE of tuna species based on logbook or observer data) (Table 3.1) while spatial resolution of explanatory variables may be 100 m (re-analyzed temperature and salinity) and 4 km (satellite-based Chl-*a*) (Table 3.2). The relative importance of explanatory variables explaining a species' distribution and abundance can be highly scale dependent (Soberón, 2007). The appropriate scale may depend on the biology of target organisms, including movement scales, longevity, and sensing ability since all these influence the scale of habitat selection by individual organisms.

There are many studies showing that the association between the density of prey and predator depends on the scales of analyses. For example, the spatial association of murre density with the density of prey (capelin, krill) is weak at the 0.2 to 1 km scale and strong at the 2 to 10 km scale (Schneider and Piatt, 1986; Mehlum *et al*., 1999). This indicates that the distribution of murres and prey overlap at a 10 km scale where density of the prey patch is high on average but murres are unable to detect each prey patch at a 0.1 km scale efficiently, presumably because of their sensory constraint and moving ability. Alternatively, sampling at a larger scale may sometimes significantly reduce the power of inference as important features may be overlooked. If a fine-scale process such as prey distribution is measured at a large scale, it may not have explanatory power in the model (Torres *et al*., 2008). The scales where strong positive associations between prey and predator are observed may depend on the scales of the searching behavior of predators (scales of Area Restricted Search: ARS) and the scales of the spatial organization of prey patches. Scales of ARS are 80–100 km for albatross species (Weimerskirch *et al*., 2007; Pinaud and Weimerskirch, 2005) and 2–5 km for murres and rhinoceros auklets (Y. Watanuki, unpublished). Usually, we do not know the scale of prey searching behavior for each species of predators *a priori*, so analyses should be carried out at various scales to find the one where explanatory power is strongest. Nishizawa *et al*. (2016) modeled the distribution of Laysan (*Phoebastria immutabilis*) and black-footed albatrosses (*P. nigripes*) at 4 to 80 km scales in the Northwestern Pacific and found a greater coefficient of determination at the 80 km scale than at the 4 km scale.

Seasonal and inter-annual variability

Organisms may have different responses to environmental variables in different seasons, different years, or under different climate phases (Grebmeier *et al*., 2006; Moore and Huntington, 2008). As well, they may respond differently to their environments, depending on their innate life cycle (breeding/foraging season), interactions with other species, and food availability (Hazen *et al*., 2012). For example, in the North Pacific, Alabia *et al*. (2015) found that preferred SST (derived from the models) of neon flying squid (*Ommastrephes bartramii*) differed between January and February (Northwestern Pacific fishing ground) and June to July (Central Pacific fishing ground). These sources of temporal variability can be treated as fixed or random effects in a habitat model. It is often difficult to separate the effects of season, breeding status, and food availability because these factors are often correlated. Furthermore, the range of environmental factors or explanatory factors (*e.g*., SST) can change seasonally or over the years. Fish respond to SST, for example, during the spring when SST may vary between 5 and 15°C, while the response may disappear during the summer when SST is more homogeneous. So, SST may be included in the best performing model in the spring but not in summer.

When we are not interested explicitly in the effects of season or year, they can be included as random effects. To construct a model with random effects, there are three general approaches: random intercept, slope or including both (Zuur *et al*., 2009b). The random intercept model assumes that the baseline varies among years and seasons. If the response variables vary with time, a random slope model can be used. The random intercept and slope models are used when variability occurs in both parameters. Kanaji *et al*. (2015) constructed habitat models for short-finned pilot whales (*Globicephala melas*) in the Northwestern to Central Pacific separately during the summer from 1983–2006. The predicted distribution looks similar among years, although the inter-annual changes of the Kuroshio might have influenced the whales' habitat. Their paper does not describe the differences in the model and those in the explanatory variables in detail among years.

Regional variability

Organisms show different responses in different regions. Organisms may adapt to regional or local environments. Stability (repeatability or persistence) of environmental factors may differ among regions. For example, Torres *et al*. (2015) constructed habitat models of grey petrels (*Procellaria cinerea*) using tracking data and oceanographic data from different colonies separately. Their results indicate that the performance of the model constructed using tracking data collected from birds breeding in the subantarctic at Antipodes Island was high when the model was applied to data collected from birds breeding at Kerguelen Island but the performance of this model was worse when the model was applied to data collected from birds breeding at Marion Island. The authors argued that the models constructed from birds breeding at the Antipodes and Kerguelen islands might be over-fitted since habitat usage of these populations might be similar. The potential environment for birds breeding at Marion Island was different from that for birds breeding at the other two islands, so the accuracy of prediction was poor when the model derived from birds breeding at Antipodes–Kerguelen islands was applied to birds breeding at Marion Island.

Another example is the study by Sundblad *et al*. (2009) who explored environmental factors (Secchi depth, salinity and wave exposure) to explain the distribution of larval northern pike (*Esox lucius* L.) and roach (*Rutilus rutilus* L.) in the Baltic Sea. They constructed a model using data from one area and year, then tested the performance of this model by predicting data collected in a separate area and year, and followed the same procedure in reverse. They found that model performances were high for both directions for roach larval presence despite an almost opposite relationship between larval presence and wave exposure, suggesting that wave exposure explained minimal variation in larval presence. For pike larvae, however, the model was less successful when tested with data collected in the other area and year. Sundblad *et al*. (2009) speculated that the species-specific difference in model performances is likely due to differences in terms of species ranges along the predictor variables, and emphasize the need to validate model predictions properly.

These regional and seasonal differences can be included in species distribution models (SDMs) as fixed or random effects. If researchers are interested in the magnitude of either regional or seasonal effects, these effects must be included as fixed effects in SDMs or separate models must be built for each region and/or season.

3.7 Case studies in the North Pacific and adjacent seas

Copepods in the Chukchi Sea

Temperature, salinity and density of water and the water current are often correlated with each other. In statistical models, these correlated variables cannot be used together in GLM and GAM. Several studies

constructed models after one (or more) of these correlated explanatory variables were removed from the analyses. Habitat models for zooplankton are good examples (*e.g.*, surface salinity, temperature and Chl-*a*) (Zarauz *et al.*, 2007, 2008; Silva *et al.*, 2014). However, when we remove some variables, we may fail to recognize important oceanographic features such as water mass defined by the combination of water properties (*e.g.*, temperature and salinity). Further specific combinations of water masses in upper and bottom layers cannot be treated as explanatory variables. To reduce these weaknesses and to catch important features of water masses, we can summarize the variable into a few indices prior to conducting statistical models (see Section 3.4).

Sasaki *et al.* (2016) constructed habitat models using GAM for Arctic copepods collected in the Chukchi Sea during the summer seasons of 2007, 2008 and 2013. The abundance of copepods, sampled using plankton nets, was the response variable. To quantify the marine environmental factors affecting copepod distributions, Sasaki *et al.* (2016) used the depth of the pycnocline (Stockwell and Peters, 1999) and the vertically averaged temperature, salinity, and log-transformed Chl-*a* concentration above (upper layer) and below (bottom layer) the depth of the pycnocline. They then compared the performance of two approaches. In the first approach (conventional technique), one of the variables that was correlated with the other was removed to mitigate the collinearity. In the second approach, Principal Component Analysis (PCA) was used to integrate several physical variables (Fig. 3.2) to produce a composite quantitative index. The water mass index was scored along the first Principal Component axis that was derived using the depth of the pycnocline and averaged physical factor in upper and bottom layers. In addition, vertically averaged Chl-*a* in the upper and bottom layers and the bottom depth were used as environmental variables. The year was included as a random effect. All best-fit models explaining abundance of copepods included water mass indices, Chl-*a* concentration in both layers and bottom depth. Sasaki *et al.* (2016) found that the performance (evaluated by R^2 and RMSE) of the best model (ΔAIC > 2.00) based on the water mass index was higher than that of the best model based on conventional methods.
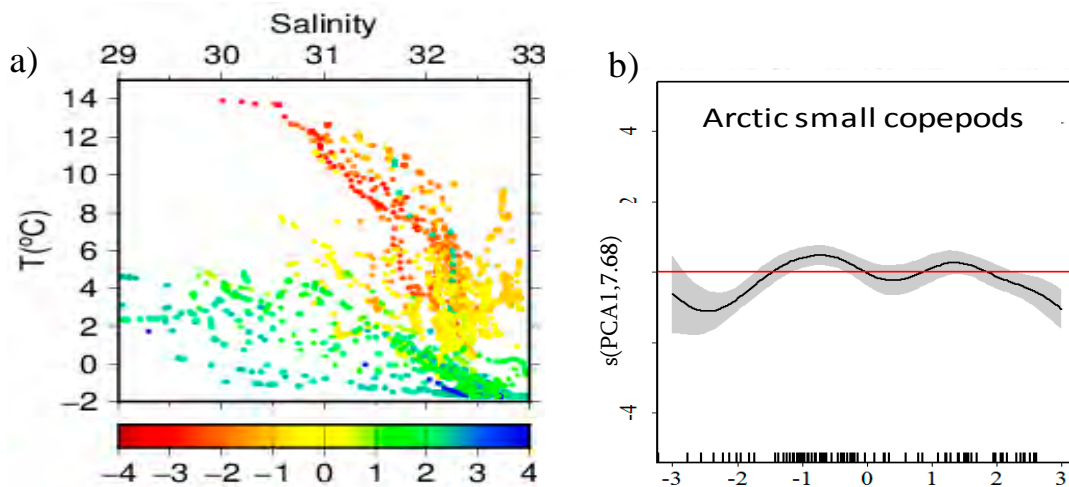
Fig. 3.2   a) T-S diagram of Principal Component 1 (PC1). Colored circles indicate the magnitude of each PC1. Water mass designations are Alaskan Coastal Water (ACW; salinity < 31.8 and temperature 2–13°C), Bering Shelf Water (BSW; 31.8–33 and 0–10°C), Anadyr Water (AW; 32.3–33.3 and 0–10°C), Bering Shelf Anadyr Water (BSW and AW combined), Ice-Melt Water (IMW; < 30 and < 2°C) and Dense Water (DW; 31–33 and < 0°C). b) GAM plot of the best model for copepod species: Arctic small (AcopeS). The vertical axis indicates the estimate smoother for the abundance of copepods. The horizontal axis shows the explanatory variable: PC1. From Sasaki *et al.* (2016).
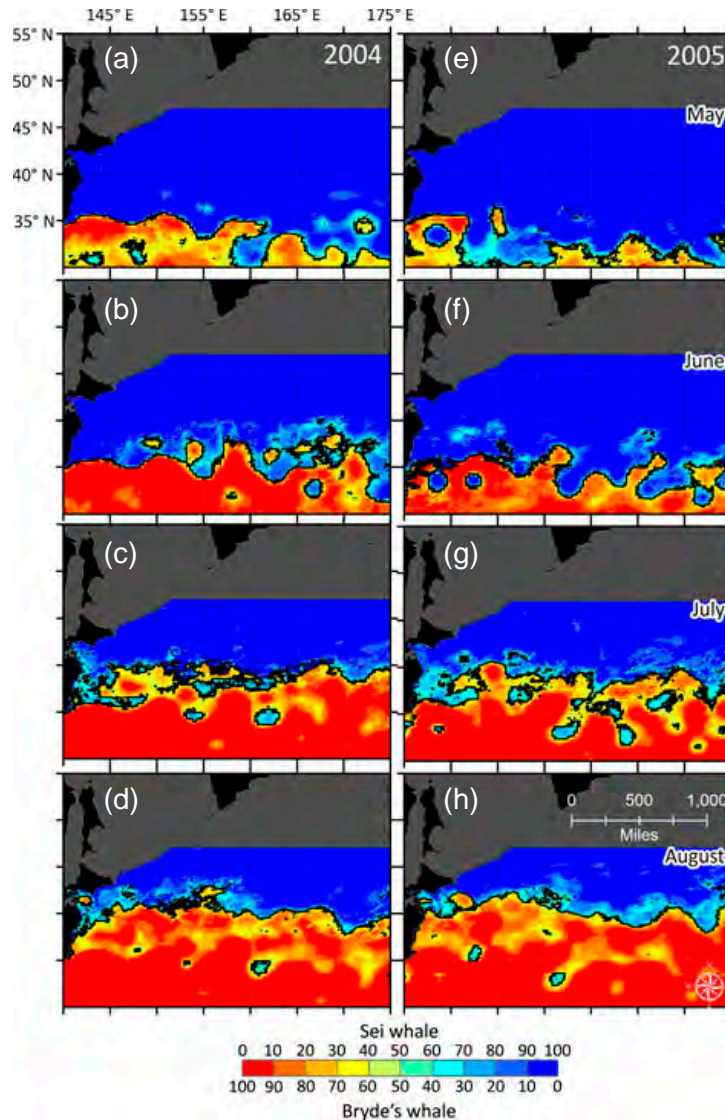
Bryde's and sei whales

