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Contribution to the Theme Section 'Beyond marine mammal habitat modeling'

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OVERVIEW

Marine mammal habitat models come of age: the emergence of ecological and management relevance

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ABSTRACT: Models for predicting marine mammal habitat are increasingly being developed to help answer questions about species' ecology, conservation, and management. Over the past 10 yr, the models and analyses presented at the Habitat Modelling Workshops of the Biennial Conference on the Biology of Marine Mammals have shown tremendous development in their breadth and complexity. At the 18th Biennial, held in Quebec City, Canada, in 2009 we noticed a change in how these models were presented. Instead of a focus on methods and model development, many researchers presented models highlighting ecological insights or management applications. We recognised this as a watershed moment for our discipline, the time when we started paying more attention to what our models were telling us than how to build them. To celebrate this progress, we invited researchers from the global marine mammal community to submit articles to this Theme Section of *Endangered Species Research* describing work that included not only advanced model development, but also emphasised ecological interpretation or management relevance. The resulting collection of articles highlights the leading science in marine mammal habitat modelling, and provides some important indications of how, as a community, we must continue to refine our methods to move beyond correlations towards understanding the processes that interact to create marine mammal habitat. While there will no doubt be future challenges to overcome, the articles in this collection raise the standard for marine mammal habitat modelling, and herald the transition from learning *how* to model, to *using* our models as a heuristic tool to support ecological understanding and marine spatial planning.

KEY WORDS: Critical habitat · Marine protected areas · MPA · Habitat suitability · Marine spatial planning · MSP · Conservation · Management

INTRODUCTION

Like all species, marine mammals are expected to be distributed, in large part, according to how they respond to their physical or biological environment. The particulars of how and why they are distributed in their ecosystems are fundamental ecological, conservation, and management questions. An increasingly accepted approach to understanding these relationships is to quantify them using a variety of correlative modelling techniques (e.g. Guisan & Zimmermann 2000, Austin 2002, Redfern et al. 2006).

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However, before ecological insights can emerge from such models, and the resulting knowledge can inform management, modellers must confront a number of confounding issues relating to environmental data collection, statistical methods, scaling, observation error, and model validation. As marine ecologists and biological oceanographers involved in habitat modelling for well over a decade, we have watched the evolution of our field since the first Habitat Modelling Workshop was held at the Society for Marine Mammalogy's 14th Biennial Conference on the Biology of Marine Mammals in 2001. The workshop attracted over 50 participants and was dominated by questions about sources of data and methods for their incorporation with marine mammal observations. Over the course of subsequent workshops (2003, 2005, 2009, 2011), we have seen not only a large increase in the number of participants, but also considerable advancements in (1) the collection of mammal observations (e.g. satellite tagging and passive acoustic monitoring; Andrews et al. 2008, Van Parijs et al. 2009, Quakenbush et al. 2010), (2) analytical methods (e.g. Pearce & Boyce 2006, Phillips et al. 2006, Aarts et al. 2008, Gregr & Trites 2008), and (3) access to environmental data (e.g. Best et al. 2007).

Initially as participants, and then as workshop organisers, we have watched this evolution of marine mammal habitat modeling first hand. Since its inception, the workshop has always been extremely popular, now regularly attracting well over 100 scientists, students, and new modellers interested in better describing and understanding marine mammal distributions. Workshop themes have included movement modelling, large-scale habitat modelling, presence-only methods, and the integration of ocean circulation models. At more recent workshops, we have witnessed an increase in the number of advanced modellers in attendance, presenting increasingly sophisticated analyses (e.g. Gurarie et al. 2009, Block et al. 2011). It is gratifying that some of these researchers attended earlier workshops as students.

At the 18th Biennial Conference in Quebec City in 2009, we noticed a surge in the ecological insights emerging from species distribution models, not just at the workshop but also as part of the main conference sessions. It became apparent to us that, for the first time, some of these insights were being considered in management decisions. Analytical methods and data access tools had also matured considerably, removing many of the early barriers to model development. We thus recognised this meeting as a watershed moment when marine mammal habitat models came of age, and set about marking this moment with a special issue capturing the state of the art.

