

## REVIEW

## Techniques for cetacean–habitat modeling

J. V. Redfern<sup>1,\*</sup>, M. C. Ferguson<sup>1,2</sup>, E. A. Becker<sup>1,3</sup>, K. D. Hyrenbach<sup>4</sup>, C. Good<sup>4</sup>,  
J. Barlow<sup>1</sup>, K. Kaschner<sup>5,6</sup>, M. F. Baumgartner<sup>7</sup>, K. A. Forney<sup>8</sup>, L. T. Ballance<sup>1</sup>,  
P. Fauchald<sup>9</sup>, P. Halpin<sup>10</sup>, T. Hamazaki<sup>11</sup>, A. J. Pershing<sup>12</sup>, S. S. Qian<sup>10</sup>, A. Read<sup>4</sup>,  
S. B. Reilly<sup>1</sup>, L. Torres<sup>4</sup>, F. Werner<sup>13</sup>

<sup>1</sup>Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, California 92037, USA

<sup>2</sup>Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California 92093, USA

<sup>3</sup>Institute for Computational Earth System Science, Marine Science Graduate Program, University of California, Santa Barbara, California 93106, USA

<sup>4</sup>Nicholas School of the Environment and Earth Sciences, Duke University, Beaufort, North Carolina 28516, USA

<sup>5</sup>Forschungs- und Technologiezentrum Westküste, Hafentörn, 25761 Büsum, Germany

<sup>6</sup>Sea Around Us Project, Fisheries Centre, University of British Columbia, Vancouver V6T 1Z4, Canada

<sup>7</sup>Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA

<sup>8</sup>Southwest Fisheries Science Center, 110 Shaffer Road, Santa Cruz, California 95060, USA

<sup>9</sup>Norwegian Institute for Nature Research, The Polar Environmental Center, 9296 Tromsø, Norway

<sup>10</sup>Nicholas School of the Environment and Earth Science, Duke University, Durham, North Carolina 27708, USA

<sup>11</sup>Alaska Department of Fish & Game, 333 Raspberry Rd, Anchorage, Alaska 99518, USA

<sup>12</sup>Department of Earth and Atmospheric Sciences, 1115 Bradfield Hall, Cornell University, Ithaca, New York 14853, USA

<sup>13</sup>Marine Sciences Department, University of North Carolina, Chapel Hill, North Carolina 27599, USA

**ABSTRACT:** Cetacean–habitat modeling, although still in the early stages of development, represents a potentially powerful tool for predicting cetacean distributions and understanding the ecological processes determining these distributions. Marine ecosystems vary temporally on diel to decadal scales and spatially on scales from several meters to 1000s of kilometers. Many cetacean species are wide-ranging and respond to this variability by changes in distribution patterns. Cetacean–habitat models have already been used to incorporate this variability into management applications, including improvement of abundance estimates, development of marine protected areas, and understanding cetacean–fisheries interactions. We present a review of the development of cetacean–habitat models, organized according to the primary steps involved in the modeling process. Topics covered include purposes for which cetacean–habitat models are developed, scale issues in marine ecosystems, cetacean and habitat data collection, descriptive and statistical modeling techniques, model selection, and model evaluation. To date, descriptive statistical techniques have been used to explore cetacean–habitat relationships for selected species in specific areas; the numbers of species and geographic areas examined using computationally intensive statistic modeling techniques are considerably less, and the development of models to test specific hypotheses about the ecological processes determining cetacean distributions has just begun. Future directions in cetacean–habitat modeling span a wide range of possibilities, from development of basic modeling techniques to addressing important ecological questions.

**KEY WORDS:** Cetacean–habitat modeling · Predictive models · Regression models · Cross validation · Spatial autocorrelation · Classification models · Ordination · Environmental envelope models

—Resale or republication not permitted without written consent of the publisher—

## INTRODUCTION

Accurately describing and understanding the processes that determine the distribution of organisms is a fundamental problem in ecology, with important conservation and management implications. Recently, there has been a rapid increase in the development of habitat distribution models and tools for the statistical analysis of spatial distribution patterns (e.g. several journal issues or profiles have been dedicated to this subject: *Ecological Modelling* 2002, Vol. 157, Issues 2/3; *Ecography* 2002, Vol. 25, Issue 5; and *Journal of Applied Ecology* 2004, Vol. 41, Issue 2). These developments highlight the widespread use of computer-intensive methods in statistics, facilitated by the increasing availability and speed of computing power. Specifically, many statistical procedures currently used for habitat modeling require complex and iterative calculations to integrate non-linear relationships and an increasing number of explanatory variables (Diaconis & Efron 1983, Efron & Tibshirani 1991, Manly 1991, Guisan & Zimmermann 2000). These developments, however, have tended to focus primarily on terrestrial ecology, particularly vegetation modeling, where habitat patches and ecosystem structure change over comparatively long temporal scales of seasons to decades.

Marine ecosystems are dynamic and fluid; temporal variability operates on diel to decadal scales, while spatial variability can be observed on scales from several meters to 1000s of kilometers. This spatio-temporal variability presents unique challenges when developing species–habitat models. For example, the dynamic nature of marine physical processes, such as upwelling and the transport of planktonic organisms in surface currents, requires careful selection of habitat predictor variables and may result in temporal or spatial lags between physical processes and biological responses. Marine species–habitat models, therefore, must be flexible enough to accommodate a wide range of potential model structures and types of habitat variables if they are to explain or predict species distributions.

In this review, we focus on cetacean–habitat modeling. Many of the questions, concerns, and methodologies that we present are applicable to other apex marine predators, such as pinnipeds, seabirds, turtles, and large fishes. Restricting the focus of this review to cetaceans was necessary to derive a cohesive manuscript from the breadth of marine ecology. Cetaceans form a unique assemblage from a natural history perspective. For example, cetaceans are entirely pelagic, whereas pinnipeds, seabirds, and turtles must return to land for pupping or nesting. Pinnipeds, seabirds, and turtles are easily accessible to land-based human

observers during this phase of their lives, frequently resulting in different sampling methodologies. More complex habitat models, such as central-place foraging models, may also be needed to capture species distributions during land-based periods. Additionally, the majority of cetacean sampling techniques must be non-invasive, in accordance with national and international protection regulations, unlike other marine species, such as fishes, whose abundance is traditionally estimated using catch-rate statistics.

Many cetacean species are wide-ranging and respond to the variability in marine ecosystems by changes in distribution patterns (Forney 2000), rather than changes in survival and reproductive success. Consequently, models that predict habitat for cetaceans are necessary as a means to incorporate this variability into management decisions regarding anthropogenic activities that increasingly threaten cetacean populations. Distribution modeling remains a relatively new tool in cetacean research, but the promise of this technique has been demonstrated in a number of applications including improvement of abundance estimates (Forney 2000), development of marine protected areas (Hooker et al. 1999, Cañadas et al. 2002), and understanding cetacean–fisheries interactions (Torres et al. 2003, Kaschner 2004).

Ideally, cetacean–habitat modeling would be based on accurate measures of population size and data characterizing habitat variability, prey populations, and predator populations at a range of temporal and spatial scales, as well as an understanding of the interactions among these components. Obtaining such data for cetacean populations presents several unique challenges. Most cetaceans are highly mobile and spend a substantial amount of time below the surface, making detection and group size estimation inherently difficult. For example, Barlow (1999) predicted that there is a low probability of detecting beaked whale species (*Mesoplodon* spp., *Ziphius cavirostris*, and *Berardius bairdii*), which dive for extended periods of time. Furthermore, challenges involved in identifying the species in detected groups, from either external characteristics or vocal repertoires, increase in areas with high diversity, which are often areas of management concern. Cetacean–habitat modeling is further complicated by the natural history of these species, particularly their social organization and behavior (Ersts & Rosenbaum 2003). For example, models developed for migrating species (e.g. humpback whales *Megaptera novaeangliae*) on high-latitude summer feeding grounds may not accurately predict distributions on low-latitude winter breeding grounds.

We present a review of the development of cetacean–habitat models, with an emphasis on the challenges inherent in and unique to studies of marine

ecosystems. This paper is organized according to the primary steps involved in the modeling process. Specifically, we begin with a discussion of the purposes for which cetacean–habitat models are developed and a general overview of scale issues in marine ecosystems, because these topics provide a framework for the modeling process. Methods of estimating cetacean abundance and collecting habitat data are discussed as the primary foundation for modeling efforts. We also discuss general data and statistical considerations, including the unit of observation, covariation of habitat variables, and spatial autocorrelation. Various statistical techniques for describing and modeling cetacean–habitat relationships, as well as the limitations of these techniques, are described in the context of specific examples. In particular, standard references are provided for commonly used descriptive statistical techniques, while statistical modeling approaches are explored in more detail. Finally, we discuss different approaches for model selection and model evaluation.

### MODELING PURPOSES

The purpose of a cetacean–habitat model guides the selection of habitat variables, determines the appropriate statistical tool, and governs the interpretation or use of the model results. Hence, defining the purpose of a model is a critical first step in the modeling process. The purpose of a model is determined by how well we understand the ecology of the species, which varies along a continuum from non-existent to abundant *a priori* knowledge (Fig. 1).

At one end of the continuum, when little is known about the ecology of a species, models can be used to explore empirical associations between cetacean distributions and the physical and biological features of the study area. These models employ a variety of descriptive statistical techniques (such as those discussed in the ‘Descriptive techniques’ section) to iden-

tify important habitat variables (Kenney & Winn 1986, Reilly 1990, Fiedler & Reilly 1994, Reilly & Fiedler 1994, Griffin 1999, Baumgartner et al. 2001). Although *a priori* knowledge of the species’ ecology is lacking, an understanding of the dominant oceanographic features in the study area or the ecology of similar species can be used to guide the selection of the habitat variables used in these analyses.

As data availability and knowledge of the potential habitat variables influencing cetacean distributions increase, the purpose of developing a model may shift to predicting cetacean distribution patterns. Although the ecological processes determining cetacean distributions may not be understood at this stage, predictive models can be used to develop hypotheses about these processes, reduce unexplained variation in population trends and abundance estimation (Forney 1999, 2000, Hedley et al. 1999), or minimize adverse anthropogenic impacts on cetacean populations. The success of these models is measured by their ability to predict novel observations; predictions from a ‘good’ model will be more accurate than predictions made without the information provided by the habitat variables. Statistical modeling techniques (see the ‘Modeling techniques’ section) are generally used at this stage as part of an iterative process in which each successive sample aids in refining the model and improving long-term predictive capabilities.

At the other end of the continuum, when substantive *a priori* knowledge exists about cetacean–habitat relationships, models can be used to test specific hypotheses about the ecological processes determining cetacean distributions. For example, Baumgartner et al. (2003) relied on previous speculation (Gaskin 1987), descriptive studies (Murison & Gaskin 1989, Woodley & Gaskin 1996), and studies of individual foraging ecology (Baumgartner & Mate 2003) to develop hypotheses about the habitat variables that influence the summertime distribution of North Atlantic right whales *Eubalaena glacialis*. Ideally, hypothesis-driven modeling will be an integral component of ecological re-

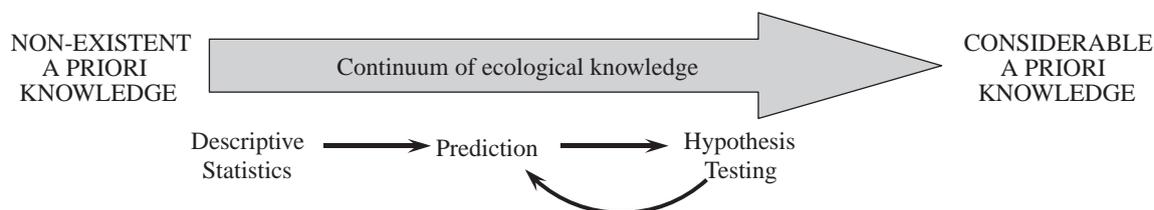


Fig. 1. When little is known about the ecology of a species, the purpose of cetacean–habitat modeling is to describe empirical associations between species’ distributions and the physical and biological features of the study area. As ecological knowledge increases, the purpose of developing a model may shift to predicting cetacean distribution patterns. When considerable *a priori* ecological knowledge exists, models can be used to test specific hypotheses about the processes determining cetacean distributions. Iteratively developing predictive and hypothesis-driven models will further advance our understanding of cetacean ecology

search that includes visual or acoustic surveys of cetacean distributions, telemetry studies, and intensive oceanographic measurements (e.g. Croll et al. 1998) designed to address specific hypotheses about cetacean–habitat relationships.

Very few cetacean species have been studied in sufficient detail to develop specific hypotheses about the ecological processes determining distributions, yet there is a growing demand for predictive models of cetacean distributions to support conservation and management efforts. Improvements in predictive models, such as reducing unexplained variability, will be gained by incorporating habitat features and oceanographic processes that have been demonstrated to affect cetacean distributions. Thus, predictive modeling and hypothesis-driven modeling can be conducted iteratively to advance our understanding of cetacean ecology, conservation, and management.