To explore the differences in habitats between the two species of whales and to identify the boundary of the distribution of these two species, different types of response variables were used. To investigate the relationship between the occurrence of closely related Bryde's and sei whales and their environments, Sasaki *et al*. (2013) used a GLM with binary response based on their occurrence in the Northwestern Pacific. The data were provided by sighting surveys of the Japanese Whale Research Program during May–August in 2004 and 2005. As the response variables, they used "(binary) rank" (presence of sei whale equal to 1 and presence of Bryde's whale equal to 0) derived from the occurrence data. Royle and Dorazio (2008) suggested that detection probability can be related to the "power" of the survey method. In case of imperfect sightings, detection probability should be calculated prior to categorizing species to rank. In Sasaki *et al*.'s (2013) study, perfect detection (all animals are sighted) and identification of Bryde's or sei whale was required. Since the data of the species' absence were not used in their study, the model could not show the condition of the species absence. Thus prediction in their study shows only the boundary of habitats between both species and does not show the potential habitats of each species. As the explanatory variables, satellite-derived oceanographic features were used, including SST (°C), sea surface Chl-*a* (mg m^{-3}) and sea surface height anomalies (SSHAs; cm) during the survey period, and water depth (m). The spatial and temporal scales were 4 km and monthly, respectively. The presence of sei whales was defined as [P(Y = 1)] and that of Bryde's whales was defined as [P(Y = 0)]. Formulae for the model were as follows:

$$P(Y = 1) = \alpha + \beta1(SST) + \beta2(Chl\text{-}a) + \beta3(SSHAs) + \beta3(\text{water depth}),$$

$$P(Y = 0) = 1 - P(Y = 1).$$

The result of the best-fit model based on AIC, included SST and Chl-*a*. The predicted distribution showed a clear separation of potential habitats of the two species and the boundary of habitats moved northward as the season progressed. Mainly SST contributed to the patterns of habitat use between the two whale species (Fig. 3.3).

Fig. 3.3   Probabilities of cetacean occurrence in the Northwestern Pacific in 2004 and 2005. Colors from blue to red indicate the probability of occurrence and which species (Bryde's or sei whales) can be found. Black lines indicate a probability of 50%. From Sasaki *et al*. (2013).

Currently, the field of habitat modeling is rapidly evolving. Although much progress has been made, especially on the side of machine learning techniques, much work remains to be done. For example, we do not have an appropriate method for extracting the distributional information contained in tracking studies and combining them with the density data sampled by the ship-based surveys. Likewise, combining the properties of tree-based and generalized linear models is a field in which we hope to see much progress in the near future. Bayesian approaches are not discussed here, but often add flexibility in incorporating multiple processes and data types (Ward *et al*., 2015; Thorson *et al*., 2015a, b).

4   Applications

Intensifying impacts in marine ecosystems worldwide from regional (*e.g*., fishing, pollution, mineral extraction, and maritime transportation) and global (*e.g*., climate change) anthropogenic stressors is causing increased public concern for the health of North Pacific marine ecosystems. These stressors can interact and impacts can be cumulative. For example, increases in sea surface temperature *via* global warming can result in changes in primary production *via* enrichment of waters and fundamentally change food web dynamics. Fundamental changes such as these that stem from global anthropogenic stressors can make marine ecosystems vulnerable to regional-scale human impacts. The distribution and abundance of MBMs provide valuable insight into how natural and anthropogenic stressors are impacting marine food webs and upper trophic level species. In this report, we reviewed the type of available data and the potential approaches to model the distribution and abundance MBMs in the North Pacific. Once reliable and robust models have been developed, they can be used for: 1) understanding and predicting the effects of climatic ("bottom-up" impacts) and anthropogenic impacts on marine ecosystems, and 2) understanding how changes in the distribution and abundance of marine bird and mammal populations influence marine ecosystems through "top-down" (predation and competition) mechanisms. Moreover, observed and predicted (*via* models) distribution of seabirds and marine mammals can be used to define ecologically and biologically important areas (EBSAs) and help inform appropriate management of the areas highly vulnerable to anthropogenic impacts. Thus understanding how and why MBMs distribute themselves as they do should help inform: 1) the conservation of populations and species of concern (endangered and threated species), and 2) the design of marine protected areas under the threats of oil and gas developments, pollutants, aquaculture, fisheries, and other anthropogenic threats or stressors.

To complement and contribute to the FUTURE program, AP-MBM should continue to work in the field of spatial ecology relative to climate variability and change, and other human impacts. Continuing to host workshops and topic sessions at PICES Annual Meetings and produce special issues in the primary literature will be one way AP-MBM can continue to contribute in meaningful ways to FUTURE.

5   References

Adams, J., MacLeod, C., Suryan, R.M., Hyrenbach, K.D. and Harvey, J.T. 2012. Summer-time use of west coast US National Marine Sanctuaries by migrating sooty shearwaters (*Puffinus griseus*). *Biol. Conserv.* **156**: 105–116.

Alabia, I.D., Saitoh, S., Mugo, R., Igarashi, H., Ishikawa, Y., Usui, N., Kamachi, M., Awaji, T. and Seito, M. 2015. Seasonal potential fishing ground prediction of neon flying squid (*Ommastrephes bartramii*) in the western and central North Pacific. *Fish. Oceanogr.* **24**: 190–203.

Allouche, O., Tsoar, A. and Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* **43**: 1223–1232.

Amante, C. and Eakins, B.W. 2009. ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis. NOAA Tech. Memo. NESDIS, NGDC-24, 19 pp.

Araújo, M.B. and Guisan, A. 2006. Five (or so) challenges for species distribution modeling. *J. Biogeogr.* **33**: 1677–1688.

Araújo, M.B. and New, M. 2007. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* **22**: 42–47.

Arrizabalaga, H., Dufour, F., Kell, L., Merino, G., Ibaibarriaga, L., Chust, G., Irigoien, X., Santiago, J., Murua, H., Fraile, I., Chifflet, M., Goikoetxea, N., Sagarminaga, Y., Aumont, O., Bopp, L., Herrera, M., Fromentin, J.-M., and Bonhomeau, S. 2014. Global habitat preferences of commercially valuable tuna. *Deep-Sea Res. II*: **113**: 102–112, doi:10.1016/j.dsr2.2014.07.00

Austin, M. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecol. Modell.* **200**: 1–19.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–71. NOAA NMFS Tech. Rep. 673, 103 pp.

Ballard, G., Jongsomjit, D., Veloz, S.D. and Ainley, D.G. 2012. Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. *Biol. Conserv.* **156**: 72–82.

Barry, S. and Elith, J, 2006. Error and uncertainty in habitat models. *J. Appl. Ecol.* **43**: 413–423.

Batten, S.D., Clarke, R.A., Flinkman, J., Hays, G.C., John, E.H., John, A.W.G., Jonas, T.J., Lindley, J.A., Stevens, D.P. and Walne, A.W. 2003. CPR sampling—the technical background, materials and methods, consistency and comparability. *Prog. Oceanogr.* **58**: 193–215.

Bearhop, S., Fiedler, W., Furness, R.W., Votier, S.C., Waldron, S., Newton, J., Bowen, G.J., Berthold, P. and Farnsworth, K. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science* **310**: 502–504.

Becker, B.H. and Beissinger, S.R. 2003. Scale-dependent habitat selection by a nearshore seabird, the Marbled Murrelet, in a highly dynamic upwelling system. *Mar. Ecol. Prog. Ser.* **256**: 243–255.

Becker, E.A., Forney, K.A., Ferguson, M.C., Foley, D.G., Smith, R.C., Barlow, J. and Redfern, J.V. 2010. Comparing California Current cetacean–habitat models developed using in situ and remotely sensed sea surface temperature data. *Mar. Ecol. Prog. Ser.* **413**: 163–183.

Bennison, A. and Jessopp, M. 2015. At-sea surveys confirm a North Atlantic biodiversity hotspot. *Bird Study* **62**: 262–266.

Benoit-Bird, K.J., Kuletz, K., Heppell, S., Jones, N. and Hoover, B. 2011. Active acoustic examination of the diving behavior of murres foraging on patchy prey. *Mar. Ecol. Prog. Ser.* **443**: 217–235.

Benoit-Bird, K.J., Battaile, B.C., Heppell, S.A., Hoover, B., Irons, D., Jones, N., Kuletz, K.J., Nordstrom, C.A., Paredes, R. and Suryan, R.M. 2013a. Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. *PloS One* **8**: doi.org/10.1371/journal.pone.0053348.

Benoit-Bird, K.J., Battaile, B.C., Nordstrom, C.A. and Trites, A.W. 2013b. Foraging behavior of northern fur seals closely matches the hierarchical patch scales of prey. *Mar. Ecol. Prog. Ser.* **479**: 283–302.

Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.L., Ganong, J.E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W. and Costa, D.P. 2011. Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**: 86–90.

Bombosch, A., Zitterbart, D.P., Van Opzeeland, I., Frickenhaus, S., Burkhardt, E., Wisz, M.S. and Boebel, O. 2014. Predictive habitat modeling of humpback (*Megaptera novaeangliae*) and Antarctic minke (*Balaenoptera bonaerensis*) whales in the Southern Ocean as a planning tool for seismic surveys. *Deep-Sea Res.* **91**: 101–114.

Breed, G.A., Bowen, W., McMillan, J. and Leonard, M.L. 2006. Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proc. R. Soc. Lond. B* **273**: 2319–2326.

Breiman, L. 2001. Random forests. *Machine Learning* **45**: 5–32.

Buckland, S., Anderson, D., Burnham, K., Laake, J., Borchers, D. and Thomas, L. 2001. Introduction to Distance Sampling Estimating Abundance of Biological Populations. Oxford University Press, Oxford.

Burger, A.E. and Shaffer, S.A. 2008. Perspectives in ornithology application of tracking and data-logging technology in research and conservation of seabirds. *Auk* **125**: 253–264.

Busby, J.R. 1986. A Biogeoclimatic analysis of *Nothofagus cunninghamii* (Hook.) Oerst. in southeastern Australia. *Austral. J. Ecol.* **11**: 1–7.

Busby, J.R. 1991. BIOCLIM – A bioclimate analysis and prediction system, pp. 64–68 *in* Nature Conservation: Cost Effective Biological Surveys and Data Analysis *edited by* C.R. Margules and M.P. Austin, CSIRO, Canberra, Australia.

Camphuysen, K., Shamoun-Baranes, J., Bouten, W. and Garthe, S. 2012. Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns. *Biol. Conserv*. **156**: 22–29.

Catry, P., Dias, M.P., Phillips, R.A. and Granadeiro, J.P. 2013. Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. *Ecology* **94**: 1230–1235.

Cayula, J.F. and Cornillon, P. 1992. Edge detection algorithm for SST images. *J. Atmos. Oceanic Technol*. **9**: 67–80.

Cayula, J.F. and Cornillon, P. 1995. Multi-image edge detection for SST images. *J. Atmos. Oceanic Technol*. **12**: 821–829.

Cayula, J.F. and Cornillon, P. 1996. Cloud detection from a sequence of SST images. *Rem. Sensing Environ*. **55**: 80–88.

Chivers, L.S., Lundy, M.G., Colhoun, K., Newton, S.F., Houghton, J.D. and Reid, N. 2013. Identifying optimal feeding habitat and proposed Marine Protected Areas (pMPAs) for the black-legged kittiwake (*Rissa tridactyla*) suggests a need for complementary management approaches. *Biol. Conserv*. **164**: 73–81.

Chust, G., Allen, J., Bopp, L., Schrum, C., Holt, J., Tsiaras, K., Zavatarelli, M., Chifflet, M., Cannaby, H. and Dadou, I. 2014. Biomass changes and trophic amplification of plankton in a warmer ocean. *Global Change Biol*. **20**: 2124–2139.