For this Theme Section of *Endangered Species Research*, entitled 'Beyond marine mammal habitat modeling: applications for ecology and conservation', we have assembled a set of peer-reviewed articles from the marine mammal community that demonstrate the maturity of our field. In our call for papers, initially targeting work presented at the 18th Biennial Conference, we emphasised our desire to showcase research that went beyond basic model development. We asked authors to emphasise the novelty of their models with respect to ecological interpretation or management relevance. The result is a collection of 15 articles that demonstrate the considerable progress our community has made in the last 10 yr. While new challenges continue to emerge, we can now look forward to an increase in the number of habitat models that move beyond methods and exploratory analysis. With a robust and increasing capability to glean ecological insight from a diversity of data, the field now appears poised to make real contributions to the protection of marine mammals and the conservation of their habitat.

BACKGROUND

A variety of terms have been applied to habitat models depending on the perspective of the researcher (e.g. habitat suitability models, species–habitat relationships, species distribution models). However, regardless of the terminology or methods applied, the fundamental objective, whether applied to the landscape or the seascape, is the same: to elucidate relationships between species occurrence (or abundance) and aspects of the physical or biological environment with sufficient accuracy to derive meaningful ecological insight and ultimately develop predictions of the species' distribution.

There are 3 principal reasons for these efforts. The first, and perhaps oldest, reason is to further our understanding of species ecology. This goal dates back to the observation by MacArthur & Wilson (1967) that landscape heterogeneity contributes to the persistence of biological diversity. Second, quantifying species–habitat relationships became important with the passage of the US Endangered Species Preservation Act (1966) and the subsequent Endangered Species Act (1973), both of which recognised the importance of habitat in maintaining species populations, and thus require critical habitat descriptions for species listed as endangered. Finally, as the oceans become more and more crowded with human activity, it is paramount to be able to identify where individuals and groups actually are — a population's realised distribution — in order to mitigate potential negative impacts on individuals. Increasing concern over the effects of sonar (e.g. Parsons et al. 2008) and seismic surveys (e.g. Gordon et al. 2004), combined with the more obvious risks from ship strikes (e.g. Jensen & Silber 2003) and fisheries interactions (e.g. Read et al. 2006), makes understanding and predicting the realised distribution of marine mammals one of the most important marine conservation challenges of our time. Developing such methods has implications beyond marine mammal conservation, as distinguishing between potential and realised habitats would inform a range of priority issues relating to both biological diversity (e.g. Sutherland et al. 2006) and conservation policy (e.g. Fleishman et al. 2011, Rudd et al. 2011).

Practical interest in the distribution of marine mammals, particularly large cetaceans, can be traced to commercial whaling interests (Maury 1852 et seq., Townsend 1935). From the 1940s to the 1960s the Japanese pioneered modern efforts, focusing on understanding how oceanographic conditions related to the location of whaling grounds in both the North Pacific and the Southern Ocean. The fundamental conclusion of this extensive body of work (comprising the bulk of material published in the Scientific Reports of the Whales Research Institute, Tokyo, Japan) was that favourable whaling grounds were delineated mainly by temperature and current fronts (e.g. Uda 1954, Nasu 1966). Other notable contributions to our understanding of cetacean ecology during the whaling era were made by Berzin (1978), Volkov & Moroz (1977), Gulland (1974) and Foerster & Thompson (1985), who investigated various aspects of large whale population dynamics in the (ultimately unfulfilled) hope of achieving sustainable harvest rates.

Early cetacean naturalists interested in the biogeography of species considered how large whales were associated with particular habitat types and sea-ice concentrations (Eschricht & Reinhardt 1861, Southwell 1898). Characterisations of species–habitat associations were pioneered by Gaskin (1968), Au & Perryman (1985), Hui (1985), Smith et al. (1986), Reilly (1990), and Viale (1991) on which more contemporary analyses (Waring et al. 1993, Reilly & Fiedler 1994, Woodley & Gaskin 1996, Baumgartner 1997, Fiedler et al. 1998, Baumgartner et al. 2001, Ballance et al. 2006) were based. This gradually led to the development of some of the earliest predictive models of marine mammal habitats (Palka 1995, Moses & Finn 1997, Cañadas & Sagarminaga 2000, Forney 2000, Gregr & Trites 2001).