### SCALE

Selection of spatial and temporal scales plays a crucial role in the development of cetacean–habitat models because cetacean–habitat relationships are scale dependent. In particular, the outcome of the model will depend upon the scale at which the data are collected and analyzed (Wiens 1989). We can begin to understand how scale influences cetacean–habitat modeling by looking at the distribution of cetacean prey species and the oceanographic variables used as proxy measurements of prey abundance. The distribution of cetacean prey species, such as small pelagic schooling fish and crustaceans, can be viewed as a hierarchical patch structure in which high-density, small-scale patches are nested within low-density, large-scale patches (Weber et al. 1986, Murphy et al. 1988, Fauchald et al. 2000). At small scales, prey species may form high-density patches of schools and swarms; for example, krill may form patches ranging in size up to 100 m (Murphy et al. 1988). The creation and location of these small-scale patches is driven by turbulent diffusion and mixing for planktonic or weakly swimming organisms or by the species' behavior (e.g. an anti-predator response or spawning) (Murphy et al. 1988).

Oceanographic features, such as fronts and eddies, aggregate these schools and swarms to form meso-scale patches, which can vary in size from approximately 10 km to 100s of kilometers (Moser & Smith 1993, Logerwell & Smith 2001). Aggregation of meso-scale patches into large-scale patches of 1000s of kilometers is driven by water masses and current systems, and reflects components of the prey species' migration, spawning, and feeding distributions (Murphy et al.

1988). In general, rates of change are expected to be high in small patches (e.g. persistence measured in hours and days), while large-scale patches may be highly predictable (e.g. persistence measured in months or years).

Although behavioral factors such as migration, predator avoidance, and social interactions influence cetacean distributions, many of the distribution patterns that we attempt to describe using cetacean–habitat models are determined by the response of cetaceans as predators foraging in this hierarchical patch structure. In general, predators are expected to track a hierarchical system using long travel distances and low turning frequencies at large scales and short travel distances and higher turning frequencies at smaller scales (Fauchald 1999). The position of predators within the patch hierarchy should be updated using knowledge gained from recent foraging experiences (Mayo & Marx 1990, Fauchald 1999).

To understand cetacean–habitat relationships at small scales, we must explore the small-scale movements and behavior of individual foragers exploiting patchy food resources. Individual tracking and active acoustics can be used to understand cetacean movement patterns relative to prey distributions or oceanographic processes, such as diffusion and mixing. For example, an active acoustic survey of Hawaiian spinner dolphins *Stenella longirostris* and their prey showed an overlap in distributions ranging from 20 m to several kilometers (Benoit-Bird & Au 2003).

The abundance of apex marine predators (marine birds and mammals) and the abundance of zooplankton or prey fishes are often strongly correlated at meso-scales (Schneider & Piatt 1986, Piatt & Methven 1992). Cetacean–habitat models developed at these scales typically examine the relationship between cetacean abundance and prey abundance or habitat variables comprised of water column data (e.g. thermocline depth and strength, mixed layer depth), surface data (e.g. temperature, salinity, chlorophyll concentrations), or oceanographic features (e.g. fronts, eddies, upwelling). For example, Ferguson et al. (2006b) used a 9 km unit of analysis to describe the relationship between beaked whale abundance in the eastern tropical Pacific and habitat variables comprised of water column data, surface data, and bathymetry. At large scales, cetacean–habitat models may be used to define a species' range relative to ocean basin characteristics, such as water masses and current systems, or shifts in population distributions relative to long-term (e.g. seasonal, annual, or decadal) oceanographic changes. For example, Kaschner et al. (2006) used long-term averages of 3 habitat variables to generate hypotheses about global cetacean distributions.

As the examples above illustrate, cetacean–habitat models have been developed at a range of spatial scales. Multi-scale studies have also been conducted, typically exploring the change in the explanatory power of the habitat variables relative to the scale of the unit of analysis (e.g. Jaquet & Whitehead 1996, Jaquet et al. 1996). Ideally, cetacean–habitat models would be developed in a hierarchical scale framework, in which patterns at small, meso-, and large scales are identified and the influence that each scale exerts on the patterns observed at other scales is taken into account (Fauchald et al. 2000). However, the design of cetacean–habitat surveys is subject to the trade-off between high sampling intensity to capture small-scale patterns and long-range or broad spatial scale sampling to capture large-scale patterns. Hence, it is of primary importance to ensure that the scale of data collection and the unit of observation used in analyses match the temporal and spatial scales determined by the purpose of the model.

## DATA COLLECTION

### Cetacean data

Cetacean data used in habitat modeling may come from designed studies including ship, aerial, and acoustic surveys, as well as individual tagging studies (Fig. 2). Ship and aerial surveys generally rely on line-transect sampling methods (Buckland et al. 2001) to make quantitative estimates of abundance. Transect lines are designed to ensure equal sampling probabilities throughout the study area. However, transect design is, in reality, a compromise between sampling theory and logistical considerations (e.g. safety, vessel re-fueling, funding, etc.), and the actual transect lines are likely to be compromised by days lost to weather and mechanical breakdowns. When strata are incorporated in survey design, transects should be allocated among strata according to expected cetacean densities (i.e. effort should be higher in areas where cetaceans are abundant). If prior knowledge of cetacean densities is not available, transects should be allocated according to the size of the strata. Ferguson & Barlow (2001) derived stratified density estimates for cetacean species in the eastern Pacific Ocean from line-transect survey data. Their analyses highlight the frequent problem that adequate sample sizes for stratified density estimates can only be obtained at a coarse spatial resolution.

In both ship and aerial cetacean surveys, animals may be missed due to perception bias (animals are at the surface and, hence, available for detection but are missed) and availability bias (animals are submerged)

(Marsh & Sinclair 1989). Perception bias is affected by factors associated with the animals (e.g. behavior and group size) and survey conditions (e.g. sea state, swell height, visibility) (Barlow et al. 2001); availability bias is affected by species' dive durations and the relative proportion of time spent at the surface. Independent observer and dual platform methods (Buckland et al. 2001) can be used to estimate these sources of bias if all cetaceans are likely to surface within the visual range of observers; simulation models may be used to estimate bias for long-diving species (Doi 1974, Barlow 1999, Okamura 2003). Acoustic methods, such as towed hydrophone arrays, may also be used to detect vocalizing submerged cetaceans on ship surveys (Barlow & Taylor 2005).

Data collection from ship or aerial surveys is expensive, and sophisticated analytical methods are required to deal with the challenges involved in detecting cetaceans from these platforms. Acoustical survey methods may provide a less expensive alternative for recording limited cetacean data (see Di Sciara & Gordon [1997] for a summary of the potential benefits of acoustic surveys). Currently, quantitative estimation of cetacean density solely from acoustic detections is not possible, because we do not know the rates at which animals vocalize or how these rates vary with season, area, and the sex and behavior of the vocalizing animal. Additionally, many vocalizations have not been identified to the species level, and it is difficult to estimate the distance to a sound source. However, acoustic data can provide information about cetacean presence on large spatial and temporal scales (Fig. 2). For example, arrays of military hydrophones have been used to study the distribution of vocalizing whales at distances of 100s of miles (Watkins et al. 2000), and autonomous seafloor instruments have been used to continuously assess cetacean presence for periods up to a year (Stafford et al. 1998, Mellinger et al. 2004).

Cetacean tagging can also provide data for habitat modeling at a range of spatial and temporal scales (Fig. 2). For example, Baumgartner & Mate (2005) were able to infer summer and fall habitat of North Atlantic right whales using satellite tagging. In particular, the temporal coverage of the satellite tags allowed them to track individual movements over 100s of kilometers. Obtaining fine-scale data on cetacean behavior, physiology, and ecology has also been facilitated by advances in cetacean tagging (e.g. Costa 1993, Mate et al. 1999) and the development of computer programs to facilitate visualization and analysis of spatial data, such as geographic information systems. Increasingly, tags are capable of recording information about an individual's location (e.g. latitude, longitude, and depth) and behavior (e.g. dive

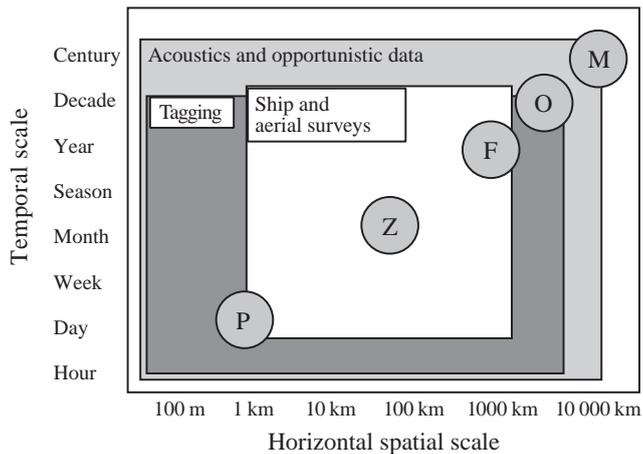


Fig. 2. A conceptual diagram showing the life-span and range of mysticete (M) and odontocete (O) cetaceans, as well as phytoplankton (P), zooplankton (Z), and fish (F) (redrawn from Steele 1978), has been overlaid on the scales at which cetacean data are typically collected. Acoustic data collection includes active devices (e.g. echosounders), towed hydrophone arrays, and autonomous seafloor instruments. Opportunistic data include whaling and fisheries observer programs, as well as data collected from non-survey dedicated platforms, such as ferries or merchant marine ships. Tagging studies include satellite tracking, radio tracking, and photo-identification

profiles), as well as fine-scale habitat data including water temperature and salinity. As tags become larger, however, they are more invasive and potentially alter the behavior of the individual (Watkins & Tyack 1991, Schneider et al. 1998). Other less invasive and relatively inexpensive data collection techniques, such as photo-identification and focal follows, can also be used to obtain information on species' habitat use and migration patterns.

The constraints on tagging studies, particularly the amount of time or expense required to collect and process the data, typically result in small sample sizes. Consequently, habitat data collected from tagging studies may span a limited range of environmental conditions, and extrapolation of results to population distribution patterns must proceed with caution. Additionally, caution is necessary when using these data to assess habitat preferences, because comparative data are not recorded in areas that are not used.

In addition to data collected using studies designed to estimate cetacean abundance and distribution (e.g. tagging studies or ship, aerial, and acoustic surveys), opportunistically collected data can be used in cetacean-habitat models (Fig. 2). Studies conducted on platforms of opportunity (e.g. situations in which an observer takes advantage of an opportunity to work from a research vessel, ferry, merchant marine ship, or

fishing vessel that is dedicated to another purpose) can result in large databases of observations, such as the atlas of cetacean distributions compiled for European waters (Reid et al. 2003). Potential limitations of data collected from platforms of opportunity include variability in the quality and reliability of the observations (e.g. the expertise of observers) and restrictions in space and time due to logistical and financial considerations of the parent project (e.g. ferries cross waterways that connect populated land masses). For cetacean-habitat modeling purposes, however, data collected from platforms of opportunity may be considered equivalent to data collected using designed surveys if trained observers and rigorous survey protocols are used and data collection is broad enough spatially and temporally to incorporate a range of habitat variability (e.g. Cañadas et al. 2005). In particular, such surveys must record effort (i.e. the time spent or distance covered searching for animals in different areas) and standardize or record conditions under which the survey is conducted (e.g. Beaufort sea state). If the goal of the model is to estimate density rather than the probability of cetacean occurrence, these surveys must also record school sizes.

Other types of opportunistic data include whaling records and information from fishery observer programs. Both sources of data typically include information about the location of the catch, as well as life-history information. For example, information on the global distribution of large whales is available from the International Whaling Commission's (IWC) extensive database of 20th century catch records. These sources of opportunistic data, however, may be subject to several important limitations that must be taken into account during the modeling process. First and foremost, effort data are frequently absent. For example, lack of effort data in the IWC whaling database makes it difficult to determine whether whales were absent from an area or simply not harvested in that area. In addition, although data from fishery observer programs typically contain effort information, absence of by-catch does not necessarily mean the absence of cetaceans, because a myriad of behavioral and ecological factors influence the probability of by-catch and some by-catch may be undetected.

### Habitat data

Habitat data used to model cetacean distributions may be collected during cetacean surveys and tagging studies or be derived from broadly available sources, including bathymetric data, remotely sensed data, and models of oceanographic processes. During ship surveys of cetacean abundance, a number of potential

habitat variables can be measured to describe surface water conditions, water column properties, or broad characteristics of the ecological community, such as densities of prey, competitor, and predator species. Measurements of surface conditions include temperature, salinity, fluorescence, chlorophyll *a*, dissolved oxygen content, and water color. Properties of the water column that may be of interest in modeling cetacean distributions include the depth and strength of the thermocline, the depth of the mixed layer, the depth of the euphotic zone, and the mean or total chlorophyll concentration in the euphotic zone (e.g. Reilly 1990, Reilly & Fiedler 1994, Ferguson et al. 2006a).