Connell, J.H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr*. **31**: 61–104.

Coyle, K.O., Hunt, G.L. Jr., Decker, M.B. and Weingartner, T.J. 1992. Murre foraging, epipelagic sound scattering and tidal advection over a shoal near St. George Island, Bering Sea. *Mar. Ecol. Prog. Ser*. **83**: 1–14.

Crawford, J.A., Frost, K.J., Quakenbush, L.T. and Whiting, A. 2012. Different habitat use strategies by subadult and adult ringed seals (*Phoca hispida*) in the Bering and Chukchi seas. *Polar Biol*. **35**: 241–255.

Dorman, J.G., Powell, T.M., Sydeman, W.J. and Bograd, S.J. 2011. Advection and starvation cause krill (*Euphausia pacifica*) decreases in 2005 Northern California coastal populations: Implications from a model study. *Geophys. Res. Lett*. **38**: L04605.

Elith, J. and Graham, C.H. 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography* **32**: 66–77.

Elith, J. and Leathwick, J.R. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst*. **40**: 677–697.

Elith, J., Kearney, M. and Phillips, S. 2010. The art of modelling range-shifting species. *Methods Ecol. Evol*. **1**: 330–342.

Etnoyer, P., Canny, D., Mate, B.R., Morgan, L.E., Ortega-Ortiz, J.G. and Nichols, W.J. 2006. Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. *Deep-Sea Res. II* **53**: 340–358.

Farley, J.H., Davis, T.L., Gunn, J.S., Clear, N.P. and Preece, A.L. 2007. Demographic patterns of southern bluefin tuna, *Thunnus maccoyii*, as inferred from direct age data. *Fish. Res*. **83**: 151–161.

Favorite, F. 1976. Oceanography of the subarctic Pacific region, 1960–1971. *Int. North Pac. Fish. Comm. Bull*. **31**: 1960–1971.

Fernández, P., Anderson, D.J., Sievert, P.R. and Huyvaert, K.P. 2001. Foraging destinations of three low-latitude albatross (*Phoebastria*) species. *J. Zool*. **254**: 391–404.

Forero, M.G., González-Solís, J., Hobson, K.A., Donázar, J.A., Bertellotti, M., Blanco, G. and Bortolotti, G.R. 2005. Stable isotopes reveal trophic segregation by sex and age in the southern giant petrel in two different food webs. *Mar. Ecol. Prog. Ser*. **296**: 107–113.

Forney, K.A., Ferguson, M.C., Becker, E.A., Fiedler, P.C., Redfern, J.V., Barlow, J., Vilchis, I.L. and Ballance, L.T. 2012. Habitat-based spatial models of cetacean density in the eastern Pacific Ocean. *Endangered Species Res*. **16**: 113–133.

Franklin, J. 2010. Mapping Species Distributions: Spatial Inference and Prediction. Cambridge University Press, Cambridge.

Franks, P.J. 2002. NPZ models of plankton dynamics: their construction, coupling to physics, and application. *J. Oceanogr*. **58**: 379–387.

Friedlaender, A.S., Hazen, E.L., Nowacek, D.P., Halpin, P.N., Ware, C., Weinrich, M.T., Hurst, T. and Wiley, D. 2009. Diel changes in humpback whale *Megaptera novaeangliae* feeding behavior in response to sand lance *Ammodytes* spp. behavior and distribution. *Mar. Ecol. Prog. Ser*. **395**: 91–100.

Fujioka, E., Kot, C.Y., Wallace, B.P., Best, B.D., Moxley, J., Cleary, J., Donnelly, B. and Halpin, P.N. 2014. Data integration for conservation: leveraging multiple data types to advance ecological assessments and habitat modeling for marine megavertebrates using OBIS–SEAMAP. *Ecol. Informatics* **20**: 13–26.

Fulton, E.A. 2010. Approaches to end-to-end ecosystem models. *J. Mar. Syst*. **81**: 171–183.

Gienapp, P., Teplitsky, C., Alho, J., Mills, J. and Merilä, J. 2008. Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecol*. **17**: 167–178.

González-Solís, J., Croxall, J.P. and Wood, A.G. 2000. Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. *Oikos* **90**: 390–398.

Grebmeier, J., Overland, J., Moore, S., Farley, E., Carmack, E., Cooper, L., Frey, K., Helle, J., McLaughlin, F. and McNutt, S. 2006. A major ecosystem shift in the northern Bering Sea. *Science* **311**: 1461–1464.

Grecian, W.J., Witt, M.J., Attrill, M.J., Bearhop, S., Godley, B.J., Grémillet, D., Hamer, K.C. and Votier, S.C. 2012. A novel projection technique to identify important at-sea areas for seabird conservation: An example using Northern Gannets breeding in the North East Atlantic. *Biol. Conserv*. **156**: 43–52.

Guisan, A. and Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. *Ecol. Modell*. **135**: 147–186.

Guy, T.J., Jennings, S.L., Suryan, R.M., Melvin, E.F., Bellman, M.A., Balance, L.T., Blackie, B.A., Croll, D.A., Deguchi, T., Geernaert, T.O., Henry, R.W., Hester, M., Hyrenbach, K.D., Jahncke, J., Kappes, M.A., Ozaki, K., Roletto, J., Sato, F., Sydeman, W.J. and Zamon, J.E. 2013. Overlap of North Pacific albatrosses with the U.S. west coast groundfish and shrimp fisheries. *Fish. Res.* **147**: 222–234.

Hastie, T.J. and Tibshirani, R.J. 1990. Generalized Additive Models. Chapman and Hall/CRC Press, Boca Raton, USA.

Hazen, E.L. and Johnston, D.W. 2010. Meridional patterns in the deep scattering layers and top predator distribution in the central equatorial Pacific. *Fish. Oceanogr.* **19**: 427–433.

Hazen, E.L., Friedlaender, A., Wiley, D., Thompson, M., Ware, C. and Weinrich, M. 2007. Three dimensional prey aggregations and fine scale foraging patterns of Humpback whales (*Megaptera novaengliae*) in Stellwagen Bank Marine Sanctuary, 2007 ICES Annual Science Conference, September 17–21, 2007, Helsinki, Finland.

Hazen, E.L., Friedlaender, A.S., Thompson, M.A., Ware, C.R., Weinrich, M.T., Halpin, P.N. and Wiley, D.N. 2009. Fine-scale prey aggregations and foraging ecology of humpback whales *Megaptera novaeangliae*. *Mar. Ecol. Prog. Ser.* **395**: 75–89.

Hazen, E.L., Nowacek, D.P., St. Laurent, L., Halpin, P.N. and Moretti, D.J. 2011. The relationship among oceanography, prey fields, and beaked whale foraging habitat in the Tongue of the Ocean. *PloS One* **6**: e19269.

Hazen, E.L., Maxwell, S.M., Bailey, H., Bograd, S.J., Hamann, M., Gaspar, P., Godley, B.J. and Shillinger, G.L. 2012. Ontogeny in marine tagging and tracking science: technologies and data gaps. *Mar. Ecol. Prog. Ser.* **457**: 221–240.

Hazen, E.L., Jorgensen, S., Rykaczewski, R.R., Bograd, S.J., Foley, D.G., Jonsen, I.D., Shaffer, S.A., Dunne, J.P., Costa, D.P. and Crowder, L.B. 2013a. Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Clim. Change* **3**: 234–238.

Hazen, E.L., Suryan, R.M., Santora, J.A., Bograd, S.J., Watanuki, Y. and Wilson, R.P. 2013b. Scales and mechanisms of marine hotspot formation. *Mar. Ecol. Prog. Ser.* **487**: 177–183.

Hijmans, R.J. and Elith, J. 2013. Species distribution modeling with R. R package version 0.8-11.

Hijmans, R.J., Phillips, S., Leathwick, J. and Elith, J. 2014. Species distribution modeling. R package version 1.0-5.

Hirzel, A., Hausser, J., Chessel, D. and Perrin, N. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* **83**: 2027–2036.

Hooker, S.K. 2008. Marine reserves and higher top predators, pp. 347–360 *in* Top Predators in Marine Ecosystems: Their Role in Monitoring and Management *edited by* I. Boyd, S. Wanless and C.J. Camphuysen, Cambridge University Press, Cambridge.

Howell, E.A. and Kobayashi, D.R. 2006. El Niño effects in the Palmyra Atoll region: oceanographic changes and bigeye tuna (*Thunnus obesus*) catch rate variability. *Fish. Oceanogr.* **15**: 477–489.

Huberty, C.J. 1994. Applied Discriminant Analysis. Wiley, New York.

Hughes, B.J., Martin, G.R., Giles, A.D. and Dickey, R.C. 2015. Identification of an assembly site for migratory and tropical seabirds in the South Atlantic Ocean. *Global Ecol. Conserv*. **4**: 38–47.

Humphries, G.R. and Huettmann, F. 2014. Putting models to a good use: a rapid assessment of Arctic seabird biodiversity indicates potential conflicts with shipping lanes and human activity. *Diversity Distrib*. **20**: 478–490.

Hunt, G.L. Jr., Harrison, N.M. and Piatt, J.F. 1993. Foraging ecology as related to the distribution of planktivorous auklets in the Bering Sea, pp. 18–26 *in* The Status, Ecology, and Conservation of Marine Birds of the North Pacific *edited by* K. Vermeer, K.T. Briggs, K.H. Morgan, D. Siegel-Causey, Canadian Wildlife Service, Ottawa.

Hunt, G.L. Jr., Kato, H. and McKinnell, S.M. (Eds.) 2000. Predation by Marine Birds and Mammals in the Subarctic North Pacific Ocean. PICES Sci. Rep. No. 14, 168 pp.

Hyrenbach, K.D. and Dotson, R.C. 2003. Assessing the susceptibility of female black-footed albatross (*Phoebastria nigripes*) to longline fisheries during their post-breeding dispersal: an integrated approach. *Biol. Conserv*. **112**: 391–404.

Hyrenbach, K.D., Forney, K.A. and Dayton, P.K. 2000. Marine protected areas and ocean basin management. *Aquat. Conserv. Mar. Freshwater Ecosyst*. **10**: 437–458.

Hyrenbach, K.D., Keiper, C., Allen, S.G., Ainley, D.G. and Anderson, D.J. 2006. Use of marine sanctuaries by far-ranging predators: commuting flights to the California Current System by breeding Hawaiian albatrosses. *Fish. Oceanogr*. **15**: 95–103.

Isojunno, S., Matthiopoulos, J. and Evans, P.G. 2011. Harbour porpoise habitat preferences: robust spatio-temporal inferences from opportunistic data. *Mar. Ecol. Prog. Ser*. **448**: 155–170.

James, G., Witten, D., Hastie, T. and Tibshirani, R. 2013. An Introduction to Statistical Learning: With Applications in R. Springer, New York.

Johnson, J.B. and Omland, K.S. 2004. Model selection in ecology and evolution. *Trends Ecol. Evol*. **19**: 101–108.

Kanaji, Y., Okazaki, M., Kishiro, T. and Miyashita, T. 2015. Estimation of habitat suitability for the southern form of the short-finned pilot whale (*Globicephala macrorhynchus*) in the North Pacific. *Fish. Oceanogr*. **24**: 14–25.

Kappes, M.A., Shaffer, S.A., Tremblay, Y., Foley, D.G., Palacios, D.M., Robinson, P.W., Bograd, S.J. and Costa, D.P. 2010. Hawaiian albatrosses track interannual variability of marine habitats in the North Pacific. *Prog. Oceanogr*. **86**: 246–260.

Kawai, H. 1969. Statistical estimation of isotherms indicative of the Kuroshio axis. *Deep-Sea Res*. **16**: 109–115.

Kishi, M.J., Kashiwai, M., Ware, D.M., Megrey, B.A., Eslinger, D.L., Werner, F.E., Noguchi-Aita, M., Azumaya, T., Fujii, M. and Hashimoto, S. 2007. NEMURO—a lower trophic level model for the North Pacific marine ecosystem. *Ecol. Modell*. **202**: 12–25.

Klemas, V. 2013. Fisheries applications of remote sensing: an overview. *Fish. Res*. **148**: 124–136.