Throughout the 1990s and into the 21st century, marine habitat modellers struggled with several fundamental challenges. These included how to deal with the variety of observational data available and the associated error, how to access geophysical data (especially remotely sensed oceanographic data), and how to apply analytical methods developed on the landscape (e.g. Guisan & Zimmermann 2000) to the more dynamic, 3-dimensional structure of the marine environment.

Observational data range in quality from historical records and opportunistically collected sighting data to well-quantified abundance estimates derived from line-transect surveys. Over the past decade or so, the evolution of satellite telemetry and passive acoustic monitoring has provided valuable new sources of observational data. Each of these observational data types provides a different perspective on how a species responds to its environment. While each can be used to develop species–habitat relationships, they require different assumptions and must therefore be analysed differently. The fundamental distinction is between presence-absence (i.e. visual survey) and presence-only data (i.e. opportunistic sightings, satellite telemetry, passive acoustic monitoring), and a variety of analytical methods are available for both (e.g. Elith & Graham 2009).

Historically, the primary sources of independent, geophysical data have been bathymetry (including depth, slope, and complexity) and remotely sensed sea surface temperature. This has largely been because of their ease of acquisition compared to other, perhaps more proximate (sensu Austin 2002) variables (e.g. subsurface temperature structure, prey distribution). Bathymetry and surface temperature are also well-suited for extending habitat predictions over broad spatial extents such as an ocean basin, or a nation's territorial waters. Fortunately, these fundamental measures of the marine environment have served as sufficient proxies for some of the features that form marine habitat (e.g. bathymetry for shelf, slope, and oceanic regions; sea surface temperature for fronts and gradients; see Bakun 1996), allowing habitat models based on them to provide limited ecological insight into habitat associations by capturing some of the variance in the observational data. Studies employing direct *in situ* sampling of oceanographic properties provide the clearest insights into species–environment relationships (e.g. Reilly 1990, Baumgartner et al. 2001), but the synoptic, high-resolution view provided by remote sensors is a challenge to replicate with *in situ* sampling. Today, ocean circulation models are providing an ever richer suite of synoptic independent variables, as demonstrated by some of the articles in this Theme Section.

Reviews of the analytical methods available to combine the dependent and independent data appear with regular frequency in the ecological literature (e.g. Guisan & Zimmermann 2000, Elith et al. 2006, Robinson et al. 2011). However, as observed by Redfern et al. (2006), marine habitat models have always faced a unique set of challenges beyond those on the landscape, on which most such reviews are based. This is because as cryptic, highly mobile species inhabiting a dynamic, 3-dimensional environment, marine fauna cross a range of ecological scales much more commonly than terrestrial species (Steele 1998). Their high mobility and expansive habitats also complicate the collection of both observational (dependent) and independent data. Thus, early modelling efforts, characterised by attempts to apply emerging terrestrial approaches to this more dynamic environment, helped bring into focus several conceptual challenges facing marine ecologists during this period. Topics discussed at our workshops included the role of scale and the hierarchical structuring of physical processes, the implications of different observational data, and how spatial autocorrelation and statistical assumptions confounded the regression methods that were dominant during this time.

Today, models incorporating animal distributions and representations of their physical environment are ubiquitous across the terrestrial and marine realms. They are used in a variety of marine disciplines such as biological oceanography, marine biogeography, endangered species research, marine spatial planning, and fisheries management. As demonstrated by the articles in this Theme Section, such models now incorporate advanced data collection technologies and sophisticated analytical methods with a predictive power that, in some cases, may outperform more traditional regression methods (Elith et al. 2006).

These advances in data collection and analytical methods have significantly reduced the barriers to developing species–habitat relationships for marine mammals, making today's challenge less about model development and increasingly about the interpretation and relevance of model results. The articles contained in this Theme Section represent the cutting edge work being done to meet that challenge.