Physical oceanographic data, however, typically represent proxies for prey abundance or availability, which are expected to directly influence cetacean distributions. Continuous vertical and horizontal distributions of prey fishes and squid can be measured directly using active acoustic devices such as echosounders. Discrete measures of the relative abundance of prey species can be obtained using net sampling. The patchy nature of marine ecosystems, however, makes it challenging to apply discrete indices of prey distribution and abundance to a broad geographic area. Estimates of the abundance of other species that may influence cetacean distributions, such as competitors and predators, can be directly incorporated into the cetacean survey (e.g. the survey can be expanded to include estimates of other cetacean densities). However, techniques for incorporating the effects of competition and predation into cetacean–habitat modeling remain to be developed.

When *in situ* oceanographic data are not available (e.g. for cetacean data collected using aerial surveys), habitat variables may be derived from bathymetric data, remotely sensed data, and models of oceanographic processes. Bathymetric data are available for many parts of the world, making it easy to include variables such as bottom depth, bottom slope, and distance to shore, or other topographic features in cetacean–habitat models. Significant relationships between bathymetric variables and population distributions have been observed for many cetaceans, including bottlenose dolphin *Tursiops truncatus* ecotypes in the northwest Atlantic (Torres et al. 2003), harbor porpoises *Phocoena phocoena* in northern California (Carretta et al. 2001), and northern bottlenose whales *Hyperoodon ampullatus* in Nova Scotia (Hooker et al. 2002).

Satellite-derived data are also readily obtainable; variables typically used in cetacean–habitat models include sea surface temperature, chlorophyll *a* concentration, and dynamic height (Smith et al. 1986, Davis et al. 2002, Baumgartner et al. 2003). Satellite-derived data can also be used to infer the presence of dynamic

oceanographic features, such as frontal regions (e.g. Baumgartner et al. 2001). For example, Smith et al. (1986) calculated the variance in satellite-derived chlorophyll concentrations and used this measure of habitat heterogeneity to examine cetacean distributions off the California coast. Perhaps the biggest challenge to using remotely sensed data is that the finest temporal resolution possible is generally daily or greater. In areas with persistent cloud cover, weekly or even monthly composites must be used for passive sensor data such as advanced very high resolution radiometer (AVHRR). Hence, there can be a temporal lag of several hours to several months between cetacean data and satellite-derived habitat data.

Numerical ocean circulation models are another source of habitat data for cetacean modeling. Circulation models provide a time-varying, 3-dimensional estimate of the state of the ocean, including sea surface temperature and salinity, mixed layer depth, and the horizontal gradients of these fields. Significant progress has been made in the development of models that couple circulation to biological processes at lower trophic levels, including simulating the timing and distribution of nutrients and phytoplankton (J. K. Moore et al. 2002, Spitz et al. 2003). Progress has also been made in modeling the transport and bioenergetics of zooplankton populations and the early life stages of fishes (Carlotti et al. 2000, Werner et al. 2001, Runge et al. 2004) that may serve as prey for cetaceans. In general, the accuracy of ocean circulation models increases as the spatial and temporal resolution increases. At fine scales, ocean circulation models can simulate realistic features and dynamics, such as variability in frontal and eddy structures and its effect on biogeochemical fields (McGillicuddy et al. 2003), but the precise timing and location of these features may not be accurately simulated. Data assimilation, a class of techniques that merges observations with models (see reviews in Bennett [1992] and Wunsch [1996]), can improve the accuracy of circulation model predictions (Stammer & Chassignet 2000, Hofmann & Friedrichs 2002, Robinson & Lermusiaux 2002). In areas where oceanographic observations are present, the output of data-assimilative models provides an interpolation of the observations in a manner that is consistent with the underlying ocean dynamics. There are currently several observing and forecasting efforts that provide daily estimates of circulation on regional (e.g. see the special issue on ocean observing systems in the Marine Technology Society Journal 2003, Vol. 37, Issue 3) and basin scales (e.g. Koblinsky & Smith 2001, Rowley et al. 2002). The amount of effort and the quality of these products is likely to increase considerably in the coming years with the establishment of international ocean observing programs such as the global

ocean observing system (GOOS) (available at: <http://ioc.unesco.org/goos/>).

Cetacean–habitat models may be built at finer spatial and temporal resolutions when using *in situ* data rather than satellite-derived data or predictions from oceanographic circulation models. *In situ* data also provide information about water-column properties that is not obtainable from satellite-derived data and that may be more accurate than predictions from circulation models. However, collection and processing of *in situ* data is time consuming and expensive, limiting the area surveyed and the frequency of such surveys. In contrast, satellite imagery can provide synoptic coverage of broad ocean areas on a repetitive basis. Additionally, the ‘real-time’ nature of satellite-derived data allows cetacean management decisions to be based on the current state of the system. Perhaps the best data for modeling cetacean distributions will be created by blending multiple sources of habitat data to enable ‘real-time’ predictions over broad geographic areas.

#### DATA CONSIDERATIONS

Critical decisions made during data processing determine the scope of the model, including selecting the habitat variables considered in the model and selecting the unit of observation. Ideally, the habitat variables will be chosen based on an *a priori* understanding of the factors influencing a species’ distribution. For species about which little is known, however, initial models may be built using a suite of available habitat variables. Latitude and longitude may be included in models as proxy variables for specific habitat features, such as water masses, bathymetric regions, or species range limitations (Forney 2000). The use of latitude and longitude as a general proxy for unmeasured variables is not recommended, because the resulting models are difficult to interpret ecologically. Similarly, the use of year as a general proxy is not recommended if the purpose of the model is prediction, because inclusion of this term precludes prediction in a novel year.

The units of observation used in cetacean–habitat models span a wide range of spatial scales (see the ‘Scale’ section). For example, Jaquet et al. (1996) used grid cells ranging in size from 220 to 1780 km<sup>2</sup> to study the relationship between sperm whale *Physeter macrocephalus* abundance, as determined from whaling data, and phytoplankton pigment concentrations, as measured from satellite data. Other units of observation that may be used in cetacean–habitat models include strata defined by relatively uniform habitat variables (e.g. water masses), segments of transect

lines (Jaquet & Whitehead 1996), or time spent sampling (e.g. dividing transects from ship surveys into units defined by daily effort, see Reilly & Fiedler 1994). Some key points to consider when choosing the unit of observation are the characteristics and resolution of the available data, the purpose of the model, and the scale at which the question of interest can be effectively analyzed.

Once a candidate unit of observation has been selected, cetacean and habitat variables need to be summarized within each unit. Depending on the type of data available and the purpose of the model, cetacean data may be summarized by presence/absence (Hamazaki 2002), abundance or relative abundance (e.g. the number of cetaceans or cetacean groups per unit of search effort, see Forney 1999), density (Benson et al. 2002), or line-transect variables, such as encounter rate and mean school size (Ferguson et al. 2006a). When habitat data are available at a finer resolution than the selected unit of observation (e.g. remotely sensed habitat variables), simple averages may be used to summarize the habitat. However, habitat data are frequently available only at a relatively coarse resolution and must be interpolated using techniques such as inverse distance weighting, negative exponential distance weighting, or kriging (Cressie 1993).

Evaluation of the candidate unit of observation should include an exploration of the autocorrelation in the summarized cetacean data, as well as exploration of the relationships among the habitat variables. Positive spatial autocorrelation (e.g. cetacean abundances measured at nearby locations are more similar than randomly associated pairs of observations) is the norm for ecological data (Lennon 2000). Spatial autocorrelation invalidates the common assumption in traditional statistical methods that observations are independent, and the frequency of Type I errors (i.e. mistakenly identifying a non-significant relationship as significant) may increase if autocorrelation is not accounted for in cetacean–habitat models. Autocorrelation can be assessed using statistical techniques such as Moran’s *I*, Geary’s *C*, Mantel tests, variograms, and correlograms (an excellent discussion of spatial statistics is provided in a special issue of *Ecography* 2002, Vol. 25, Issue 5).

Methods for addressing spatial autocorrelation may be separated into 2 general categories: (1) removing autocorrelation from the data and (2) explicitly accounting for autocorrelation in statistical tests and models. Autocorrelation may be removed from the data to investigate the influence of habitat variables on cetacean distributions in the absence of spatial structure. The simplest technique for removing autocorrelation is to discard intermediate observations until spatial independence is achieved, a process called rarefaction. This approach may not be satisfac-

tory for cetacean–habitat modeling in which initial sample sizes are typically small. Alternatively, the unit of observation can be increased to achieve spatial independence.

The effects of spatial autocorrelation can also be explicitly taken into account in statistical tests and models. Tests of statistical significance may be modified by penalizing the number of degrees of freedom (see Legendre 1993 for an overview of these techniques). Another option is to assess statistical significance using permutation tests (e.g. random re-assignment of the observations among the units of observation) rather than traditional statistical tests. For example, Schick & Urban (2000) used resampling and Mantel tests to show that the distribution of bowhead whales in the Alaskan Beaufort Sea is affected by the presence of oil-exploration activities. Alternatively, the information contained in the spatial structure of the cetacean data may be directly incorporated into cetacean–habitat models. Specifically, autocorrelation can be included in cetacean–habitat models by extending the predictor variables to include spatial measures, such as sampling locations or geographic distances (Legendre 1993), or measures of the autocorrelation structure (Augustin et al. 1996, Keitt et al. 2002).

An exploration of the relationships among habitat variables may also influence the final selection of the unit of observation. Interpretation of statistical models is easier if all predictor variables are uncorrelated. For example, the effects attributed to uncorrelated predictor variables in a regression model (see 'Regression models' in the 'Modeling techniques' section) are independent of the other variables in the model (Neter et al. 1996). The habitat variables used to model cetacean distributions may be correlated, in which case multicollinearity among the variables is said to exist (Neter et al. 1996). The presence of multicollinearity does not prohibit the development of models that provide a good fit to the data, nor does it affect inferences about the mean response or predictions of the mean response within the range of observed habitat values (Neter et al. 1996). However, multicollinearity does affect the interpretation of model coefficients. In particular, the coefficients for correlated variables in regression models will have large sampling variances and cannot be interpreted as measuring the marginal effects of the variables (Neter et al. 1996). Gregor & Trites (2001) tested the colinearity of predictor variables used to model critical habitat for sperm, sei *Balaenoptera borealis*, fin *B. physalus*, humpback, and blue *B. musculus* whales off the coast of British Columbia. The predictor variables did not show significant colinearity at the chosen unit of observation; hence, all predictor variables were considered in the models.

## DESCRIPTIVE TECHNIQUES

### Overlay of sightings and maps of habitat variables

The simplest and most frequently used technique to describe cetacean distributions consists of plotting species locations on maps of habitat variables, such as bathymetry (S. E. Moore et al. 2002, D'Amico et al. 2003, Fulling et al. 2003), sea surface temperature (Gaskin 1968, Au & Perryman 1985, Kasamatsu et al. 2000b), or the edges of sea ice (Murase et al. 2002). Frequency of occurrence may also be calculated in pre-defined habitat categories. For example, several studies have mapped the frequency of species occurrence in regions defined by sea floor depth (Fertl et al. 2003, Naud et al. 2003).

These overlay techniques can be used to develop a general understanding of species spatial patterns and distribution boundaries. However, the lack of consideration or documentation of effort information in many published overlays of species' occurrence and habitat variables may render the resulting maps misleading or difficult to interpret. For example, an analysis of 70 yr of IWC data by Kaschner et al. (2006) showed that the majority of minke whale *Balaenoptera bonaerensis* catches around the Antarctic continent occurred at depths between 2000 and 4000 m. These results could be interpreted as suggesting that minke whales, generally considered to prefer coastal or shelf water, predominately occurred in the deeper waters around the Antarctic continent during the time period examined (Kaschner et al. 2006). Simple catch frequencies per environmental stratum are misleading, however, because effort data must be included in the analysis. When relative encounter rates, defined as the proportion of minke whale catches in the total catch, were plotted, it was apparent that minke whales were more frequently encountered at shallower depths (Kaschner et al. 2006).

Although whaling operations may represent an extreme case of skewed effort distributions, heterogeneous survey effort relative to habitat variables can occur in designed surveys. Therefore, correcting sighting frequencies for effort, using relative indices of abundance or encounter rates (Kasamatsu et al. 2000b, Griffin & Griffin 2003, MacLeod et al. 2003), or producing stratified estimates of cetacean densities is recommended. Alternatively, categories of habitat variables may be defined so that they contain equal effort. For example, Baumgartner (1997) defined depth categories containing equal survey effort to understand the distribution of Risso's dolphins *Grampus griseus* in the northern Gulf of Mexico.