Ladd, C. and Stabeno, P.J. 2012. Stratification on the Eastern Bering Sea shelf revisited. *Deep-Sea Res. II* **65**: 72–83.

Laidre, K.L., Heide-Jørgensen, M.P., Heagerty, P., Cossio, A., Bergström, B. and Simon, M. 2010. Spatial associations between large baleen whales and their prey in West Greenland. *Mar. Ecol. Prog. Ser*. **402**: 269–284.

Lewis, S., Schreiber, E., Daunt, F., Schenk, G.A., Orr, K., Adams, A., Wanless, S. and Hamer, K.C. 2005. Sex-specific foraging behaviour in tropical boobies: does size matter? *Ibis* **147**: 408–414.

Louzao, M., Hyrenbach, K.D., Arcos, J.M., Abello, P., Gil de Sola L. and Oro, D. 2006. Oceanographic habitat of an endangered Mediterranean procellariiform: Implications for marine protected areas. *Ecol. Appl*. **16**: 1683–1695.

Louzao, M., Becares, J., Rodriguez, B., Hyrenbach, K.D., Ruiz, A. and Arcos, J.M. 2009. Combining ship-based surveys and tracking data to identify key marine areas for seabirds. *Mar. Ecol. Prog. Ser*. **391**: 183–197.

Macleod, K., Fairbairns, R., Gill, A., Fairbairns, B., Gordon, J., Blair-Myers, C. and Parsons, E.C. 2004. Seasonal distribution of minke whales *Balaenoptera acutorostrata* in relation to physiography and prey off the Isle of Mull, Scotland. *Mar. Ecol. Prog. Ser*. **277**: 263–274.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. and Thuiller, W. 2009. Evaluation of consensus methods in predictive species distribution modeling. *Diversity Distrib*. **15**: 59–69.

Mehlum, F., Klusek, Z. and Decker, M.B. 1999. Scale dependent correlations between the abundance of Brünnich's guillemots and their prey. *J. Animal Ecol*. **68**: 60–72.

Mizuno, K. and White, W.B. 1983. Annual and interannual variability in the Kuroshio current system. *J. Phys. Oceanogr*. **13**: 1847–1867.

Moore, S. and Huntington, H. 2008. Arctic marine mammals and climate change: impacts and resilience. *Ecol. Appl*. **18**: 157–165.

Mugo, R., Saitoh, S.-I., Nihira, A. and Kuroyama, T. 2010. Habitat characteristics of skipjack tuna (*Katsuwonus pelamis*) in the western North Pacific: a remote sensing perspective. *Fish. Oceanogr*. **19**: 382–396.

Mugo, R.M., Saitoh, S.I., Takahashi, F., Nihira, A. and Kuroyama, T. 2014. Evaluating the role of fronts in habitat overlaps between cold and warm water species in the western North Pacific: A proof of concept. *Deep-Sea Res. II* **107**: 29–39.

Mundry, R. and Nunn, C.L. 2009. Stepwise model fitting and statistical inference: Turning noise into signal pollution. *Amer. Naturalist* **173**: 119–123.

Murase, H., Matsuoka, K., Ichii, T. and Nishiwaki, S. 2002. Relationship between the distribution of euphausiids and baleen whales in the Antarctic (35°E–145°W). *Polar Biol.* **25**: 135–145.

Murase, H., Kitakado, T., Kanaji, Y., Sasaki, H., Mitani, Y., Matsuoka, K., Okazaki, M. and Kanda, N. 2014. Application of habitat models to highly mobile marine animals – Cetaceans in the North Pacific as case studies. Invited presentation in Topic Session S2, PICES-2014, Yeosu, Korea, October, 16–26, 2014.

Nishizawa, B., Ochi, D., Minami, H., Yokawa, K., Saitoh, S.-I. and Watanuki, Y. 2015. Habitats of two albatross species during the non-breeding season in the North Pacific Transition Zone. *Mar. Biol.* **162**: 743–752.

Oppel, S., Meirinho, A., Ramírez, I., Gardner, B., O'Connell, A.F., Miller, P.I. and Louzao, M. 2012. Comparison of five modeling techniques to predict the spatial distribution and abundance of seabirds. *Biol. Conserv.* **156**: 94–104.

Panigada, S., Zanardelli, M., MacKenzie, M., Donovan, C., Mélin, F. and Hammond, P.S. 2008. Modeling habitat preferences for fin whales and striped dolphins in the Pelagos Sanctuary (Western Mediterranean Sea) with physiographic and remote sensing variables. *Rem. Sensing Environ.* **112**: 3400–3412.

Paredes, R., Harding, A.M.A., Irons, D.B., Roby, D.D., Suryan, R.M., Orben, R.A., Renner, H., Young, R. and Kitaysky, A. 2012. Proximity to multiple foraging habitats enhances seabirds' resilience to local food shortages. *Mar. Ecol. Prog. Ser.* **471**: 253–269.

Paredes, R., Orben, R.A., Suryan, R.M., Irons, D.B., Roby, D.D., Harding, A.M.A., Young, R.C., Benoit-Bird, K., Ladd, C., Renner, H., Heppell, S., Phillips, R.A. and Kitaysky, A. 2014. Foraging responses of black-legged kittiwakes to prolonged food-shortages around colonies on the Bering Sea Shelf. *PloS One* **9**: e92520.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**: 637–669.

Patterson, B.D. 1999. Contingency and determinism in mammalian biogeography: the role of history. *J. Mammal.* **80**: 345–360.

Perrow, M.R., Harwood, A.J.P., Skeate, E.R., Praca, E. and Eglington, S.M. 2015. Use of multiple data sources and analytical approaches to derive a marine protected area for a breeding seabird. *Biol. Conserv.* **191**: 729–738.

Peterson, A.T. 2005. Predicting potential geographic distributions of invading species. *Current Sci.* **89**: 9–9.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. and Araújo, M.B. 2011. Ecological Niches and Geographic Distributions. Princeton University Press, UK.

Phillips, R., Silk, J., Phalan, B., Catry, P. and Croxall, J. 2004. Seasonal sexual segregation in two Thalassarche albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc. R. Soc. Lond. B* **271**: 1283–1291.

Phillips, S.J., Anderson, R.P. and Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**: 231–259.

Phillips, S.J. and Elith, J. 2010. POC plots: calibrating species distribution models with presence-only data. *Ecology* **91**: 2476–2484.

Pinaud, D. and Weimerskirch, H. 2005. Scale-dependent habitat use in a long-ranging central place predator. *J. Anim. Ecol.* **74**: 852–863.

Potts, J.M. and Elith, J. 2006. Comparing species abundance models. *Ecol. Modell.* **199**: 153–163.

Praca, E., Gannier, A., Das, K. and Laran, S. 2009. Modeling the habitat suitability of cetaceans: Example of the sperm whale in the northwestern Mediterranean Sea. *Deep-Sea Res.* **56**: 648–657.

Priddel, D., Carlile, N., Portelli, D., Kim, Y. and O'Neill, L. 2014. Pelagic distribution of Gould's Petrel *Pterodroma leucoptera*: linking ship-based and beached bird sightings with remote tracking data. *Emu* **114**: 360–370.

Raymond, B., Lea, M.A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J.B., Cottin, M., Emmerson, L., Gales, N., Gales, R. and Goldsworthy, S.D. 2015. Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography* **38**: 121–129.

Redfern, J.V., Ferguson, M.C., Becker, E.A., Hyrenbach, K.D., Good, C., Barlow, J., Kaschner, K., Baumgartner, M.F., Forney, K.A., Ballance, L.T., Fauchald, P., Halpin, P., Hamazaki, T., Pershing, A.J., Qian, S.S., Read, A., Reilly, S.B., Torres, L. and Werner, F. 2006. Techniques for cetacean–habitat modeling. *Mar. Ecol. Prog. Ser.* **310**: 271–295.

Renner, M., Parrish, J.K., Piatt, J.F., Kuletz, K.J., Edwards, A.E. and Hunt, G.L. Jr. 2013. Modeled distribution and abundance of a pelagic seabird reveal trends in relation to fisheries. *Mar. Ecol. Prog. Ser.* **484**: 259–277.

Robinson, L., Hobday, A., Possingham, H. and Richardson, A. 2015. Trailing edges projected to move faster than leading edges for large pelagic fish habitats under climate change. *Deep-Sea Res II* **113**: 225–234.

Rooper, C., Zimmermann, M., Sigler, M. and Hoff, J. 2014. Distribution modeling for deep-sea corals and sponges in Alaska. Presentation in Topic Session S2, PICES-2014, Yeosu, Korea, October 16–26, 2014.

Royle, J.A. and Dorazio, R.M. 2008. Hierarchical Modeling and Inference in Ecology. Academic Press, New York.

Ruckstuhl, K. and Neuhaus, P. 2005. Sexual Segregation in Vertebrates. Cambridge University Press, Cambridge.

Rutz, C. and Hays, G.C. 2009. New frontiers in biologging science. *Biol. Lett.* **5**: 289–292.

Santora, J.A., Ralston, S. and Sydeman, W.J. 2011. Spatial organization of krill and seabirds in the central California Current. *ICES J. Mar. Sci.* **68**: 1391–1402.

Santora, J.A., Sydeman, W.J., Schroeder, I.D., Reiss, C.S., Wells, B.K., Field, J.C., Cossio, A.M. and Loeb, V.J. 2012. Krill space: a comparative assessment of mesoscale structuring in polar and temperate marine ecosystems. *ICES J. Mar. Sci.* **69**: doi:10.1093/icesjms/fss048.

Santos, A.M.P. 2000. Fisheries oceanography using satellite and airborne remote sensing methods: a review. *Fish. Res*. **49**: 1–20.

Sasaki, H., Murase, H., Kiwada, H., Matsuoka, K., Mitani, Y. and Saitoh, S.-I. 2013. Habitat differentiation between sei (*Balaenoptera borealis*) and Bryde's whales (*B. brydei*) in the western North Pacific. *Fish. Oceanogr*. **22**: 496–508.

Sasaki, H., Matsuno, K., Fujiwara, A., Onuka, M., Yamaguchi, A., Ueno, H., Watanuki, Y. and Kikuchi, T. 2016. Distribution of Arctic and Pacific copepods and their habitat in the northern Bering Sea and Chukchi seas. *Biogeosciences* **13**: 4555–4567.

Scales, K.L., Miller, P.I., Hawkes, L.A., Ingram, S.N., Sims, D.W. and Votier, S.C. 2014. On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *J. Appl. Ecol*. **51**: 1575–1583.

Schneider, D.C. and Piatt, J.F. 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. *Mar. Ecol. Prog. Ser*. **32**: 237–246.

Sebastián-González, E., Sánchez-Zapata, J.A., Botella, F. and Ovaskainen, O. 2010. Testing the heterospecific attraction hypothesis with time-series data on species co-occurrence. *Proc. R. Soc. Lond. B* **277**: 2983–2990.

Silva, T., Gislason, A., Licandro, P., Marteinsdóttir, G., Ferreira, A.S.A., Gudmundsson, K. and Astthorsson, O.S. 2014. Long-term changes of euphausiids in shelf and oceanic habitats southwest, south and southeast of Iceland. *J. Plankton Res*. **36**: 1262–1278.

Sims, D.W. 2005. Differences in habitat selection and reproductive strategies of male and female sharks, pp. 127–147 *in* Sexual Segregation in Vertebrates: Ecology of the Two Sexes *edited by* K.E. Ruckstuhl and P. Neuhaus, Cambridge University Press, Cambridge.

Skov, H., Humphreys, E., Garthe, S., Geitner, K., Grémillet, D., Hamer, K.C., Hennicke, J., Parner, H. and Wanless, S. 2008. Application of habitat suitability modelling to tracking data of marine animals as a means of analyzing their feeding habitats. *Ecol. Modell*. **212**: 504–512.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett*. **10**: 1115–1123.

Spear, L.B., Nur, N. and Ainley, D.G. 1992. Estimating absolute densities of flying seabirds using analyses of relative movement. *Auk* **109**: 385–389.

Stockwell, D. and Peters, D. 1999. The GARP modeling system: problems and solutions to automated spatial prediction. *Int. J. Geogr. Info. Syst*. **13**: 143–158.