CONTRIBUTIONS TO THE THEME SECTION

Every article in this collection extends existing modelling methods, and many emphasise some of the emerging challenges we are facing. Corkeron et al. (2011) address spatial autocorrelation in opportunistically collected data, Gerrodette & Eguchi (2011) show how uncertainty can be included in the design of Marine Protected Areas, and Forney et al. (2012) provide an extensive investigation of statistical methods for predicting encounter rates and group size. Blasi & Boitani (2012) show how a collection of methods can be integrated to describe 2 types of critical habitat at small scales, based on different behaviours, while Doniol-Valcroze et al. (2012) combine ecological-niche factor analysis and cluster analysis to characterise the influence of the tidal cycle on foraging habitats using high-frequency tagging data. Wheeler et al. (2012) show how different sources of dependent data can be combined, and Goetz et al. (2012) use advanced regression techniques to combine count and presence data. Gregr (2011) provides one of the first applications of maximum entropy modelling to marine systems while exploring the effect of scaling physical processes, something Becker et al. (2012) also explore in the context of generating forecasts of species distributions. Lambert et al. (2011) push the forecasting envelope further by driving their predictive models with climate forecasts. Pendleton et al. (2012) explore the utility of including prey distributions derived from a bio-physical ocean model. Gilles et al. (2011) provide a compelling example of model validation, and Best et al. (2012) combine model performance metrics with model results into a multi-species decision support system for marine spatial planning. Finally, Keller et al. (2012) provide a refreshingly explicit regression treatment complete with autocorrelation analysis, while Gallus et al. (2012) demonstrate the use of passive acoustic data in a predictive model.

In addition to the significant technical advances represented by this body of work, the collected articles span several space and time scales. High-resolution studies include the description of blue whale foraging habitat and how it changes on an hourly basis (Doniol-Valcroze et al. 2012), near real-time forecasts of cetacean distributions (Becker et al. 2012), and weekly predictions of right whale habitat suitability based on modeled prey distribution (Pendleton et al. 2012). In contrast, habitat suitability at basin scales is explored by considering the long-term persistence of oceanic right whale habitats (Gregr 2011), and the potential for climate effects to displace dolphin habitat (Lambert et al. 2011). These studies highlight the importance of correctly coupling space and time scales (Wiens 1989), a topic that is critical to correctly structuring the hierarchical interactions between physical and biological processes.

The scaling question is also reflected in the dependent data used in the various analyses. These range from historic presence-only data (Gregr 2011, Wheeler et al. 2012) to multi-year line transect surveys (Becker et al. 2012, Best et al. 2012, Forney et al. 2012). The spatial resolution of these data and the degree to which they can be associated with concurrent oceanographic conditions helps determine the appropriate model resolution. Understanding the resolution of modelled processes and how they interact is key to moving model predictions along the continuum from predictions of potential to realised, or occupied habitat.

This distinction between where animals are versus where they could potentially be is critical for management since these cannot be equated unless a species is near its carrying capacity — an unlikely situation for most marine mammals today. This is also dependent on the temporal resolution of the study, and again, the articles in this Theme Section span the range of possibilities from the potential habitat end of the spectrum (Gregr 2011, Lambert et al. 2011, Wheeler et al. 2012) to the occupied habitat end (Becker et al. 2012, Forney et al. 2012, Pendleton et al. 2012). Studies considering dependent and independent data averaged over a number of years to improve sample sizes are more in the middle of the spectrum (Gilles et al. 2011, Best et al. 2012). Yet another perspective is provided by investigations of how foraging habitat is influenced by the dynamics of prey in addition to oceanography (Goetz et al. 2012, Pendleton et al. 2012).