### Correlation analysis

Correlation analysis can be used to investigate the relationship between species occurrence and a single habitat variable (e.g. Kasamatsu et al. 2000a). Parametric correlation analyses assume that all variables have a normal distribution. Griffin (1997) used data transformations to achieve normality in a parametric correlation analysis of the relationship between odontocete distributions and habitat variables along the southern edge of Georges Bank. Alternatively, Jaquet et al. (1996) used Spearman's rank correlation analysis, a non-parametric technique, to relate the distribution of sperm whale catches to chlorophyll concentration.

The most important assumption in both parametric and non-parametric correlation analyses is that the functional relationship between variables is linear. Linear relationships, effectively representing simple direct or indirect resource selection along a habitat gradient, are considered rare or unlikely (Austin 2002, Oksanen & Minchin 2002). Hence, although exploring simple linear relationships may be an appropriate starting point for species about which little is known, lack of a significant correlation does not necessarily imply that there is no relationship between the species and the habitat variable.

### Goodness-of-fit metrics

Goodness-of-fit techniques can be used to test hypotheses concerning frequencies of observations. This section focuses on the use of goodness-of-fit techniques for hypothesis testing, and thus is included under the general framework of descriptive techniques; goodness-of-fit techniques can also be used in model evaluation, which is discussed in the 'Model evaluation' section. In a hypothesis testing context, goodness-of-fit tests have been used to determine whether cetacean occurrence is evenly distributed with respect to one or more classes of habitat variables (Hui 1979, 1985, Smith et al. 1986, Selzer & Payne 1988, Brown & Winn 1989, Ribic et al. 1991, Waring et al. 1993, Woodley & Gaskin 1996, Baumgartner 1997, Raum-Suryan & Harvey 1998, Davis et al. 2002, Elwen & Best 2004a,b). The chi-squared test and *G*-test (or log-likelihood ratio test) are the most commonly used goodness-of-fit techniques in cetacean-habitat studies. These tests are well suited to handle categorical habitat variables; continuous habitat variables must be divided into 2 or more contiguous classes.

Smith et al. (1986) used chi-squared techniques to test the null hypothesis that cetacean occurrence was randomly distributed with respect to chlorophyll concentrations off the California coast. Results indicated

that some cetacean species occurred more frequently in regions of higher chlorophyll concentration, providing a foundation to help interpret observed distribution patterns. Moore et al. (2000) also used chi-squared goodness-of-fit tests to investigate habitat selection for 3 cetacean species off the northern coast of Alaska. Approximately 2000 cetacean sightings, collected during 10 yr of aerial surveys, were available for this study; however, the only habitat features recorded on the same temporal and spatial scale as the cetacean sightings were water depth and sea ice cover. Moore et al. (2000) stratified the study area using these 2 habitat variables to test the null hypothesis that the distribution of cetacean sightings was proportional to survey effort in all habitat categories. Results from the chi-squared analysis were used to describe seasonal depth and ice cover habitats. Jaquet & Gendron (2002) used the *G*-test to determine whether sperm whales were uniformly distributed with respect to 3 habitat variables (depth, underwater relief, and sea surface temperature) at a range of spatial scales in the Gulf of California. The significance of the *G*-test was dependent on both the scale and oceanographic feature.

The Kolmogorov-Smirnov test is a non-parametric goodness-of-fit test that is applicable to continuous frequency distributions and is useful for small sample sizes. This test can be used to evaluate whether a species is distributed randomly with respect to a habitat variable (i.e. the distributions of cetacean abundance and the values of the habitat variable are identical), without the arbitrary categorization of continuous habitat variables that is necessary for both the chi-squared test and *G*-test. Hooker et al. (2002) used the Kolmogorov-Smirnov test to compare the distribution of effort and encounter data relative to 2 habitat variables, bottom depth and slope, for northern bottlenose whales near a submarine canyon and found that both bathymetric features may influence the population's distribution.

Goodness-of-fit techniques are computationally simple, can be used with relatively small sample sizes, and can be applied to continuous and categorical data. These attributes make goodness-of-fit techniques a popular choice for cetacean-habitat analyses, because it is often difficult to obtain a large number of cetacean sightings with simultaneous habitat data collected at an appropriate resolution. However, caution is needed when applying chi-squared tests and *G*-tests, because the definition of habitat categories affects the outcome of the tests. In particular, the selection of categories for continuous habitat data is subjective; alternative definitions may reveal different relationships, making Kolmogorov-Smirnov tests generally preferred. Additionally, goodness-of-fit metrics cannot be used to quantify cetacean-habitat relationships, although use of these techniques may indicate that a relationship exists.

### Analysis of variance

Analysis of variance (ANOVA) techniques have been used to examine whether cetacean species or species groups can be differentiated with respect to habitat variables (Mullin et al. 1994, Davis et al. 1998, Gardner & Chavez-Rosales 2000). This section describes the use of ANOVA techniques for hypothesis testing, and thus is included under the general framework of descriptive techniques; use of ANOVA for predictive modeling is a special form of generalized linear modeling, which is discussed in 'Regression models' in the 'Modeling techniques' section. In hypothesis testing, ANOVA is used to compare the means of a single habitat variable for several cetacean species or species groups. Statistically significant results provide evidence of differences among groups, but do not identify which means differ from one another. Multiple, unplanned comparison tests (e.g. Tukey–Kramer, Scheffé's) can be used to identify differences among means. For example, Mullin et al. (1994) detected differences in mean water depths among 7 cetacean species or species groups in the northern Gulf of Mexico using ANOVA. Using Duncan's multiple range test, Mullin et al. (1994) were able to identify depth characteristics for pantropical spotted dolphins and sperm whales (lower continental slope), pygmy and dwarf sperm whales and Risso's dolphins (upper continental slope), and Atlantic spotted dolphins and bottlenose dolphins (continental shelf and upper continental slope).

Multivariate analysis of variance (MANOVA) is an extension of ANOVA that is used to detect differences among group means for many habitat variables simultaneously. As with ANOVA, identification of detected differences requires the use of additional techniques, such as discriminant function analysis (DFA). DFA is an ordination technique (see 'Ordination', this section, for a discussion of other ordination techniques) that reduces the dimensionality of multivariate data by finding linear combinations of the habitat variables that best differentiate among species or species groups. Often 1 or 2 of the linear combinations of habitat variables will capture most of the variability. These linear combinations can be used to determine which habitat characteristics influence the species differences detected by MANOVA and to evaluate success in classifying sightings among species based on habitat variables. Baumgartner et al. (2001) used MANOVA and DFA to examine habitat differences among several cetacean species and species groups found in the northern Gulf of Mexico. Like Mullin et al. (1994), Baumgartner et al. (2001) found cetacean habitat to be strongly partitioned by water depth. However, the DFA also indicated that sperm whales were found in waters with a shallower 15°C isotherm than the

other cetaceans. These results suggested that sperm whales avoided warm-core eddies in the northern Gulf of Mexico. Reilly (1990) used MANOVA techniques to examine differences in water column properties among 3 dolphin groups in the eastern tropical Pacific Ocean; DFA was then used to assess success in classifying sightings among the 3 dolphin groups based on water column properties.

ANOVA and MANOVA can be used to compare habitat among different species or groups. Both techniques assume that the data for each group are normally distributed and that the group variances are similar. Although these techniques are valid for small departures from these assumptions, large departures may require data transformation or the use of non-parametric statistics (e.g. rank-transformation of habitat data used in MANOVA or Mood's median or Kruskal–Wallis tests as non-parametric substitutes for ANOVA). Direct comparisons of habitat data for different species also assume that sighting conditions and detection probabilities are identical for all groups. This assumption of similar sighting conditions is typically valid when all sightings are derived from the same source (e.g. a platform used during a single survey). Caution, however, is warranted when comparisons are made between species with vastly different detection probabilities (e.g. harbor porpoise and humpback whales). Similar to other descriptive techniques, classification studies using ANOVA, MANOVA, or their non-parametric equivalents can only be used to detect a relationship between cetacean distributions and habitat variables; these techniques, however, cannot be used to quantify the relationship.

### Ordination

Ordination is a class of multivariate statistical techniques used to arrange species along habitat gradients (Jongman et al. 1995). These techniques partition the variance in cetacean abundance among axes that are orthogonal, or mutually independent, linear combinations of measured or latent (i.e. unknown or theoretical) habitat variables (Jongman et al. 1995). Ordination axes represent a smaller set of new predictor variables that capture the patterns in the original predictor variables (Jongman et al. 1995). The power of ordination techniques lies in this ability to reduce the dimension of multivariate data to a level that is easier to interpret. Hence, ordination techniques are valuable tools for exploring relationships in community ecology, which typically involve multiple species and habitat variables that may be best analyzed simultaneously.

Examples of ordination techniques include principal components analysis (PCA), redundancy analysis

(RDA), correspondence analysis (CA), and canonical correspondence analyses (CCA) (Jongman et al. 1995). PCA and RDA assume linear relationships between cetacean distributions and the latent or measured habitat variables. CA and CCA assume unimodal relationships between cetacean distributions and habitat variables (Jongman et al. 1995), thereby avoiding the potentially unrealistic assumption of linear species–habitat relationships. PCA and CA are ‘indirect gradient analysis’ techniques, because the axes are comprised of latent habitat variables and are typically interpreted indirectly using additional information about the habitat characteristics of the sampling sites. RDA and CCA are ‘direct gradient analysis’ techniques that extend PCA and CA by incorporating measured habitat variables directly into the ordination. For example, in CCA, the canonical axes are linear combinations of the measured habitat variables. The axes are chosen to maximize the dispersion, or spread, of the species scores, which are defined as the average of the measured habitat values at the sites where the species was present (Jongman et al. 1995). Hence, the canonical axes are comprised of the habitat characteristics that provide the maximum differentiation among species.

The results of PCA, RDA, CA, and CCA can be easily interpreted from ordination diagrams (Fig. 3). In PCA, each species is represented by a vector, graphically displayed as an arrow, indicating the direction

in which the species’ abundance increases most with respect to the latent habitat variables represented by the axes (Jongman et al. 1995). The length of the arrow is proportional to the corresponding rate of change in abundance. In CA, arrows are used to represent the latent habitat variables, while in RDA and CCA arrows represent specific habitat variables. Longer arrows are associated with the latent or measured habitat variables that have the greatest explanatory power (Jongman et al. 1995). In RDA, CA, and CCA, species and sampling sites are represented by points. Sites that tend to have a high abundance of a given species are located close to the point for that species in the ordination diagram (Jongman et al. 1995).

Reilly & Fiedler (1994) used CCA to examine habitat use by the dominant dolphin species in the eastern tropical Pacific. Species studied included spotted *Stenella attenuata*, spinner, common *Delphinus delphis*, and striped *S. coeruleoalba* dolphins; all of these species are affected by the purse seine tuna fishery. Common dolphins were separated from spotted and spinner dolphins based on their associations with cool upwelling habitat and warm tropical habitat, respectively (Fig. 3). Whitebelly and eastern spinner dolphins both occurred in tropical water, but were separated by thermocline topography (Fig. 3). Overall, the habitat data explained 15% of the variance in the species data, ranging from 34% of the variance for common dol-

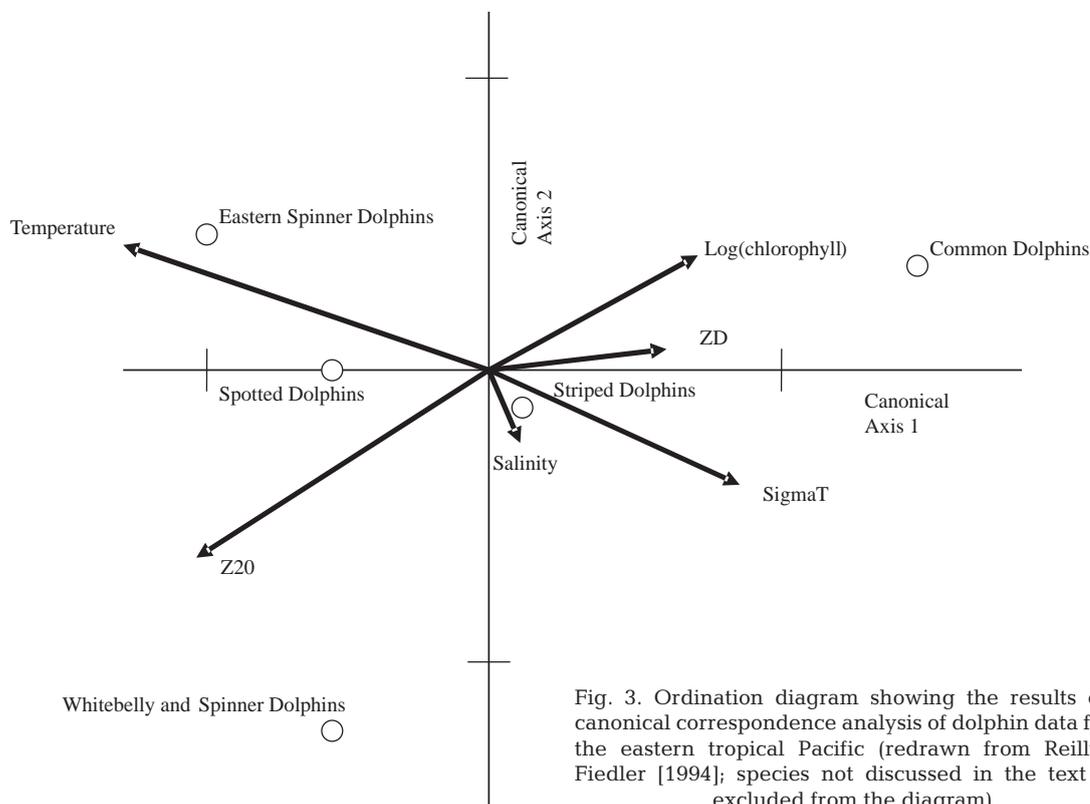


Fig. 3. Ordination diagram showing the results of a canonical correspondence analysis of dolphin data from the eastern tropical Pacific (redrawn from Reilly & Fiedler [1994]; species not discussed in the text are excluded from the diagram)

phins to 5% of the variance for whitebelly spinner dolphins.