Stoner, A.W., Manderson, J.P. and Pessutti, J.P. 2001. Spatially explicit analysis of estuarine habitat for juvenile winter flounder: combining generalized additive models and geographic information systems. *Mar. Ecol. Prog. Ser*. **213**: 253–271.

Su, N.J., Sun, C.L., Punt, A.E., Yeh, S.Z. and DiNardo, G. 2011. Modelling the impacts of environmental variation on the distribution of blue marlin, *Makaira nigricans*, in the Pacific Ocean. *ICES J. Mar. Sci*. **68**: 1072–1080.

Sundblad, G., Härmä, M., Lappalainen, A., Urho, L. and Bergström, U. 2009. Transferability of predictive fish distribution models in two coastal systems. *Estuar. Coast. Shelf Sci.* **83**: 90–96.

Suryan, R.M., Sato, F., Balogh, G.R., Hyrenbach, D.K., Sievert, P.R. and Ozaki, K. 2006. Foraging destinations and marine habitat use of short-tailed albatrosses: a multi-scale approach using first-passage time analysis. *Deep-Sea Res II* **53**: 370−386.

Syamsuddin, M.L., Saitoh, S.-I., Hirawake, T., Bachri, S. and Harto, A.B. 2013. Effects of El Niño–Southern Oscillation events on catches of Bigeye Tuna (*Thunnus obesus*) in the eastern Indian Ocean off Java. *Fish. Bull.* **111**: 175–188.

Sydeman, W.J., Brodeur, R., Grimes, C.B., Bychkov, A.S. and McKinnell, S. 2006. Marine habitat "hotspots" and their use by migratory species and top predators in the North Pacific Ocean. *Deep-Sea Res II* **53**: 247–249.

Tasker, M.L., Jones, P.H., Dixon, T. and Blake, B.F. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *Auk* **101**: 567–577.

Thiers, L., Louzao, M., Ridoux, V., Le Corre, M., Jaquemet, S. and Weimerskirch, H. 2014. Combining methods to describe important marine habitats for top predators: Application to identify biological hotspots in tropical waters. *PLoS One* **9**: e115057.

Thorson, J.T., Scheuerell, M.D., Shelton, A.O., See, K.E., Skaug, H.J. and Kristensen, K. 2015a. Spatial factor analysis: a new tool for estimating joint species distributions and correlations in species range. *Methods Ecol. Evol.* **6**: 627–637.

Thorson, J.T., Skaug, H.J., Kristensen, K., Shelton, A.O., Ward, E.J., Harms, J.H. and Benante, J.A. 2015b. The importance of spatial models for estimating the strength of density dependence. *Ecology* **96**: 1202–1212.

Thuiller, W., Lafourcade, B., Engler, R. and Araújo, M.B. 2009. BIOMOD–a platform for ensemble forecasting of species distributions. *Ecography* **32**: 369–373.

Torres, L.G., Read, A.J. and Halpin, P. 2008. Fine-scale habitat modeling of a top marine predator: do prey data improve predictive capacity? *Ecol. Appl.* **18**: 1702–1717.

Torres, L.G., Sutton, P.J., Thompson, D.R., Delord, K., Weimerskirch, H., Sagar, P.M., Sommer, E., Dilley, B.J., Ryan, P.G. and Phillips, R.A. 2015. Poor transferability of species distribution models for a pelagic predator, the grey petrel, indicates contrasting habitat preferences across ocean basins. *PloS One* **10**: e0120014.

VanDerWal, J., Shoo, L.P., Graham, C. and Williams, S.E. 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecol. Modell.* **220**: 589–594.

Visser, M.E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc. R. Soc. Lond. B* **275**: 649–659.

Ward, E.J., Jannot, J.E., Lee, Y.-W., Ono, K., Shelton, A.O. and Thorson, J.T. 2015. Using spatiotemporal species distribution models to identify temporally evolving hotspots of species co-occurrence. *Ecol. Appl.* **25**: 2198–2209.

Wearmouth, V.J. and Sims, D.W. 2008. Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Adv. Mar. Biol.* **54**: 107–170.

Weimerskirch, H., Pinaud, D., Pawlowski, F. and Bost, C.A. 2007. Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *Amer. Naturalist* **170**: 734–743.

Weimerskirch, H., Louzao, M., de Grissac, S. and Delord, K. 2012. Changes in wind pattern alter albatross distribution and life-history traits. *Science* **335**: 211–214.

Whitehead, H. and Jonsen, I.D. 2013. Inferring animal densities from tracking data using Markov chains. *Plos One* **8**: e60901.

Willis-Norton, E., Hazen, E.L., Fossette, S., Shillinger, G., Rykaczewski, R.R., Foley, D.G., Dunne, J.P. and Bograd, S.J. 2015. Climate change impacts on leatherback turtle pelagic habitat in the Southeast Pacific. *Deep-Sea Res. II* **113**: 260–267.

Wingfield, D.K., Peckham, S.H., Foley, D.G., Palacios, D.M., Lavaniegos, B.E., Durazo, R., Nichols, W.J., Croll, D.A. and Bograd, S.J. 2011. The making of a productivity hotspot in the coastal ocean. *PloS One* **6**: e27874.

Wisz, M.S. and Guisan, A. 2009. Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. *BMC Ecology* **9**: doi: 10.1186/1472-6785-9-8.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.A. and Guisan, A. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modeling. *Biol. Rev.* **88**: 15–30.

Wood, S. 2006. Generalized Additive Models: An Introduction with R. CRC Press, Boca Raton, USA.

Worm, B., Lotze, H.K. and Myers, R.A. 2003. Predator diversity hotspots in the blue ocean. *Proc. Natl. Acad. Sci.* **100**: 9884–9888.

Yamamoto, T., Takahashi, A., Oka, N., Iida, T., Katsumata, N., Sato, K. and Trathan, P.N. 2011. Foraging areas of streaked shearwaters in relation to seasonal changes in the marine environment of the Northwestern Pacific: inter-colony and sex-related differences. *Mar. Ecol. Prog. Ser.* **424**: 191–204.

Yamamoto, T., Watanuki, Y., Hazen, E.L., Nishizawa, B., Sasaki, H. and Takahashi, A. 2015. Statistical integration of tracking and vessel survey data to incorporate life history differences in habitat models. *Ecol. Appl.* **25**: 2349–2406.

Yen, P.P., Sydeman, W.J. and Hyrenbach, K.D. 2004. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. *J. Mar. Syst.* **50**: 79–99.

Zarauz, L., Irigoien, X., Urtizberea, A. and Gonzalez, M. 2007. Mapping plankton distribution in the Bay of Biscay during three consecutive spring surveys. *Mar. Ecol. Prog. Ser.* **345**: 27–39.

Zarauz, L., Irigoien, X. and Fernandes, J.A. 2008. Modeling the influence of abiotic and biotic factors on plankton distribution in the Bay of Biscay, during three consecutive years (2004–06). *J. Plankton Res.* **30**: 857–872.

Zhang, X., Saitoh, S.I., Hirawake, T., Nakada, S., Koyamada, K., Awaji, T., Ishikawa, Y. and Igarashi, H. 2013. An attempt of dissemination of potential fishing zones prediction map of Japanese common squid in the coastal water, southwestern Hokkaido, Japan. *Proc. Asia-Pacific Advanced Network* **36**: 132–141.

Zuur, A., Ieno, E.N. and Smith, G.M. 2007. Analysing Ecological Data. Springer Science + Business Media LLC, New York.

Zuur, A.F., Ieno, E.N., Walker. N.J., Saveliev, A.A. and Smith, G.M. 2009a. GLM and GAM for count data, *in* Mixed Effects Models and Extensions in Ecology with R. Springer, New York, pp. 209–243.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. and Smith, G.M. 2009b. Mixed effects modeling for nested data, *in* Mixed Effects Models and Extensions in Ecology with R, Springer, New York, pp. 101–142.

Zydelis, R., Lewison, R.L., Shaffer, S.A., Moore, J.E., Boustany, A.M., Roberts, J.J., Sims, M., Dunn, D.C., Best, B.D., Tremblay, Y., Kappes, M.A., Halpin, P.N., Costa, D.P. and Crowder, L.B. 2011. Dynamic habitat models: using telemetry data to project fisheries bycatch. *Proc. R. Soc. Lond. B* **278**: 3191–3200.

Appendix
PICES Annual Meeting Topic Session and Workshop Summaries Linked to the Goals of the Spatial Ecology Project (2012–2014)

PICES-2012, Hiroshima, Japan
October 12–21, 2012

BIO/MEQ Topic Session (S6)
Environmental contaminants in marine ecosystems: Seabirds and marine mammals as sentinels of ecosystem health

Co-sponsored by: *JSPS*

Co-convenors: *Peter Ross (Canada), Hideshige Takada (Japan) and Yutaka Watanuki (Japan)*

Background

Urban and industrial developments in the world's coastal regions have led to the release of a large number of pollutants (heavy metals, POPs, plastics, oils, radioactive substances) into the marine environment. In some cases, these have detrimental effects on variety of marine resources in coastal and offshore areas. It is increasingly important to identify sources, subsequent transport through marine physical systems and resulting spatial patterns of these anthropogenic stressors. Compared to river-lake systems, knowledge of anthropogenic stressors in marine systems is less understood due to difficulties with detection over wide areas and in offshore regions. As top predators, such as many marine mammals and seabirds, bio-magnify some of these pollutants, these organisms can be used as bio-indicators of coastal, marine and/or food web contamination. The utility of these 'sentinels' was discussed at the PICES-2011 MEQ Workshop. This session: 1) identified spatial patterns and geographic areas of concern (high concentrations) of pollutants or other stressors in the PICES region using bio-indicator species, 2) examined mechanisms of transport, and ultimate disposition, of contaminants in marine ecosystems, and 3) discussed health risks for certain predators and human consumers. Review papers, case studies, and innovative methods papers on anthropogenic stressors in marine predators were invited, as well as papers that distinguished between the effects of natural and anthropogenic stressors. In particular, studies linking predator habitat use with spatial aspects of stressors in the environment and in predators were encouraged.

Summary of presentations

Ten talks (5 from Japan, 2 from Canada, 1 from Korea, 1 from Russia, and 1 from UK,) and 4 posters (all from Russia) were given. Spatial patterns and interannual changes in POPs (Persistent Organic Pollutants), including PCBs, DDTs, HCHs, and PBDs in marine birds and some terrestrial birds were presented, and their usefulness as bio-indicators was discussed. A common theme among many of the presentations was the need to consider age and the trophic level as important factors when evaluating and comparing contaminants levels among species or populations. Case studies of monitoring marine debris ashore and POPs in plastic pellets were also presented. Forty to 50 people, including bird and mammal researchers, geochemists, and biochemists attended the session and gave useful discussion. The co-convenors discussed the potential for a review paper on the usefulness and limitation of marine birds and mammals as indicators of marine pollutants, and the spatial patterns of POPs shown by them in the PICES region.

List of papers

Oral presentations
Andy Sweetman, John Crosse, Richard Shore, Gloria Pereira and Kevin Jones (Invited)
Long term trends in PBDE concentrations in gannet (*Morus bassanus*) eggs from two UK colonies

Rei Yamashita, Hideshige Takada, Mai Miyazaki, Takashi Yamamoto, Akinori Takahashi, Maki Yamamoto, Philip N. Trathan and Yutaka Watanuki (Invited)
Persistent organic pollutants (POPs) in preen gland oils from streaked shearwaters reflect exposure in overwintering areas

Sang Hee Hong, Gi Myung Han, Won Joon Shim, Sung Yong Ha and Nak Won Heo
Concentrations and profiles of persistent organic pollutants (POPs) in birds collected from an urbanized coastal region of South Korea

Annamalai Subramanian and Shinsuke Tanabe
Developing Asian countries as sources of pollutants to the Asia-Pacific region

John E. Elliott, Kyle H. Elliott, Melanie F. Guigueno, Laurie K. Wilson, Sandi Lee and Abde Idrissi (Invited)
Seabirds are indicators of persistent contaminants in the marine environment: Examples from the Pacific Coast of Canada

Peter S. Ross
Persistent Organic Pollutants (POPs) in marine mammals: Harmless chemicals or lingering poisons?