The question of delineating habitat boundaries is addressed both from a methodological perspective (Gerrodette & Eguchi 2011, Gregr 2011) and from a definitional one. This includes considering the dynamic nature of foraging habitats (Doniol-Valcrose et al. 2012, Pendleton et al. 2012), and the extension of critical habitat boundaries to calving grounds (Keller et al. 2012). The question is also informed by studies showing that sparse data can yield meaningful ecological results (Corkeron et al. 2011), and that larger collections of data can be marshalled in a decision support system integrating predictive models for multiple species (Best et al. 2012).

As data access improves (e.g. Best et al. 2012) we will need to become more circumspect in our selection of independent variables. We need to pay closer attention to the principle of parsimony, and strive to represent only ecologically defensible relationships in our models. Overly complex relationships that defy ecological explanation (e.g. see the 'skyline' plots described in Fig. 2 in Gregr 2011) may describe correlations well, but do little to further our ecological understanding. Explicitly including process hypotheses (e.g. Gregr 2011, Becker et al. 2012, Keller et al. 2012) can lead to a more parsimonious selection of independent variables and significantly improve model performance and interpretability by guiding the selection, resolution, form of, and interaction between, the potential independent variables.

Several articles also consider the effect of seasonality on spatial boundaries (Gilles et al. 2011, Gregr 2011, Gallus et al. 2012). These studies demonstrate the importance of seasonal variability when considering wide-ranging marine species, and show how model performance improves when oceanographic processes are scaled by season instead of pooled into annual averages. The effect of temporal refinement is also evident in a comparison of average and nowcast models (Becker et al. 2012).

The work in this collection represents the leading edge of scientific advice on marine mammal distributions for management. This includes studies explicitly intended to mitigate the potential of injury due to interactions with military and industrial sonar use (Becker et al. 2012, Forney et al. 2012), ship strikes (Pendleton et al. 2012), and the possible longer-term impact of coastal development (Gilles et al. 2011). Critical habitat designations (Blasi & Boitani 2012, Goetz et al. 2012, Keller et al. 2012, Wheeler et al. 2012) and marine protected area strategies more broadly are also represented (Gerrodette & Eguchi 2011, Gregr 2011, Lambert et al. 2011, Gallus et al. 2012).

CONCLUSIONS

The old mariner's adage, 'red skies at night, sailor's delight; red skies in the morning, sailor's warning' predicts the likelihood of storminess from atmospheric colour. While such correlations can be useful when no other information is available, we generally demand much greater accuracy from our weather forecasts, now regularly provided by models that encapsulate our fundamental understanding of the physical processes that govern atmospheric dynamics. In contrast to modern weather forecasting, predictive modelling of marine mammal distributions continues to depend on correlations, much the way early mariners used atmospheric 'signs' to predict weather. However, technical advances in observational data collection, access to environmental data, and analytical methods have made building habitat models much more straightforward compared to 10 yr ago. It is therefore no longer enough to simply explore correlations between a species and its environment.

The articles in this Theme Section, in addition to being examples of the state of the art in marine mammal habitat modelling, provide some important indications of how we can move beyond a correlative approach. Much like weather forecasts moved from correlative analyses to process-based predictions, we anticipate that future advances in habitat modelling will also be best achieved by elucidating the physical and biological processes underlying habitat formation. As a community, we must continue to push our methods to address questions of process dynamics and scaling, furthering our ability to interpret ecological linkages and to develop management applications. This will require becoming explicit about our model assumptions, and carefully justifying the selection of variables and scale to avoid building models with high statistical but little ecological significance. It also means focusing on the ecology of both our study species and their prey to improve the hypotheses included in our models. Finally, it will also require some consideration of behavioural states, and an exploration of how other motivating factors beyond foraging may influence habitat selection and animal distributions. In Palacios et al. (2013, this Theme Section), we examine these processes in detail, advocate an approach to fill modelling gaps, and outline a progression of modelling stages that we believe will lead us to generate increasingly robust predictions of species distributions rooted in greater ecological understanding.

While there will no doubt be significant challenges in the future, we believe that, with this collection of articles, the standard for marine mammal habitat modelling has now been raised. We are on the cusp of making the transition from learning how to model to using our models as a heuristic tool to support ecological understanding and marine spatial planning. This is something worth celebrating as a community.

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