Ordination techniques reduce the dimensionality of many, potentially interacting, variables to provide quantitative habitat definitions. CCA can be used to understand species distributions relative to the original habitat variables included in the analysis, the habitat gradients defined by the axes, and the habitat characteristics of the other species included in the analysis. Advantages of CCA over other ordination techniques include the assumption of unimodal, rather than linear, species–habitat relationships and the direct incorporation of habitat variables in the ordination. Additionally, CCA is insensitive to the high frequency of zero observations common in most cetacean surveys. A disadvantage of CCA is that it typically explains less variance than indirect gradient methods, such as CA, because the axes are restricted to linear combinations of the measured habitat variables (Jongman et al. 1995). Application of both CA and CCA is restricted to species–habitat relationships that are predominantly unimodal. The most common application of all ordination techniques is the exploration of species–habitat relationships, making them subject to the general limitations of descriptive techniques.

## MODELING TECHNIQUES

### Environmental envelope models

Environmental envelope modeling is the simplest technique available for quantifying large-scale relationships between cetacean distributions and habitat variables. Traditionally, subjective outlines of species ranges were derived from overlay analyses (see overlay of sightings and maps of habitat variables in the

‘Descriptive techniques’ section) to define potentially suitable habitat (e.g. Jefferson et al. 1993). Species’ ranges produced using this technique can show considerable variation. Environmental envelope modeling is a more objective approach that generates reproducible results using clear and modifiable assumptions. Specifically, an envelope defined by minimum and maximum values of the habitat variables is calculated so that the envelope encompasses a predetermined percentage of the observed species’ occurrences. Fitted envelopes are generally multi-dimensional and may range from simple rectilinear shapes to more complex polytopes. Although envelope models are an objective approach, extrapolations based on these models or the results of models built from sparse data may benefit from cross checking against expert opinion.

Kaschner et al. (2006) developed a rule-based envelope model to map global distributions of 115 marine mammal species. Species were assigned to broad-scale habitat categories defined by depth, sea surface temperature, and ice edge association based on published quantitative and qualitative habitat preference data (Fig. 4). Habitat variables were averaged within 0.5° latitude and longitude grid cells; relative habitat suitability for a particular species was determined by relating the broad-scale habitat categories to the habitat averages for each cell. Validation of the model using large-scale, long-term data sets indicated that the model captured a significant amount of the observed variability in occurrence for several well-studied species. Additionally, the distributions predicted by the model closely matched published ranges for most species. The model results, however, provide more information about species distributions than the published ranges, because they illustrate the heterogeneity in suitable habitat within a species’ range.

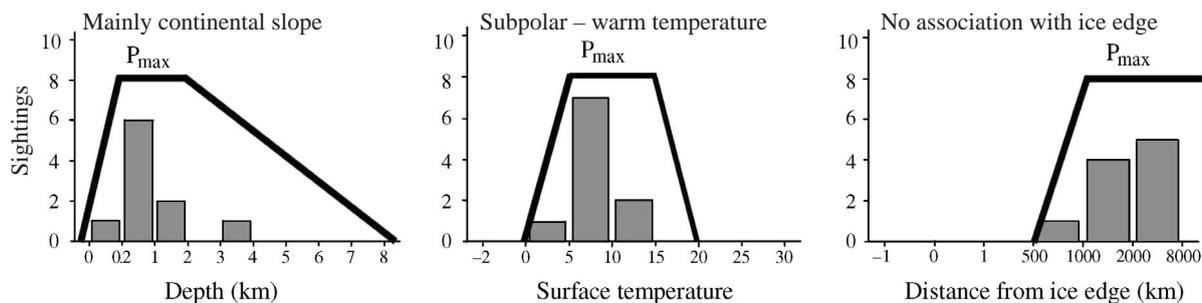


Fig. 4. An environmental envelope model, developed by Kaschner et al. (2006), assigning Sowerby's beaked whales *Mesoplodon bidens* to broad-scale habitat categories defined by depth, sea surface temperature, and ice edge association based on published quantitative and qualitative (e.g. expert opinion) habitat usage data. The habitat categories are represented by the trapezoidal probability distributions; frequency distributions of ‘presence’ cells are included for comparison. The analyses suggest that this species occurs mainly on the continental slope in subpolar (e.g. warm temperature) waters and has no association with the ice edge. Envelope models were also developed for 115 other species of marine mammals. These models were used to map global species distributions, which can be viewed in Kaschner (2004)

The vast distribution of many cetacean species, as well as the difficulty of conducting dedicated cetacean surveys, restricts the application of data-intensive modeling techniques to select species and regions. Environmental envelope models do not require large samples sizes and can be applied to data sets in which effort information is missing. Hence, these models can be used to evaluate assumptions about the occurrence of infrequently studied species. Envelope models can also be used to test hypothesized ecological relationships between species distributions and habitat characteristics because of their simple conceptual framework. The benefits of envelope models, however, come with a sacrifice of 'detail for generality' (Gaston & McArdle 1994). Hence, these models are best applied to broad questions about large-scale species distributions. Interpolation to finer scales or novel geographic areas must proceed with caution because the broad, static nature of environmental envelope models may obscure important cetacean–habitat relationships.

### Regression models

Regression is one of the most commonly used techniques to model the relationship between cetacean distributions and one or more habitat variables. Regression encompasses a broad range of techniques that differ in their assumptions about the distribution of the variables and the functional form of the relationship. The simplest technique is linear regression, which relates the variability in  $n$  observed values,  $Y_i$  ( $i = 1, \dots, n$ ), to a sum of linear functions of  $k$  predictor variables,  $X_{ij}$  ( $j = 1, \dots, k$ ), such that:

$$Y_i = \alpha + \sum_{j=1}^k \beta_j X_{ij} + \varepsilon_i$$

where  $\alpha$  is the intercept term,  $\varepsilon_i$  is a stochastic error term, and the coefficients,  $\beta_j$ , represent the change in the mean response,  $\hat{Y}_i$ , for a unit change in the independent variable  $X_{ij}$ , assuming all other independent variables are held constant. Both the mean response,  $\hat{Y}_i$ , and the error terms are assumed to have a normal distribution. The predictor variables,  $X_{ij}$ , can either be categorical or continuous. Many classical significance tests (e.g. the  $t$ -test and ANOVA) are special forms of linear regression.

Linear regression produces a model that is relatively simple to understand and apply. Hooker et al. (1999) used linear regression to understand cetacean habitats in a proposed marine protected area on the Scotian Shelf. Their results quantitatively demonstrate significant depth preferences for the species in their study area, from which they were able to propose reserve boundaries. Data transformations can be used to

achieve normal error distributions or to better approximate a linear relationship between the response and one or more predictors. For example, Benson et al. (2002) used linear regression of log-transformed cetacean densities to investigate the effects of habitat variables in Monterey Bay, California. This analysis helped interpret changes in cetacean assemblages relative to large-scale changes in oceanographic conditions (e.g. El Niño and La Niña). Higher-order terms of predictor variables and interactions among predictor variables can also be included in linear regression models. Additionally, regression models are ideally suited for dealing with variables that are not of immediate interest in habitat analyses but which may affect the response variable. For example, although sea state is not a habitat variable, it may be included as an independent variable in habitat regression analyses, because it can affect cetacean encounter rates.

Situations may arise, however, in which more sophisticated techniques are needed to deal with discrete response variables and non-normal error distributions. Generalized linear models (GLMs) use a link function to induce linearity between response and predictor variables, incorporate non-constant variances directly into analyses, and constrain the response within a specific range (e.g. a positive response or a response from 0 to 1). For example, logistic regression can be used to relate binary response variables, such as cetacean presence/absence, to habitat variables. In a logistic GLM, the logit transformation of the probability,  $p$ , that  $y = 1$  (e.g. indicating cetacean presence) is a linear function of predictor variables, such that:

$$\text{logit}(p_i) = \ln\left(\frac{p_i}{1-p_i}\right) = \alpha + \sum_{j=1}^k \beta_j X_{ij}$$

Logistic regression has been used to investigate habitat for a number of cetacean species, including North Atlantic right whales (Moses & Finn 1997, Baumgartner et al. 2003), sperm whales (Waring et al. 2001, Davis et al. 2002), humpback whales (Yen et al. 2004b, Tynan et al. 2005), beaked whales (Waring et al. 2001), and small cetaceans (Davis et al. 2002, Hamazaki 2002, Yen et al. 2004b, Tynan et al. 2005). Poisson regression, another form of GLM, can be used when the response variable is a count, with large outcomes being rare events. Cañadas et al. (2002) used Poisson regression to relate cetacean encounter rates to physiographic habitats defined by depth and slope. Gregr & Trites (2001) used Poisson regression to predict critical habitat off the coast of British Columbia for 5 whale species (sperm, fin, sei, humpback, and blue whales).

Both linear regression and GLM assume that the relationship between the response variable (or some linking function of the response variable) and the predictor variables is parametric (for example, a linear or

quadratic relationship), which may be an unrealistic assumption for many cetacean–habitat relationships. Generalized additive models (GAMs, Hastie & Tibshirani 1990) are a non-parametric extension of GLMs, in which the linear function of the predictor variables is replaced by a smoothing function,  $f_j(X_{ij})$ , such that:

$$\text{link}(Y_i) = \alpha + \sum_{j=1}^k f_j(X_{ij}) + \varepsilon_i$$

(Fig. 5). Smoothing functions include moving averages, running medians (Goodall 1990), smoothing splines (Eubank 1988, Wood 2003, Wood & Augustin 2003), and kernel smoothers (Härdle 1991). Selection of a smoothing function may be based on ease of calculation, weighting schemes, degree of smoothness, or resistance to outliers (see Goodall [1990] for a discussion of these issues).

Hedley et al. (1999) developed methods for applying GAMs to cetacean–habitat data collected during strip and line-transect surveys. Forney (1999) detected a significant, non-linear effect of sea surface temperature on harbor porpoise sighting rates using a Poisson-based GAM. Forney (2000) applied GAMs to understand the effect of habitat variability on estimates of cetacean abundance and showed that variability in sighting rates for Dall’s porpoise *Phocoenoides dalli* and short-beaked common dolphins were partially accounted for by changes in habitat variables. Most of the cetacean–habitat relationships in Forney’s (2000) study were non-linear. Ferguson et al. (2006b) also used GAMs to examine beaked whale habitat in the eastern Pacific Ocean.

GAMs can be used when the response variable is binary (i.e. presence/absence data), discrete (e.g. count data), or continuous. Perhaps the greatest benefit of using GAMs, however, is their flexibility in capturing non-linear cetacean–habitat relationships (Fig. 5). A major assumption of GAMs is that the effects of predic-

tor variables are additive; GAMs are less efficient than GLMs when interactions among predictor variables are present, especially when the number of predictor variables is large. The results of GAMs may also be more difficult to interpret ecologically than GLM results, because the smoothed cetacean–habitat relationships produced by GAMs may not be a simple functional form.

Currently, regression is the most common technique for modeling cetacean–habitat relationships. Choice of a specific regression technique depends upon the characteristics of the data set and the purpose of the model. Caution must be used to ensure that the theoretical assumptions of the technique are not violated. All regression techniques assume independence among the observations of the response variable; this assumption is violated by spatially or temporally autocorrelated data (see the ‘Data considerations’ section). Caution is also needed when using regression models to predict cetacean distributions. Cetacean–habitat regression models must be developed using observations that span a wide range of spatial and temporal habitat variability to describe general ecological relationships. Additionally, the parameter  $\alpha$  in cetacean–habitat regression models represents a baseline, such as the probability of a cetacean sighting in logistic regression, which may vary spatially or temporally. Consequently, application of regression models to predict cetacean distributions may be limited by the spatial and temporal availability of survey and habitat data.