Vasiliy Yu. Tsygankov, Margarita D. Boyarova, Anna A. Lukashkina, Peter A. Tyupeleev, Ilya A. Shcherbakov, Yuri V. Prikhodko and Olga N. Lukyanova
Marine mammals as bioindicators of persistent toxic substance (PTS) contamination in Russian Subarctic marine ecosystems

Atsuo Ito, Rei Yamashita, Hideshige Takada, Takashi Yamamoto, Kozue Shiomi, Carlos Zavalaga, Takuya Abe, Shinichi Watanabe, Maki Yamamoto, Katsufumi Sato, Hiromi Kohno, Ken Yoda, Tomohiko Iida and Yutaka Watanuki
POPs in the preen gland oil of streaked shearwaters breeding on the islands in Japan reflect marine pollution in western North Pacific

Atsuhiko Isobe, Shin'ichiro Kako and Etsuko Nakashima (Invited)
Marine/beach plastic litter as a transport vector of pollutants

Kosuke Tanaka, Hideshige Takada, Rei Yamashita and Yutaka Watanuki (Invited)
Marine plastics: Monitoring matrix for persistent organic pollutants (POPs) and carrier of POPs to seabirds

Poster presentations

Andrey S. Neroda, Vasily F. Mishukov, Vladimir A. Goryachev, Denis V. Simonenkov and Anna A. Goncharova
Radioactive isotopes in atmospheric aerosols over Russia and the Sea of Japan following the nuclear accident at Fukushima nr. 1 Daiichi nuclear power station in March 2011

Tatiana Chizhova, Pavel Tishchenko, Liubov Kondratieva and Takuya Kawanishi
Polycyclic aromatic hydrocarbon (PAH) distribution in the Amur River estuary

Yulia Koudryashova, Natalia Prokuda, Natalia Khodorenko, Tatiana Chizhova and Pavel Tishchenko
PAHs in sediments of rivers of the Primorsky Region, Far East of Russia

Mikhail V. Simokon
Ecological risk evaluation of metals in the coastal areas of Peter the Great Bay, Japan/East Sea

PICES-2013, Nanaimo, Canada
October 11–20, 2013

BIO Workshop (W3)
Marine bird and mammal spatial ecology

Co-Convenors: *Robert Suryan (USA), William Sydeman (USA), Yutaka Watanuki (Japan) and Rolf Ream (USA)**
_____

* Rolf Ream was unable to attend PICES-2013 due to the U.S. government partial shutdown.

Invited Speaker: *Martin Renner (Tern Again Consulting, USA)*

Background

Marine birds and mammals (MBMs) are highly mobile, yet relatively easily observed and tracked to determine their spatial distribution throughout the North Pacific Ocean. They are important marine top predators that consume substantial amounts of zooplankton and fish, and are susceptible to changes in marine food web structure, productivity, and a variety of anthropogenic impacts. Therefore, MBMs are highly visible sentinels of ecosystem health and its change. To incorporate MBMs into ecosystem based management and meet objectives of FUTURE, the PICES Advisory Panel on MBM (AP-MBM) proposed to focus on MBM spatial ecology and conservation as a priority topic for their 2012–2014 activities.

Over the past several decades, a wide variety of research programs have collected observational and tracking data of MBMs throughout the North Pacific. Portions of these data have been compiled into large databases, such as the North Pacific Pelagic Seabird Database (NPPSD). Other data sets, however, still need to be integrated for more complete coverage of the PICES regions. Holding the proposed workshop is an important first step to compiling and integrating these massive datasets. In February 2012, we held discussions with several of the main data holders/contributors and they expressed broad support for this effort. Workshop invitees were contacted over the past year which included data holders, spatial analysis experts, and end product users.

Summary of the workshop

There were 29 attendees at the workshop (Table 1). The structure of the workshop was organized to address three main objectives: 1) Datasets, 2) Applications, and 3) Integration.

1. Datasets

The first four presentations highlighted examples of existing databases that include data representing large spatial scales (100,000s km^2) spanning multiple decades. Examples of these large databases include the NPPSD that contains over 370,571 records (3 km transect segments) covering 282,035 km^2 spanning 1974–2012. Total counts of organisms include over 17 million seabirds and 241 thousand marine mammals. Spatial coverage from this dataset is best within or adjacent to the Exclusive Economic Zones of Pacific Rim countries where the majority of cruises have occurred. Other datasets include additional regions such as the Eastern Tropical Pacific. Regions of limited vessel survey coverage include the low to mid latitude central and Western Pacific. Individual tracking data from marine birds and mammals will help to fill some of these gaps, as well as provide greater temporal coverage in some instances, for example during winter.

2. Applications

Three presentations provided examples of individual studies describing how distributional patterns of birds (Cassin's auklets) and whales (minke, sei, and Bryde's) can change over time, affecting the types of prey that they consume or in response to changing prey distribution and abundance. A fourth presentation used a larger animal tracking dataset from the Tagging of Pacific Predators (TOPP) program and a cumulative human impact assessment to identify areas of highest cumulative impact. Interestingly, they found that marine sanctuaries were hotspots for use and risk. It was also discussed that birds and mammals do not always co-occur in the areas of greatest prey abundance since their relationship with prey is typically non-linear, only requiring enough to satisfy their immediate needs.

3. Integration

Three of the four presentations described regional studies in the Western Pacific, Bering Sea, and California Current where both vessel-based survey data and individual tracking data exist for a model species. One study where only a single vessel cruise through a region in a given year showed how restrictive vessel survey data can be relative to individual tracking. At the broad scale, there was some coherence in distribution where the ship and bird tracks overlapped. However, habitat models from vessel- and tracking-based data were quite different. In other regions, longer time series of repeated vessel-based surveys demonstrate how powerful these datasets are relative to the often shorter-duration tacking datasets. Presenters agreed that survey and tracking data are very different, yet highly complementary, especially for filling data gaps in perceived species habitat use and seasonal occurrence. A fourth presentation described an approach using tracking and environmental data to model habitat use, producing a density grid that shows similar patterns to density estimates from vessel surveys in regions where vessel and tracking data overlap.

Decisions from the workshop

1. Datasets

Compiling all available vessel survey and tracking data into single databases for each data type is much needed. This is, however, an enormous undertaking. The NPPSD represents one such effort occurring over many years, yet does not include tracking data. Although there are still many datasets that have yet to be included in this database, the database is extremely comprehensive and represents the best single data source for many species of marine birds and mammals in the North Pacific. The most comprehensive database for individual tracking data is the Tagging of Pacific Predators, but this database does not include data from multiple independent programs over many years, like the NPPSD. It was agreed that our group's effort moving forward should be focused on compiling a list of existing datasets, their temporal and spatial extent, and contact information for the data holder. This could be used in future efforts to secure much needed funding for integrating these data into central databases and proposing additional studies to fill the spatial or temporal gaps in the data.

2. Applications

Comprehensive distribution and abundance maps for the North Pacific are extremely valuable for many scientific and conservation efforts. In addition, it was noted that such accurate and comprehensive species abundance and distribution maps for marine birds and mammals are unique among marine organisms owing to the relative ease of collecting these data. Furthermore, because broad scale distribution of micronekton is poorly understood, the distribution and intensity of MBM aggregations may be valuable indicators of key micronekton. From the AP-MBM perspective, the first application of these data layers is to revisit prey consumption estimates for North Pacific marine birds and mammals (*e.g.*, Hunt *et al.*) With more comprehensive distribution and diet information, the spatially explicit prey consumption estimates will be greatly improved over previous efforts, which have received wide usage to date, indicating the value and demand for these efforts.

Additional uses for comprehensive marine bird and mammal distribution data include calibrating outputs from regional and basin scale ocean models and projecting future impacts of changing marine ecosystems. This is particularly relevant for identifying conservation hotspots and spatial distribution of contaminants in upper trophic level consumers (*e.g.*, Ross, Watanuki *et al.*).

An important consideration is to produce distribution data layers in metrics that are most relevant to modelers and other end product users, especially within the PICES community (*e.g.*, FUTURE).

3. Integration

The group was unanimous in the conclusion that the two types of data are highly complementary, but for various sampling and empirical reasons it is not prudent to integrate vessel survey and tracking data outright, either quantitatively or qualitatively. Instead, the two types of data should first be used independently to create habitat use models, then secondarily combined in habitat use models to create a single predicted distribution (or density) layer from the two datasets.

Report outline and section leads:
The report documenting AP-MBM's three-year "spatial ecology" effort will follow the outline of the workshop with the respective section leads.
Introduction: R. Suryan (lead), B. Sydeman, R. Ream, Y. Watanuki
Chapter 1: Datasets, R. Ream (lead), R. Suryan, with contributions from many others
Chapter 2: Integration, R. Suryan (lead), Y. Watanuki, E. Hazen, M. Renner
Chapter 3: Habitat Modeling, Y. Watanuki (lead), J. Santora, R. Suryan, E. Hazen, M. Renner
Chapter 4: Uses, W. Sydeman (lead), A. Trites

Acknowledgements: We thank the presenters for taking the time to summarize their data for presentation, travel to attend the workshop, and contribute to a fruitful discussion. We would especially like to thank those individuals who contributed additional time to analyze new datasets specifically for this workshop. We thank BIO, Science Board and the PICES Secretariat for supporting the workshop and for providing travel for our invited speaker.

Table 1   Workshop W3 attendees.

Sonia Batten	Canada
Douglas Bertram	Canada
Bryan Black	USA
Carrie Eischens	USA
Jerome Fiechter	USA
Marisol Garcia-Reyes	USA
Tracee Geernaert	USA
Kaoru Hattori	Japan
Elliott L Hazen	USA
George Hunt	USA
Trevor Joyce	USA
Ken Morgan	Canada
Chad Nordstrom	Canada
Patrick O'Hara	Canada
Mayuko Otsuki	Japan
Corinne Pomerleau	Canada
Martin Renner	USA

Tamara Russell	Canada
Ryan Rykaczewski	USA
Hiroaki Saito	Japan
Jarrod Santora	USA
Hiroko Sasaki	Japan
Huamei Shao	Japan
Melanie Smith	USA
William Sydeman	USA
Tsutomu Tamura	Japan
Andrew Trites	Canada
Atsushi Tsuda	Japan
Yutaka Watanuki	Japan

List of papers

Oral presentations

Tracee O. Geernaert
Trends in seabird occurrence on Pacific halibut assessment surveys (2002-2012)

Lisa T. Ballance, Jay P. Barlow and Trevor W. Joyce
At sea marine mammal, seabird, and ecosystem assessment surveys in the eastern Pacific: An overview of Southwest Fisheries Science Center's 23-year time series

Tsutomu Tamura, Kenji Konishi, Koji Matsuoka and Takashi Hakamada
Geographical and temporal distribution of common minke, sei and Bryde's whales in the western North Pacific in relation to prey availability

Sara M. Maxwell, Elliott L. Hazen, Steven J. Bograd, Benjamin S. Halpern, Greg A. Breed, Barry Nickel, Nicole M. Teutschel, Larry B. Crowder, Scott Benson, Peter H. Dutton, Helen Bailey, Michelle A., Carey E. Kuhn, Michael J. Weise, Bruce Mate, Scott A. Shaffer, Jason L. Hassrick, Robert W. Henry, Ladd Irvine, Birgitte I. McDonald, Patrick W. Robinson, Barbara A. Block and Daniel P. Costa
Understanding spatial overlap of human impacts and marine predator distributions

Hiroko Sasaki, Hiroto Murase, Koji Matsuoka, Yoko Mitani and Sei-Ichi Saitoh
Seasonal shift of Bryde's and sei whale habitat in the western North Pacific

D.F. Bertram, Dave Mackas, D.W. Welch, W.S. Boyd, J.L. Ryder and A. Hedd
Interannual variation in zooplankton prey distribution determines marine breeding distributions of Cassin's Auklet in the proposed Scott Islands National Marine Wildlife Area in Canada

Martin Renner (Invited)
Combining tracking and transect data - Issues and possible solutions

Yutaka Watanuki, Bungo Nishizawa, Takashi Yamamoto, Elizabeth Labunski, Kathy Kuletz, Catherine Meathrel and R.A. Phillips
Distribution of short-tailed shearwaters in the northern North Pacific: A comparison between geolocator-based tracking of individuals and boat-based surveys