### Classification and regression trees

Tree-based models provide a completely non-parametric alternative to linear and additive regression models; classification trees are used when the response variable is categorical, and regression trees are used when the response variable is numeric. The goal of a tree-based model is to resolve relationships within a complex data set by producing the best empirical classifier (Breiman et al. 1984). This classifier is a binary tree that is created by a recursive partitioning method that successively divides the data into increasingly homogeneous subgroups. Specifically, the tree originates from a single ‘root’ that includes the entire data set. At each split, 2 ‘daughter nodes’ containing subsets of the data are produced; these nodes are then evaluated for further splitting. Each split is based on the single predictor variable that produces the most homogeneous data sub-

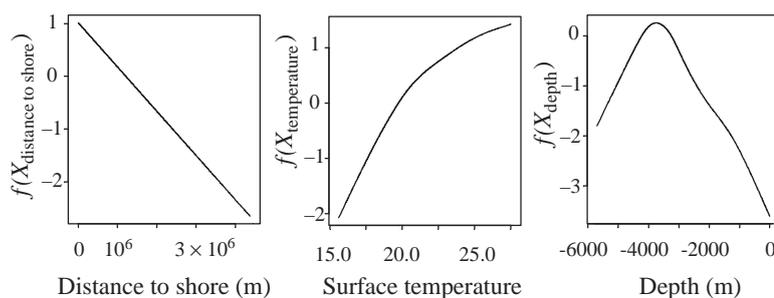


Fig. 5. Generalized additive models can be used to explore the shape of cetacean–habitat relationships. In this hypothetical example, smoothing splines were used to model the relationship between cetacean encounter rate and several habitat variables. A linear fit was selected between encounter rate and distance to shore. A smoothing spline with 2 degrees of freedom suggests that encounter rates may level off with increasing temperature, while a smoothing spline with 3 degrees of freedom captures a peak in encounter rate at a depth of approximately 3500 m

sets as evaluated by a statistical metric such as the deviance (see the 'Model fitting' section). The tree ends with a set of 'terminal nodes' that show the prediction or classification rules. Without a rule that determines when to stop the binary partitioning, these 'terminal nodes' would contain only 1 data point. Cross validation is commonly used to determine an appropriate stopping point; it selects the tree-based model that has the highest prediction accuracy for an independent data set (see the 'Model evaluation' section for further details).

Tree-based models have been used to predict the at-sea distribution of marbled murrelets (Yen et al. 2004a) and to identify odontocete species from acoustic recordings (Oswald et al. 2003); currently there are no published examples using tree-based models to explore cetacean–habitat relationships. One potential advantage that can be gained from using tree-based rather than regression models to explore cetacean–habitat relationships is the ability of tree-based models to explicitly and intuitively capture non-additive relationships (i.e. interactions) among predictor variables. Tree-based models are also easy to interpret, particularly when categorical and numeric predictor variables are combined. Only predictor variables that create homogeneous data subsets, and hence explain some of the variation in the response variable, are retained in the model. Classification and regression trees, however, require large data sets (Michaelsen et al. 1994), which are not common in cetacean–habitat studies. Tree-based models also produce discrete predictions of cetacean–habitat relationships; hence, they cannot capture smooth gradients in the response of cetaceans to habitat variables. Caution is also needed when using tree-based models, because the tree structure may be unstable (i.e. small changes in the data may lead to a different series of splits).

## MODEL FITTING: PARAMETER ESTIMATION, MODEL SELECTION, UNCERTAINTY ESTIMATION

### Parameter estimation

Fitting a statistical model consists of 3 steps: parameter estimation, model selection, and uncertainty estimation. Parameter estimation is an integral component of the model selection process, and the 2 steps are often conducted iteratively because the appropriate model form is not known *a priori* and parameter estimates are necessary to evaluate candidate models. The third step, estimating uncertainty, is infrequently included in the model fitting process, but it is a critical component in quantifying the limitations of our knowledge and modeling techniques.

Statistical modeling techniques rely on parameter estimation to quantify cetacean–habitat relationships. The primary methods used to estimate parameters include least squares, maximum-likelihood, and Bayesian techniques. The method of least squares is commonly used to estimate parameters in linear regression models; it assumes a normal (i.e. Gaussian) error distribution for the response variable. In particular, least squares methods use analytical solutions or numerical search procedures to find the parameter values that minimize  $\sum(Y_i - \hat{Y})^2$ , where  $Y_i$  is the observed value of the response variable and  $\hat{Y}$  is the value predicted by the model (Neter et al. 1996). If the distribution of the response variable is not normal, maximum-likelihood methods are typically used to derive parameter estimates (Sokal & Rohlf 1995). The likelihood function summarizes the information about the unknown parameters provided by the data (Collett 1991). Specifically, the likelihood defines the probability density of the data as a function of the unknown parameters. Maximum-likelihood methods use analytical solutions or numerical search procedures to find the parameter values that maximize the probability of obtaining the observed data given the hypothesized model and parameter estimates (Hilborn & Mangel 1997). Consequently, maximum-likelihood methods require explicit knowledge or assumptions about the probabilistic mechanisms generating the observed values of the response variable (i.e. the probability distribution of the response variable).

Bayesian techniques provide a framework for incorporating prior information (such as data from previous studies or expert opinion) about the distribution of the parameters into estimation procedures (Hilborn & Mangel 1997). Specifically, Bayes' theorem updates the prior information with the likelihood of the data to derive the posterior probability distribution, which is the probability of the hypothesized parameter estimates given the observed data and the specified model structure (Hilborn & Mangel 1997). For most cetacean species, little information exists from which to construct prior probability distributions. Consequently, it may be necessary to use information from other species, regions, or time periods.

One advantage of using Bayesian techniques is that the prior probabilities define the uncertainty associated with the range of parameter values considered in model fitting, clarifying the assumptions used in the parameter estimation process. Additionally, new data can easily be incorporated into a Bayesian analysis by using the posterior distribution from the original analysis as the prior distribution for the new analysis. This prior distribution is updated with the likelihood function of the new data to create a new posterior distribution, which gives the probabilities of the revised parameter estimates.

Historically, the application of Bayesian techniques was limited to simple models for which analytical solutions could be derived (e.g. linear regression with a normally distributed response variable). The advent of fast computers has made it possible to apply Bayesian techniques to a wide range of models, including non-linear models and models with a large number of variables. For example, Qian et al. (2003) discuss using Markov chain Monte Carlo simulation techniques to solve the difficult problem of sampling from a high-dimensional distribution, which arises for models with a large number of variables.

### Model selection

Parameter estimation is the common element in the wide variety of approaches to model selection. Typically, model selection is not used when the purpose of a model is to test specific hypotheses (e.g. Baumgartner et al. 2003). Model selection, or determining which variables should be included in a model, is an important component of developing predictive models. A computationally simple approach to model selection consists of simultaneously estimating the parameters for all variables in a model and retaining only those variables for which the parameter estimate is significantly different from 0, as assessed using statistical tests such as a *t*-test (Neter et al. 1996). At the other end of the spectrum, separate tests can be used to assess the significance of the relationship between the response variable and each predictor variable; a multivariate model is then fit, and parameter values are estimated using all variables for which a significant relationship existed. A primary problem with both of these approaches is that the Type I error rate is compromised because multiple comparisons are made using the same data.

Model selection can also proceed by evaluating candidate models composed of different combinations of the predictor variables to determine the best fit to the observed data. For example, sequential selection methods can be used to serially test each predictor variable for inclusion in a model. Forward selection starts with a null model to which a single predictor variable is added at each step in the procedure. Predictor variables are added in the order that optimizes the model selection criterion; the procedure is terminated when the addition of variables no longer increases the fit of the model, as judged by the model selection criterion. Backward selection, by contrast, begins with the global model (the model containing all of the variables) from which variables are sequentially removed to optimize the model selection criterion. Forward–backward selection is an amalgam in which previously selected

variables are re-examined for inclusion in the model each time a new variable is added to the model (Burnham & Anderson 1998). Alternatives to sequential selection procedures include testing all possible variable combinations (also known as ‘all subsets’ or ‘exhaustive search’ selection methods) or testing a specific subset of candidate models. The exhaustive search method requires computation and evaluation of all  $2^K$  candidate models, where  $K$  is the number of variables in the model; this approach can be prohibitively time consuming. In contrast, a subset of candidate models may be selected for evaluation if *a priori* information exists about the cetacean–habitat relationship.

Evaluation of the candidate models to determine which combination of variables provides the best fit to the observed data proceeds using a model selection criterion. Common model selection criteria include deviance (i.e. likelihood ratio tests), Akaike’s information criterion (AIC), and Bayesian information criterion (BIC). Deviance ( $D$ ) is calculated using likelihood functions, such that:

$$D = -2(\log \hat{L}_c - \log \hat{L}_f)$$

where  $\hat{L}_c$  is the maximized likelihood of the current model and  $\hat{L}_f$  is the maximized likelihood of a full model that fits the data perfectly (i.e. a model in which the number of parameters is equal to the number of data points) (Collett 1991). The full model is not useful except as a measure of comparison, because it does not provide any summarization of the data. However, the change in the deviance between 2 nested models (i.e.  $D_1 - D_2$ , where  $D_i$  is the deviance for model  $i$  and Model 2 contains a subset of the variables considered in Model 1) allows a relative assessment of which model provides a better fit to the data (Collett 1991). The statistical significance of the change in deviance can be assessed, because the change in deviance approximates a chi-squared distribution in which the degrees of freedom are equal to the difference in the degrees of freedom between the 2 models (Collett 1991). In general, a large decrease in deviance indicates that the variable under consideration should be included in the model. Caution is needed when using the change in deviance to select the best-fit model, because comparisons are restricted to nested models (Burnham & Anderson 1998, Anderson et al. 2000, Johnson & Omland 2004) and the results may depend upon the order in which models are compared (Johnson & Omland 2004).

AIC can be used to compare nested or non-nested models (Hilborn & Mangel 1997). AIC attempts to select the model that provides the best fit to the data, as measured by a decrease in variance, while minimizing the number of variables included in the model, which reduces the bias in the model. Specifically, AIC

is defined as  $2\log \hat{L}_c + 2p_i$ , where  $\hat{L}_c$  is the maximized likelihood of the current model and  $p_i$  is the number of variables in the model (Hilborn & Mangel 1997). The term  $2p_i$  is a penalty term; the strength of the penalty increases with the number of variables included in the model. Thus, the AIC model selection criterion optimizes the trade-off between bias and variance. AIC is meaningful only on a relative scale; therefore, AIC differences between models are more important than the AIC values themselves. AIC differences  $<2$  provide no credible evidence that one model is better than another, while AIC differences  $>4$  provide evidence that the model with the smaller AIC value provides a better fit to the observed data (Burnham & Anderson 1998). In general, larger AIC differences provide stronger evidence that one model provides a better fit. Alternative forms of AIC have been developed to deal with small-sample bias (AIC<sub>c</sub>) and overdispersion (QAIC and QAIC<sub>c</sub>) (Burnham & Anderson 1998). While AIC does provide a solution to comparing non-nested models, this model selection criterion can only be used to test competing models fit to the same data set, using the same definitions of the predictor variables (e.g. data cannot be grouped in one model and ungrouped in another model) and the same response variable (e.g. it is not valid to compare  $\ln[y]$  with  $y$ ) (Burnham & Anderson 1998).

Two Bayesian techniques, the Bayes factor and the BIC, can also be used as model selection criteria. The Bayes factor is defined as the ratio of the posterior odds (defined as the ratio of the posterior probabilities of the 2 models under consideration) to the prior odds (defined as the ratio of prior probabilities of the 2 models) (Kass & Raftery 1995). Hence, the Bayes factor summarizes the evidence in the observed data for one model over another (Kass & Raftery 1995). The Bayes factor can be used to compare non-nested models and has the advantage of explicitly incorporating prior information into the model selection process. However, the Bayes factor is sensitive to the assumptions in the likelihood function and the prior distribution, and an assessment of this sensitivity should be conducted as part of the model selection process (Kass & Raftery 1995). The BIC (also known as the Schwarz criterion) approximates the logarithm of the Bayes factor in large samples. It assumes that the prior distribution is normal rather than requiring an explicit definition of the distribution (Wintle et al. 2003). In general, BIC selects simpler models than AIC and its derivatives, because BIC penalizes additional variables more heavily.

Cross validation can be combined with any of the model selection criteria to determine the model that gives the most accurate predictions. In cross validation, subsets of the original data set are iteratively withheld during model fitting. During model selection, the

predictive accuracies of the resulting best-fit models are evaluated using the withheld data. For example, Ferguson et al. (2006a) used 6 yr of data to model delphinid–habitat relationships in the eastern tropical Pacific Ocean. Their original data set was divided into 5 subsets, each of which excluded a single year of data. They fit GAMs of delphinid encounter rates and school sizes to these 5 data subsets using a forward–backward procedure with AIC as the model selection criterion. The resulting 5 best-fit models were used to predict delphinid encounter rates and school sizes for the excluded year of data. The model with greatest agreement between observed and predicted values was selected as the final model.

### Estimating uncertainty

The final step in model fitting is determining the uncertainty in the parameter estimates of the selected model as well as the uncertainty in the model predictions. Sampling, process, and model selection errors contribute to model uncertainty. Sampling error occurs during data collection and arises due to the sample design and the resolution of collected data. Attempts to minimize sampling error occur during sample design, and this source of uncertainty is not generally addressed during model fitting. Process error arises from the inherent stochasticity in ecological processes. For example, the mechanistic processes determining cetacean distributions are not, and may never be, fully understood; consequently, cetacean–habitat models do not perfectly predict cetacean distributions. Additional sources of error result from the model selection process. Model selection criteria are restricted to evaluating specific types of models (e.g. nested vs. non-nested models), and the output of model selection procedures may be subject to the order in which variables are considered. Furthermore, selecting a single best model can lead to biased parameter estimates, implying that the expected value or mean parameter estimate differs from the true, but unknown, value of the parameter (Burnham & Anderson 1998). If the optimal model is not selected or the parameter estimates are biased, predictions derived from the model will be subject to error. The precision or amount of variability in parameter estimates and model predictions are another component of model uncertainty. Factors that may influence the precision of parameter estimates include correlations among predictor variables and overfitting the model (i.e. including non-significant predictor variables).

A variety of methods exist to assess uncertainty in parameter estimates and model predictions arising from process and model selection error. For example,

uncertainty may be represented by confidence intervals. In classical (Neyman–Pearson) statistics, confidence intervals define the upper and lower limits that would contain the true mean of the parameters or model predictions in a specified percentage of samples (typically 95%) if the samples were repeatedly drawn from the population and the analytical methods used to derive estimates or predictions remained constant (Sokal & Rohlf 1995). Confidence intervals are derived from other measures of uncertainty, including variance and standard error. Analytical formulae are usually available for calculating these metrics, but care must be taken to account for departures from the assumptions used in the formulae (e.g. a normal error distribution is often assumed). Frequently, analytical formulae are not available to quantify uncertainty and alternative methods are used, such as the bootstrap, jackknife, or model averaging.

The bootstrap can account for model selection uncertainty and process error when estimating uncertainty metrics for model parameter estimates and predictions. The bootstrap is a Monte Carlo technique, meaning that the data are stochastically or randomly generated (Hilborn & Mangel 1997). In the non-parametric bootstrap, a new data set is created by sampling with replacement from the original data set. The parametric bootstrap, in contrast, creates a new data set from a sampling distribution such as the normal, Poisson, gamma, or beta distributions, which is selected using knowledge or assumptions about the sampling process producing the data. One method for estimating the parameter values of the sampling distribution is to use the sample mean and variance from the original data set. In both the non-parametric and parametric bootstrap, the number of samples drawn is equal to the sample size of the original data. Parameter estimates for the best-fit model can be derived from the new data set, or a new model can be fit using the pre-specified model selection criterion to account for model selection uncertainty. The entire process is repeated, and the resultant parameter estimates and model predictions are accumulated; the number of replications needed varies, but is typically within the range of 1000 to estimate standard errors and within 100000 to accurately determine the tails of a distribution. The accumulated parameter estimates and model predictions are used to calculate the uncertainty metrics of interest, such as the standard error and confidence intervals. To calculate confidence intervals for parameter estimates or model predictions, values from the bootstrap replications are placed in an ordered list and values at the desired percentile are extracted (Efron & Tibshirani 1993). Hedley et al. (1999) developed a parametric bootstrap algorithm to estimate uncertainty in abundance estimates of minke whales in the Antarctic.

The jackknife is essentially similar to the non-parametric bootstrap algorithm; the primary difference is that the jackknife constructs new data sets by sequentially excluding some portion of samples (usually a single sample) from the original data set (Sokal & Rohlf 1995). Hence, the number of new data sets evaluated using the jackknife is determined by the size of the original data set and the number of the samples excluded in each iteration. The bootstrap and jackknife techniques are powerful tools for assessing uncertainty that can be applied to many statistical estimation problems (Efron & Tibshirani 1991), can generate a variety of uncertainty metrics, and can incorporate both model selection and process error. The primary disadvantage of these techniques is the computational power and time required to evaluate the replications.

If *a priori* information exists about the cetacean–habitat relationship, a subset of candidate models may be selected for evaluation, the best-fit model may be determined using a model selection criterion, and uncertainty may be assessed using the bootstrap or jackknife. An alternative to choosing a single best-fit model is to derive parameter estimates and predictions from all candidate models using weights such as the AIC values, the inverse of the variance, or the posterior probabilities derived in a Bayesian framework. This technique, known as model averaging, is recommended if the goal of the analysis is to determine the best estimates of a set of parameters or model predictions that are common to all models (Burnham & Anderson 1998). Model averaging can reduce uncertainty arising from the model selection process if the correct set of predictor variables, the functional form of the relationships, or the distributional assumptions are unknown (Anderson et al. 2000, Wintle et al. 2003, Johnson & Omland 2004).

## MODEL EVALUATION

The final stage of the modeling process is to assess the predictive accuracy of the model and determine its applicability to particular ecological, management, and conservation questions. To assess the accuracy of model predictions, comparisons are made between observed and predicted values using an independent data set; the statistical technique used for the comparison depends on whether the response variable is quantitative or qualitative. The independent data set can be derived from additional survey effort in the study area or by withholding a portion of the original data set from the model-building process. The latter scenario requires a large original data set to ensure adequate samples sizes for model fitting. It is also

important that the data subsets used in model fitting and model evaluation include the full range of variability in the habitat data, or the applicability of the resulting best-fit model may be restricted to a limited range of habitat conditions. In practice, it may be difficult to achieve such a division.

Agreement between observed and predicted values can be evaluated using a number of statistical tests; the particular test selected depends on the type of response variable. For numeric response variables the evaluation is generally straightforward and uses simple statistical tests, including the correlation between the observed and predicted values and goodness-of-fit tests (see 'Goodness-of-fit metrics' in the 'Descriptive techniques' section). The mean square prediction error,

$$\frac{\sum(\text{observed} - \text{predicted})^2}{n}$$

where  $n$  is the number of observations, is also commonly used to compare the predictive power of multiple models.

When the response variable is categorical, such as cetacean presence/absence, model outcomes are typically expressed as probabilities (e.g. probability of a 'presence'). Hence, to determine the predictive accuracy of the model, a probability threshold must be chosen to classify predictions as presences or absences. Selection of the threshold is critical; thresholds that are too low result in too few presences (errors of omission), while thresholds that are too high result in too few absences (errors of commission). For optimal habitat classifications we would like to minimize both errors of omission and errors of commission. For particular management applications, however, these errors may have qualitatively different costs or risks. Consequently, it may be more important to minimize one type of error. Receiver operating characteristic (ROC) curves provide a tool for selecting the 'optimal' threshold, minimizing both errors of omission and commission, or selecting alternative thresholds to minimize a particular source of error (Pearce & Ferrier 2000, Pontius 2000, Cummings 2001). Once the predicted number of presences and absences is obtained, classification accuracy can be examined using classification error (confusion) matrices (Pearce & Ferrier 2000, Pontius 2000, Cummings 2001) and Kappa (Foody 1992) or Tau (Ma & Redmond 1995) statistics.

An additional goal of model evaluation may be to determine the applicability of the best-fit model to particular ecological, management, and conservation questions. This type of evaluation may be more qualitative in practice, involving an assessment of the relative costs associated with the different types of model error for the particular application. For example,

managers evaluating the utility of a habitat model for reducing ship encounters with endangered cetaceans may wish to reduce errors of omission at the expense of overall model performance to ensure that the model yields broad predictions of cetacean occurrence.

## CONCLUSIONS

Cetacean–habitat modeling, although still in the early stages of development, represents potentially powerful techniques for predicting cetacean distributions and understanding the mechanisms determining these distributions. Consequently, cetacean–habitat models may be an important tool for mitigating anthropogenic impacts on these species, many of which are endangered. To date, descriptive statistical techniques have been used to explore cetacean–habitat relationships for selected species in specific areas. The number of species and geographic areas examined using computationally intensive statistic modeling techniques are considerably less, and the development of mechanistic models of cetacean distributions has just begun. Consequently, future cetacean–habitat research spans a wide range of possibilities, from development of basic modeling techniques to addressing important ecological questions.

Future development of cetacean–habitat modeling techniques should be driven by the need to integrate data across multiple spatial and temporal scales, understand the ecological processes determining cetacean distributions, and quantify the uncertainty in model-derived estimates of cetacean distributions. Predictions from cetacean–habitat models are constrained by the spatial and temporal resolution of the habitat data used to fit the models. For example, models built using seasonally averaged habitat data cannot accurately predict cetacean distributions at shorter time scales, because the habitat data do not capture the daily or weekly dynamics of the system. To solve the problem of simultaneously modeling cetacean distributions across scales, a hierarchical analysis framework incorporating tiers of generalized, broad-scale models and models of increasingly smaller-scale dynamics is needed. Development of this hierarchical framework will require the application of modeling techniques not currently used by the cetacean research community, such as the Bayesian maximum entropy approach, non-linear state–space models, conditional autoregressive models, neural network models, and individual-based models. It will also entail the integration of data collected using field methods specific to each spatial scale (Croll et al. 1998). Cetacean researchers may gain insight from terrestrial studies in which these approaches have been successfully used

to address ecological, management, and conservation questions.

Regardless of the modeling technique used, conservation and management applications of cetacean–habitat models require quantification of the uncertainty in model predictions. Without quantification of uncertainty, the accuracy of the model output and, hence, the utility of the model to address particular real-world questions cannot be understood. Methods developed to quantify uncertainty in cetacean–habitat models must address autocorrelation in cetacean distributions. Potentially powerful techniques for modeling cetacean distributions and quantifying uncertainty in the presence of autocorrelation may be derived from spatial statistics (Ecography 2002, Vol. 25, Issue 5). Once uncertainty has been quantified, techniques for presenting the uncertainty in model predictions must also be developed. For example, if the model output can be represented as a spatial map of cetacean abundances, the uncertainty in the estimated abundances needs to be reflected on the map.

Perhaps the most immediate progress in cetacean–habitat modeling will come from expanding the currently used modeling techniques to include a greater variety of species, geographic areas, and habitat conditions. Very little is known about the habitat or ecology of a vast number of cetacean species. Data from large-scale surveys can be used to develop cetacean–habitat models, which may increase our understanding of the habitat variables influencing species distributions. It may also be beneficial to take a community ecology approach to cetacean–habitat modeling by including abundances of prey species, competitors, and predators in models. Inclusion of these community ecology variables will provide insight into the mechanistic processes determining cetacean distributions. Expanding the range of habitat variability incorporated in models of cetacean distributions may also increase the predictive power of the models. Cetacean–habitat relationships are expected to be non-linear; consequently, models must be fit using the entire range of habitat variability to accurately describe the functional form of the relationship (Fig. 6). To expand the range of habitat variability included in cetacean–habitat models, we need long time series of data to capture interannual variability (such as the El Niño Southern Oscillation), decadal oscillations (such as the Pacific Decadal Oscillation), and ‘regime shifts,’ which may produce changes in the mean and variance of habitat variables, as well as changes in the sign and magnitude of cetacean–habitat relationships.

The future directions for cetacean–habitat modeling identified in this paper require additional data collection to provide a foundation for new model development and to evaluate and refine existing models. Sub-

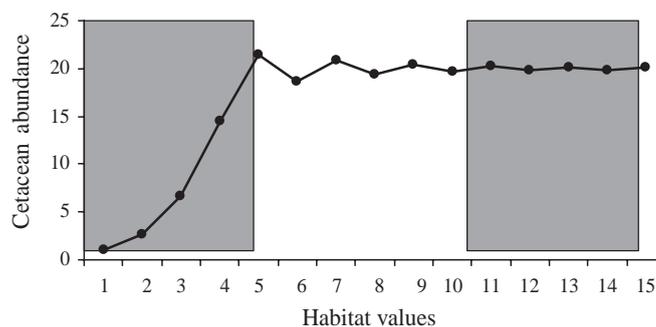


Fig. 6. The functional form of cetacean–habitat relationships may change across the range of habitat values. For example, an increasing exponential relationship would be described by models built using habitat data values from 1 to 5 (corresponding to the range shaded by the rectangle on the left), while no relationship would be described by models built using habitat data values from 11 to 15 (corresponding to the range shaded by the rectangle on the right). The entire range of habitat values is needed to show that the cetacean–habitat relationship increases until the habitat value of 5 and then levels off

stantial quantities of data are currently available from large-scale surveys designed to estimate cetacean abundance in particular geographic locations. For example, large-scale surveys have been conducted by the National Oceanic and Atmospheric Administration (NOAA) Fisheries in the eastern tropical Pacific Ocean since the 1980s, to estimate the abundance of dolphin species impacted by tuna fishing. Continuation of such surveys is essential to increase the time series of cetacean and habitat data in these locations. Surveys also need to be conducted on broader geographic scales; in particular, it is important that surveys include areas of high and low cetacean densities, so that habitat may be clearly differentiated from non-habitat. Perhaps, most importantly, surveys of cetacean abundance need to be supplemented with studies designed to address specific ecological questions about the mechanistic processes determining cetacean distributions. Future data collection efforts should be implemented using an iterative approach in which models are used to explore cetacean–habitat relationships and agreement between observations and model predictions are used to guide further research efforts.