Jarrod A. Santora, Josh Adams, Bill Henry, K. David Hyrenbach, Jim T. Harvey and David G. Ainley
Comparative habitat use and spatial overlap of sooty shearwaters using shipboard surveys and satellite-tracking

Helen Bailey, Steven J. Bograd, Elliott L. Hazen, Bruce Mate, Ladd Irvine, Daniel M. Palacios, Karin A. Forney and Evan Howell
Whale Watch: Integrating blue whale satellite telemetry and oceanographic data to develop habitat models for conservation management

PICES-2014, Yeosu, Korea
October 16–26, 2014

BIO Topic Session (S2)
Strengths and limitations of habitat modeling: Techniques, data sources, and predictive capabilities

Co-Convenors: *Enyuan Fan (China), Elliott Hazen (USA), Sei-Ichi Saitoh (Japan), William Sydeman (USA), Yutaka Watanuki (Japan)*

Invited Speakers:
Hiroto Murase (National Research Institute of Far Seas Fisheries, Japan)
Martin Renner (University of Washington, USA)

Background

Habitat modeling is a powerful tool used to identify key factors affecting the distribution of marine organisms and underlying mechanisms, to predict optimal fishing grounds, to evaluate human impacts on ecosystems, and to project distribution shifts in the face of climate change. Given their broad application and utility, evaluation of the strengths and weakness of various modeling approaches is becoming increasingly important. Environmental data primarily come from satellite-based SST, SST gradient, SSH, Chl-*a* and their variation across time, and geographic features such as shelf breaks. Distribution data are collected from various sources, including ship-based line transect surveys, animal tracking, fisheries activities (log data, satellite-based fishing light distribution) and hence contain inevitable biases, including the selection of the survey line and season, tagging location of tracked animals, sample sizes, and type of the fishing activities. Biases are also inherent in the models being used – Generalized linear and additive models (GLMs and GAMs), Random Forests, boosted regression approaches, and Maximum Entropy modeling (MaxEnt). The intention of the session was to examine factors causing biases, identify the direction of biases, discuss techniques for mitigating or accounting for biases, and create a best-practices guide for using habitat modeling approaches to predict the distribution of marine organisms in dynamic marine environments.

Summary of presentations

This session was a welcome addition to common themes explored in PICES meetings and focused on mechanisms of habitat modeling analysis rather than focusing on a specific type of study organism. It was well-attended and there was a variety of topics in the presentations, focusing on different ecosystems, trophic levels (coral to whales) and at many different scales – from fine-scale predictions to basin-wide.

In his invited lecture, Dr. Hiroto Murase discussed many of the pros and cons between habitat and mechanistic models. The former is good for understanding static pictures while the latter is better for understanding processes. He used an ensemble of statistical models to predict sei whale abundance in the western Pacific and found a range of both predictive accuracy and overall predicted spatial scales. The take-home message was that for sei-whale sightings data, Machine-learning models (Random Forests and Boosted Regression Trees) and generalized additive models (GAMs) performed best (sequentially). However, satellite tracks from sei whales did not seem to match well with the modeled habitat, highlighting the need for examining both datasets.

The second invited lecture by Dr. Martin Renner focused on the North Pacific seabird database using climatological sightings data. He, like Dr. Murase, used a suite of models, and found that model success varied quite a bit. In fact, the ensemble model performed more poorly than some of the individual models. In addition, Martin presented that kriging may outperform kernel density for filling the gaps between observations.

Dr. Chris Rooper gave a presentation on the habitat modeling of deep sea corals in the Gulf of Alaska and Bering Strait. Given the zero-inflated nature of the data, he modeled presence/absence and abundance separately in what is termed a hurdle model. He also used a camera sled to groundtruth the trawl catches of corals, finding that the camera sled did a better job sampling corals than the benthic trawls.

Dr. Bill Sydeman gave a talk for Jarrod Santora on mechanistically modeling krill hotspots in the California Current. He showed that ROMS-model based predictions of krill patch size, intensity and persistence were centered at 37° latitude, and intensity and persistence both related well to seabird densities that foraged in the California Current. The contrast between mechanistic, individual based models presented by Bill and the statistical models presented by the other speakers highlighted the need to look at both approaches in concert.

Dr. Hiroko Sasaki gave a talk on predicting zooplankton abundance as a function of the environment. She focused specifically on arctic and Pacific copepods and used GAMMs to predict their distribution relative to environmental variables with year as a random covariate. Interestingly, the habitat envelopes of the two groups of copepods were quite similar, with Pacific copepods having a slightly stronger relationship with temperature.

Dr. Irene Alabia gave a talk on habitat suitability models for neon flying squid in the western Pacific. Rather than using a single model, she used a model ensemble and like Dr. Murase, compared the results from each of the models. The ensemble models were chosen and weighted based on the prediction-based validation. There was also quite a bit of variability among years in model success, potentially because of the nature of the resource (less *vs*. more densely aggregated).

Dr. Yoon-Kyung Lee presented on a GIS based habitat map for common squid. Her research used a more qualitative method with strong predictive success to sum up the correlations among environmental variables and common squid CPUE on a pixel-by-pixel basis. The weighting of each parameter was decided based on the frequency of catch and each environmental variable and ultimately the habitat envelope data were summed into a habitat probability index.

Dr. Yukiko Inoue presented bycatch models of wandering and black-browed albatross using tag-based and fisheries bycatch data. As bycatch is a function of species distribution and fishing effort, multiple models were used sequentially. Distribution was predicted as a function of environmental variables and predicted for islands without tracking data. Bycatch was predicted in two models: as a function of environmental variables and gear type. Unfortunately, the models showed that bycatch mitigation techniques did not show an across the board reduction in bycatch but more data are likely needed to make a conclusive decision.

Dr. Patrick O'Hara gave a talk on predicting Cassin's Auklet habitat relative to environmental stressors of microplastics and oil. His models were very robust in predicting both survey and tracking-based distribution of birds. When overlaying the modeled habitat with microplastics, there was little overlap but vessel traffic was directed through important areas. Cassin's Auklets are of conservation concern for Canada and there are ongoing efforts for spatial management around Triangle Island to protect this important population.

The final talk was given by Dr. Hiromichi Igarashi who created a near-real time model of neon flying squid using ROMS model output. He used a suite of modeling techniques, and created a complex super-ensemble, regressing the suite of models against CPUE rather than the common approach of weighted averaging. Using an EOF on the super-ensemble output he was able to decompose the results based on spatio-temporal scale into fine, medium, and large scale. He then was able to highlight how the various scales improved in their predictive capacity, in addition to the single vs. super-ensemble, as a function of good and bad fishing years.

Conclusions

The suite of modeling techniques presented, with some authors using up to 10 different models, highlights the importance of comparing model results. As technological capability continues to increase, more complex multi-model ensembles can improve our predictive capacity. In addition, the talks examined multiple trophic levels from copepods up to marine mammals, highlighting the need for statistical habitat modeling. Finally, the difference between mechanistic (individual-based models) *vs*. statistical (many presented here) was highlighted by a number of speakers. In fact, the possibility of combining these approaches, *e.g*., using the habitat model output as an input for mechanistic models was suggested by one of the speakers. This has the potential to greatly improve our capabilities in predicting habitat, including for use in near-real time management of fisheries resources.

This session shows the successes of the Spatial Ecology plan by AP-MBM and will contribute to the 3-year project report.

List of papers

Oral presentations

Application of habitat models to highly mobile marine animals – Cetaceans in the North Pacific as case studies (Invited)
Hiroto Murase, Toshihide Kitakado, Yu Kanaji, Hiroko Sasaki, Yoko Mitani, Koji Matsuoka, Makoto Okazaki and Naohisa Kanda

Crossvalidating approaches to modeling habitat and distribution of seabirds at-sea (Invited)
Martin Renner

Distribution modeling for deep-sea corals and sponges in Alaska
Chris Rooper, Mark Zimmermann, Mike Sigler and Jerry Hoff

Modeling temporal variation in krill "hotspots": Size, intensity, persistence and coherence with krill predators
Jarrod A. Santora, Jeffrey Dorman and William J. Sydeman

Prediction of zooplankton community Spatial-Temporal patterns in the Chukchi Sea – Case study using habitat modeling approach
Hiroko Sasaki, Kohei Matsuno, Atsushi Yamaguchi, Yutaka Watanuki and Takashi Kikuchi

Comparison of habitat suitability models for neon flying squid (*Ommastrephes bartramii*) in western and central North Pacific
Irene Alabia, Sei-Ichi Saitoh, Hiromichi Igarashi, Yoichi Ishikawa, Norihisa Usui, Masafumi Kamachi, Awaji Toshiyuki and Masaki Seito

GIS-based potential habitat mapping for *Todarodes pacificus* (common squid)
Yoon-Kyung Lee, Inhye Park, Sang-Woo Kim, Jong-Kuk Choi, Saro Lee and Joo-Hyung Ryu

Is seabird bycatch rate affected by the seabird distribution? Estimation of seabird distribution for bycatch risk assessment
Yukiko Inoue, Makoto Okazaki, Maria P. Dias, Cleo Small and Hiroshi Minami

Cassin's Auklet at-sea distribution and exposure to stressors such as ship-source oil pollution and microplastics
Patrick D. O'Hara, Ken Morgan, Jamie McDevitt-Irwin, Jean-Pierre W. Desforges, Peter S. Ross and Sean Boyd

A multi-model ensemble prediction of habitat suitability index (HSI) models for neon flying squid in central North Pacific by using 3-D ocean data assimilation product
Hiromichi Igarashi, Toshiyuki Awaji, Masafumi Kamachi, Yoichi Ishikawa, Norihisa Usui, Masaaki Iiyama, Yosuke Onoue, Mitsuo Sakai, Yoshiki Kato, Irene Alabia, Sei-ichi Saitoh and Masaki Seitoh

Poster presentations

Developing the suitable operation prediction model of neon flying squid in the central North Pacific using Satellite images and VMS
Yang <u>Liu</u>, Sei-Ichi Saitoh, Hiroki Takegawa and Toru Hirawake

Effect of 3-D physical structures on spatial distributions of Japanese common squid in the coastal waters of southwestern Hokkaido, Japan
Xun <u>Zhang</u>, Sei-Ichi Saitoh, Toru Hirawake, Satoshi Nakada, Koji Koyamada, Toshiyuki Awaji, Yoichi Ishikawa and Hiromichi Igarashi

Habitat model development of Japanese common squid in Japan Sea using satellite remotely sensed data
Mariko <u>Dehara</u>, Sei-Ichi Saitoh and Toru Hirawake

Predicting the potential invasion in Korean waters of the saltmarsh grass *Spartina alterniflora* from China – A joint proposal by KIOST and Nanjing University
Keun-Hyung <u>Choi</u> and Changyong Wang

Jamieson, G. and Zhang, C.-I. (Eds.) 2005. Report of the Study Group on Ecosystem-Based Management Science and its Application to the North Pacific. **PICES Sci. Rep. No. 29**, 77 pp.

Brodeur, R. and Yamamura, O. (Eds.) 2005. Micronekton of the North Pacific. **PICES Sci. Rep. No. 30**, 115 pp.

Takeda, S. and Wong, C.S. (Eds.) 2006. Report of the 2004 Workshop on *In Situ* Iron Enrichment Experiments in the Eastern and Western Subarctic Pacific. **PICES Sci. Rep. No. 31**, 187 pp.

Miller, C.B. and Ikeda, T. (Eds.) 2006. Report of the 2005 Workshop on Ocean Ecodynamics Comparison in the Subarctic Pacific. **PICES Sci. Rep. No. 32**, 103 pp.

Kruse, G.H., Livingston, P., Overland, J.E., Jamieson, G.S., McKinnell, S. and Perry, R.I. (Eds.) 2006. Report of the PICES/NPRB Workshop on Integration of Ecological Indicators of the North Pacific with Emphasis on the Bering Sea. **PICES Sci. Rep. No. 33**, 109 pp.

Hollowed, A.B., Beamish, R.J., Okey, T.A. and Schirripa, M.J. (Eds.) 2008. Forecasting Climate Impacts on Future Production of Commercially Exploited Fish and Shellfish. **PICES Sci. Rep. No. 34**, 101 pp.

Beamish, R.J. (Ed.) 2008. Impacts of Climate and Climate Change on the Key Species in the Fisheries in the North Pacific. **PICES Sci. Rep. No. 35**, 217 pp.

Kashiwai, M. and Kantakov, G.A. (Eds.) 2009. Proceedings of the Fourth Workshop on the Okhotsk Sea and Adjacent Areas. **PICES Sci. Rep. No. 36**, 305 pp.

Jamieson, G., Livingston, P. and Zhang, C.-I. (Eds.) 2010. Report of Working Group 19 on Ecosystem-based Management Science and its Application to the North Pacific. **PICES Sci. Rep. No. 37**, 166 pp.

Pakhomov, E. and Yamamura, O. (Eds.) 2010. Report of the Advisory Panel on Micronekton Sampling Intercalibration Experiment. **PICES Sci. Rep. No. 38**, 108 pp.

Makino, M. and Fluharty, D.L. (Eds.) 2011. Report of the Study Group on Human Dimensions. **PICES Sci. Rep. No. 39**, 40 pp.

Foreman, M.G. and Yamanaka, Y. (Eds.) 2011. Report of Working Group 20 on Evaluations of Climate Change Projections. **PICES Sci. Rep. No. 40**, 165 pp.

McKinnell, S.M., Curchitser, E., Groot, C., Kaeriyama, M. and Myers, K.W. 2012. PICES Advisory Report on the Decline of Fraser River Sockeye Salmon *Oncorhynchus nerka* (Steller, 1743) in Relation to Marine Ecology. **PICES Sci. Rep. No. 41**, 149 pp.

Takeda, S., Chai, F. and Nishioka, J. (Eds.) 2013. Report of Working Group 22 on Iron Supply and its Impact on Biogeochemistry and Ecosystems in the North Pacific Ocean. **PICES Sci. Rep. No. 42**, 60 pp.

Shaw, C.T., Peterson, W.T. and Sun, S. (Eds.) 2013. Report of Working Group 23 on Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim. **PICES Sci. Rep. No. 43**, 100 pp.

Abo, K., Burgetz, I. and Dumbauld, B. (Eds.) 2013. Report of Working Group 24 on Environmental Interactions of Marine Aquaculture. **PICES Sci. Rep. No. 44**, 122 pp.

Hollowed, A.B., Kim, S., Barange, M. and Loeng, H. (Eds.) 2013. Report of the PICES/ICES Working Group on Forecasting Climate Change Impacts on Fish and Shellfish. **PICES Sci. Rep. No. 45**, 197 pp.

Ross, P.S. (Ed.) 2013. Report of the Study Group on Marine Pollutants. **PICES Sci. Rep. No. 46**, 49 pp.

Trainer, V.L. and Yoshida, T. (Eds.) 2014. Proceedings of the Workshop on Economic Impacts of Harmful Algal Blooms on Fisheries and Aquaculture. **PICES Sci. Rep. No. 47**, 85 pp.

Kestrup, Åsa M., Smith, D.L. and Therriault, T.W. (Eds.) 2015. Report of Working Group 21 on Non-indigenous Aquatic Species. **PICES Sci. Rep. No. 48**, 176 pp.

Curtis, J.M.R. (Ed.) 2015. Report of the Study Group on Biodiversity Conservation. **PICES Sci. Rep. No. 49**, 61 pp.

Watanuki, Y., Suryan, R.M., Sasaki, H., Yamamoto, T., Hazen, E.L., Renner, M., Santora, J.A., O'Hara, P.D. and Sydeman, W.J. (Eds.) 2016. Spatial Ecology of Marine Top Predators in the North Pacific: Tools for Integrating across Datasets and Identifying High Use Areas. **PICES Sci. Rep. No. 50**, 55 pp.

PICES Scientific Reports

Hargreaves, N.B., Hunter, J.R., Sugimoto, T. and Wada, T. (Eds.) 1993. Coastal Pelagic Fishes (Report of Working Group 3); Subarctic Gyre (Report of Working Group 6). **PICES Sci. Rep. No. 1**, 130 pp.

Talley, L.D. and Nagata, Y. (Eds.) 1995. The Okhotsk Sea and Oyashio Region (Report of Working Group 1). **PICES Sci. Rep. No. 2**, 227 pp.

Anonymous. 1995. Report of the PICES-STA Workshop on Monitoring Subarctic North Pacific Variability. **PICES Sci. Rep. No. 3**, 94 pp.

Hargreaves, N.B. (Ed.) 1996. Science Plan, Implementation Plan (Report of the PICES-GLOBEC International Program on Climate Change and Carrying Capacity). **PICES Sci. Rep. No. 4**, 64 pp.

LeBlond, P.H. and Endoh, M. (Eds.) 1996. Modelling of the Subarctic North Pacific Circulation (Report of Working Group 7). **PICES Sci. Rep. No. 5**, 91 pp.

Anonymous. 1996. Proceedings of the Workshop on the Okhotsk Sea and Adjacent Areas. **PICES Sci. Rep. No. 6**, 426 pp.

Beamish, R.J., Hollowed, A.B., Perry, R.I., Radchenko, V.I., Yoo, S. and Terazaki, M. (Eds.) 1997. Summary of the Workshop on Conceptual/Theoretical Studies and Model Development and the 1996 MODEL, BASS and REX Task Team Reports. **PICES Sci. Rep. No. 7**, 93 pp.

Nagata, Y. and Lobanov, V.B. (Eds.) 1998. Multilingual Nomenclature of Place and Oceanographic Names in the Region of the Okhotsk Sea. **PICES Sci. Rep. No. 8**, 57 pp. (Reprint from MIRC Science Report, No. 1, 1998)

Hollowed, A.B., Ikeda, T., Radchenko, V.I. and Wada, T. (Organizers) 1998. PICES Climate Change and Carrying Capacity Workshop on the Development of Cooperative Research in Coastal Regions of the North Pacific. **PICES Sci. Rep. No. 9**, 59 pp.

Freeland, H.J., Peterson, W.T. and Tyler, A. (Eds.) 1999. Proceedings of the 1998 Science Board Symposium on The Impacts of the 1997/98 El Niño Event on the North Pacific Ocean and Its Marginal Seas. **PICES Sci. Rep. No. 10**, 110 pp.

Dugdale, R.C., Hay, D.E., McFarlane, G.A., Taft, B.A. and Yoo, S. (Eds.) 1999. PICES-GLOBEC International Program on Climate Change and Carrying Capacity: Summary of the 1998 MODEL, MONITOR and REX Workshops, and Task Team Reports. **PICES Sci. Rep. No. 11**, 88 pp.

Lobanov, V.B., Nagata, Y. and Riser, S.C. (Eds.) 1999. Proceedings of the Second PICES Workshop on the Okhotsk Sea and Adjacent Areas. **PICES Sci. Rep. No. 12**, 203 pp.

Danchenkov, M.A., Aubrey, D.G. and Hong, G.H. 2000. Bibliography of the Oceanography of the Japan/East Sea. **PICES Sci. Rep. No. 13**, 99 pp.

Hunt, G.L. Jr., Kato, H. and McKinnell, S.M. (Eds.) 2000. Predation by Marine Birds and Mammals in the Subarctic North Pacific Ocean. **PICES Sci. Rep. No. 14**, 168 pp.

Megrey, B.A., Taft, B.A. and Peterson, W.T. (Eds.) 2000. PICES-GLOBEC International Program on Climate Change and Carrying Capacity: Report of the 1999 MONITOR and REX Workshops, and the 2000 MODEL Workshop on Lower Trophic Level Modelling. **PICES Sci. Rep. No. 15**, 148 pp.

Stehr, C.M. and Horiguchi, T. (Eds.) 2001. Environmental Assessment of Vancouver Harbour Data Report for the PICES MEQ Practical Workshop. **PICES Sci. Rep. No. 16**, 213 pp.

Megrey, B.A., Taft, B.A. and Peterson, W.T. (Eds.) 2001. PICES-GLOBEC International Program on Climate Change and Carrying Capacity: Report of the 2000 BASS, MODEL, MONITOR and REX Workshops, and the 2001 BASS/MODEL Workshop. **PICES Sci. Rep. No. 17**, 125 pp.

Alexander, V., Bychkov, A.S., Livingston, P. and McKinnell, S.M. (Eds.) 2001. Proceedings of the PICES/CoML/IPRC Workshop on "Impact of Climate Variability on Observation and Prediction of Ecosystem and Biodiversity Changes in the North Pacific". **PICES Sci. Rep. No. 18**, 210 pp.

Otto, R.S. and Jamieson, G.S. (Eds.) 2001. Commercially Important Crabs, Shrimps and Lobsters of the North Pacific Ocean. **PICES Sci. Rep. No. 19**, 79 pp.

Batchelder, H.P., McFarlane, G.A., Megrey, B.A., Mackas, D.L. and Peterson, W.T. (Eds.) 2002. PICES-GLOBEC International Program on Climate Change and Carrying Capacity: Report of the 2001 BASS/MODEL, MONITOR and REX Workshops, and the 2002 MODEL/REX Workshop. **PICES Sci. Rep. No. 20**, 176 pp.

Miller, C.B. (Ed.) 2002. PICES-GLOBEC International Program on Climate Change and Carrying Capacity: Report of the PICES 2002 Volunteer Observing Ship Workshop. **PICES Sci. Rep. No. 21**, 38 pp.

Perry, R.I., Livingston, P. and Bychkov, A.S. (Eds.) 2002. PICES Science: The First Ten Years and a Look to the Future. **PICES Sci. Rep. No. 22**, 102 pp.

Taylor, F.J.R. and Trainer, V.L. (Eds.) 2002. Harmful Algal Blooms in the PICES Region of the North Pacific. **PICES Sci. Rep. No. 23**, 152 pp.

Feely, R.A. (Ed.) 2003. CO_2 in the North Pacific Ocean (Working Group 13 Final Report). **PICES Sci. Rep. No. 24**, 49 pp.

Aydin, K.Y., McFarlane, G.A., King, J.R. and Megrey, B.A. (Eds.) 2003. PICES-GLOBEC International Program on Climate Change and Carrying Capacity: The BASS/MODEL Report on Trophic Models of the Subarctic Pacific Basin Ecosystems. **PICES Sci. Rep. No. 25**, 93 pp.

McKinnell, S.M. (Ed.) 2004. Proceedings of the Third Workshop on the Okhotsk Sea and Adjacent Areas. **PICES Sci. Rep. No. 26**, 275 pp.

Kishi, M.J. (Ed.) 2004. Report of the MODEL Task Team Second Workshop to Develop a Marine Ecosystem Model of the North Pacific Ocean including Pelagic Fishes. **PICES Sci. Rep. No. 27**, 49 pp.

King, J.R. (Ed.) 2005. Report of the Study Group on the Fisheries and Ecosystem Responses to Recent Regime Shifts. **PICES Sci. Rep. No. 28**, 162 pp.

PICES PUBLICATIONS

The North Pacific Marine Science Organization (PICES) was established by an international convention in 1992 to promote international cooperative research efforts to solve key scientific problems in the North Pacific Ocean.

PICES regularly publishes various types of general, scientific, and technical information in the following publications:

PICES ANNUAL REPORTS – are major products of PICES Annual Meetings which document the administrative and scientific activities of the Organization, and its formal decisions, by calendar year.

PICES SCIENTIFIC REPORTS – include proceedings of PICES workshops, final reports of PICES expert groups, data reports and planning reports.

PICES TECHNICAL REPORTS – are on-line reports published on data/monitoring activities that require frequent updates.

SPECIAL PUBLICATIONS – are products that are destined for general or specific audiences.

JOURNAL SPECIAL ISSUES – are peer-reviewed publications resulting from symposia and Annual Meeting scientific sessions and workshops that are published in conjunction with commercial scientific journals.

BOOKS – are peer-reviewed, journal-quality publications of broad interest.

PICES PRESS – is a semi-annual newsletter providing timely updates on the state of the ocean/climate in the North Pacific, with highlights of current research and associated activities of PICES.

ABSTRACT BOOKS – are prepared for PICES Annual Meetings and symposia (co-)organized by PICES.

For further information on our publications, visit PICES at www.pices.int.

Front cover figure

Photo of a Short-tailed Albatross, *Phoebastria albatrus*, taken in the Bering Sea during the 2013 cruise aboard the T/S *Oshoro-maru*. Credit: Bungo Nishizawa, Hokkaido University.