*Acknowledgements.* This paper is an outcome of the ‘SERDP Marine Mammal Modeling Experts’ Workshop’ hosted by A.R. and P.H. at Duke University. We thank all workshop participants for their contributions. We also thank B. Best and S. Freeman for their help in structuring and coordinating the paper, and we appreciate insightful comments from anonymous reviewers. Funding from the U.S. Navy and the Strategic Environmental Research and Development Program (SERDP) supported this research under Projects CS-1390 and CS-1391.

## LITERATURE CITED

- Anderson DR, Burnham KP, Thompson WL (2000) Null hypothesis testing: problems, prevalence, and an alternative. *J Wildl Manage* 64:912–923
- Au DWK, Perryman WL (1985) Dolphin habitats in the Eastern Tropical Pacific. *Fish Bull* (Wash DC) 83:623–643
- Augustin NH, Muggleston MA, Buckland ST (1996) An autologistic model for the spatial distribution of wildlife. *J Appl Ecol* 33:339–347
- Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol Model* 157:101–118
- Barlow J (1999) Trackline detection probability for long-diving whales. In: Garner GW, Amstrup SC, Laake JL, Manly BFJ, McDonald LL, Robertson DG (eds) *Marine mammal survey and assessment methods*. AA Balkema, Rotterdam, p 209–221
- Barlow J, Taylor BL (2005) Estimates of sperm whale abundance in the northeastern temperate Pacific from a combined acoustic and visual survey. *Mar Mamm Sci* 21:429–445
- Barlow J, Gerrodette T, Forcada J (2001) Factors affecting perpendicular sighting distances on shipboard line-transect surveys for cetaceans. *J Cetacean Res Manage* 3:201–212
- Baumgartner MF (1997) The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiology of the northern Gulf of Mexico. *Mar Mamm Sci* 13:614–638
- Baumgartner MF, Mate BR (2003) Summertime foraging ecology of North Atlantic right whales. *Mar Ecol Prog Ser* 264:123–135
- Baumgartner MF, Mate BR (2005) Summer and fall habitat of North Atlantic right whales (*Eubalaena glacialis*) inferred from satellite telemetry. *Can J Fish Aquat Sci* 62:527–543
- Baumgartner MF, Mullin KD, May LN, Leming TD (2001) Cetacean habitats in the northern Gulf of Mexico. *Fish Bull* (Wash DC) 99:219–239
- Baumgartner MF, Cole TVN, Clapham PJ, Mate BR (2003) North Atlantic right whale habitat in the lower Bay of Fundy and on the SW Scotian Shelf during 1999–2001. *Mar Ecol Prog Ser* 264:137–154
- Bennett AF (1992) *Inverse methods in physical oceanography*. Cambridge University Press, Cambridge
- Benoit-Bird KJ, Au WWL (2003) Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behav Ecol Sociobiol* 53:364–373
- Benson SR, Croll DA, Marinovic BB, Chavez FP, Harvey JT (2002) Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Niño 1997–98 and La Niña 1999. *Prog Oceanogr* 54:279–291
- Breiman L, Friedman JH, Olshen RA, Stone CJ (1984) *Classification and regression trees*. Wadsworth, Belmont, CA
- Brown CW, Winn HE (1989) Relationship between the distribution pattern of right whales, *Eubalaena glacialis*, and satellite-derived sea surface thermal structure in the Great South Channel. *Cont Shelf Res* 9:247–260
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press, Oxford
- Burnham KP, Anderson DR (1998) *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York
- Cañadas A, Sagarminaga R, García-Tiscar S (2002) Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. *Deep-Sea Res I* 49:2053–2073
- Cañadas A, Sagarminaga R, De Stephanis R, Urquiola E, Hammond PS (2005) Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquat Conserv* 15:495–521
- Carlotti F, Giske J, Werner FE (2000) Modeling zooplankton dynamics. In: Harris RP, Wiebe PH, Lenz J, Skjoldal HR, Huntley M (eds) *ICES zooplankton methodology manual*. Academic Press, San Diego, CA, p 571–667
- Carretta JV, Taylor BL, Chivers SJ (2001) Abundance and depth distribution of harbor porpoise (*Phocoena phocoena*) in northern California determined from a 1995 ship survey. *Fish Bull* (Wash DC) 99:29–39
- Collett D (1991) *Modelling binary data*. Chapman & Hall/CRC, London
- Costa DP (1993) The secret life of marine mammals. *Oceanography* 6:120–128
- Cressie NAC (1993) *Statistics for spatial data*. John Wiley & Sons, New York
- Croll DA, Tershy BR, Hewitt RP, Demer DA and 8 others (1998) An integrated approach to the foraging ecology of marine birds and mammals. *Deep-Sea Res II* 45:1353–1371
- Cummings G (2001) Using between-model comparisons to fine-tune linear models of species ranges. *J Biogeogr* 27:441–455
- D'Amico A, Bergamasco A, Zanasca P, Carniel S and 5 others (2003) Qualitative correlation of marine mammals with physical and biological parameters in the Ligurian Sea. *IEEE J Ocean Eng* 28:29–43
- Davis RW, Fargion GS, May N, Leming TD, Baumgartner M, Evans WE, Hansen LJ, Mullin K (1998) Physical habitat of cetaceans along the continental slope in the north-central and western Gulf of Mexico. *Mar Mamm Sci* 14:490–507
- Davis RW, Ortega-Ortiz JG, Ribic CA, Evans WE and 6 others (2002) Cetacean habitat in the northern oceanic Gulf of Mexico. *Deep-Sea Res I* 49:121–142
- Diaconis P, Efron B (1983) Computer intensive methods in statistics. *Sci Am* 248:116–130
- Di Sciara GN, Gordon J (1997) Bioacoustics: a tool for the conservation of cetaceans in the Mediterranean Sea. *Mar Freshw Behav Physiol* 30:125–146
- Doi T (1974) Further development of whale sighting theory. In: Schevill WE (ed) *The whale problem: a status report*. Harvard University Press, Cambridge, MA, p 359–368
- Efron B, Tibshirani R (1991) *Statistical data analysis in the computer age*. Science 253:390–395
- Efron B, Tibshirani RJ (1993) *An introduction to the bootstrap*. Chapman & Hall, New York
- Elwen SH, Best PB (2004a) Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa. I. Broad scale patterns. *Mar Mamm Sci* 20:567–582
- Elwen SH, Best PB (2004b) Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa. II. Within bay distribution. *Mar Mamm Sci* 20:583–601
- Ersts PJ, Rosenbaum HC (2003) Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. *J Zool* 260:337–345
- Eubank RL (1988) *Spline smoothing and nonparametric regression*. Marcel Dekker, New York
- Fauchald P (1999) Foraging in a hierarchical patch system. *Am Nat* 153:603–613
- Fauchald P, Erikstad KE, Skarsfjord H (2000) Scale-dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. *Ecology* 81:773–783

- Ferguson MC, Barlow J (2001) Spatial distribution and density of cetaceans in the eastern tropical Pacific Ocean based on summer/fall research vessel surveys in 1986–96. Report No. LJ-01-04, Southwest Fisheries Science Center, La Jolla, CA
- Ferguson MC, Barlow J, Fiedler P, Reilly SB, Gerrodette T (2006a) Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. *Ecol Model* 193:645–662
- Ferguson MC, Barlow J, Reilly SB, Gerrodette T (2006b) Predicting Cuvier's (*Ziphius cavirostris*) and Mesoplodon beaked whale densities as functions of the environment in the eastern tropical Pacific Ocean. *J Cetacean Res Manage* (in press)
- Fertl D, Jefferson TA, Moreno IB, Zerbini AN, Mullin KD (2003) Distribution of the Clymene dolphin *Stenella clymene*. *Mamm Rev* 33:253–271
- Fiedler PC, Reilly SB (1994) Interannual variability in dolphin habitats in the eastern tropical Pacific. II. Effects on abundances estimated from tuna vessel sightings, 1975–1990. *Fish Bull* (Wash DC) 92:451–463
- Foody GM (1992) On the compensation for chance agreement in image classification accuracy assessment. *Photogramm Eng Remote Sens* 58:1459–1460
- Forney KA (1999) Trends in harbour porpoise abundance off central California, 1986–1995: Evidence for interannual changes in distributions? *J Cetacean Res Manage* 1:73–80
- Forney KA (2000) Environmental models of cetacean abundance: reducing uncertainty in population trends. *Conserv Biol* 14:1271–1286
- Fulling GL, Mullin KD, Hubard CW (2003) Abundance and distribution of cetaceans in outer continental shelf waters of the U.S. Gulf of Mexico. *Fish Bull* (Wash DC) 101:923–932
- Gardner SC, Chavez-Rosales S (2000) Changes in the relative abundance and distribution of gray whales (*Eschrichtius robustus*) in Magdalena Bay, Mexico during an El Niño event. *Mar Mamm Sci* 16:728–738
- Gaskin DE (1968) Distribution of Delphinidae (Cetacea) in relation to sea surface temperatures off eastern and southern New Zealand (*Delphinus delphis*, *Lissodelphis peroni*, *Lagenorhynchus obscurus*, *Lagenorhynchus cruciger*). *NZ J Mar Freshw Res* 2:527–534
- Gaskin DE (1987) Updated status of the right whale, *Eubalaena glacialis*, in Canada. *Can Field Nat* 101:295–309
- Gaston KJ, McArdle BH (1994) The temporal variability of animal abundances: measures, methods and patterns. *Phil Trans R Soc Lond B* 345:335–358
- Goodall C (1990) A survey of smoothing techniques. In: Fox J, Long JS (eds) *Modern methods of data analysis*. Sage Publications, Beverly Hills, CA, p 126–176
- Gregg EJ, Trites AW (2001) Predictions of critical habitat for five whale species in the waters of coastal British Columbia. *Can J Fish Aquat Sci* 58:1265–1285
- Griffin RB (1997) Relationships between odontocete distributions and zooplankton community structure along the southern edge of Georges bank. *J Northwest Atl Fish Soc* 22:27–36
- Griffin RB (1999) Sperm whale distributions and community ecology associated with a warm-core ring off Georges Bank. *Mar Mamm Sci* 15:33–51
- Griffin RB, Griffin NJ (2003) Distribution, habitat partitioning, and abundance of Atlantic spotted dolphins, bottlenose dolphins, and loggerhead sea turtles on the eastern Gulf of Mexico continental shelf. *Gulf Mex Sci* 1:23–34
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol Model* 135:147–186
- Hamazaki T (2002) Spatiotemporal prediction models of cetacean habitats in the mid-western North Atlantic Ocean (from Cape Hatteras, North Carolina, USA to Nova Scotia, Canada). *Mar Mamm Sci* 18:920–939
- Hardle W (1991) *Smoothing techniques: with implementation in S*. Springer-Verlag, New York
- Hastie TJ, Tibshirani RJ (1990) *Generalized additive models*. Chapman & Hall/CRC, Boca Raton, FL
- Hedley SL, Buckland ST, Borchers DL (1999) Spatial modelling from line transect data. *J Cetacean Res Manage* 1: 255–264
- Hilborn R, Mangel M (1997) *The ecological detective: confronting models with data*. Princeton University Press, Princeton, NJ
- Hofmann EE, Friedrichs MAM (2002) Predictive modeling for marine ecosystems. In: Robinson AR, McCarthy JJ, Rothschild BJ (eds) *The sea*. John Wiley & Sons, New York, p 537–565
- Hooker SK, Whitehead H, Gowans S (1999) Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. *Conserv Biol* 13: 592–602
- Hooker SK, Whitehead H, Gowans S, Baird RW (2002) Fluctuations in distribution and patterns of individual range use of northern bottlenose whales. *Mar Ecol Prog Ser* 225: 287–297
- Hui CA (1979) Undersea topography and distribution of dolphins of the genus *Delphinus* in the southern California Bight. *J Mamm* 60:521–527
- Hui CA (1985) Undersea topography and the comparative distributions of 2 pelagic cetaceans. *Fish Bull* (Wash DC) 83:472–475
- Jaquet N, Gendron D (2002) Distribution and relative abundance of sperm whales in relation to key environmental features, squid landings and the distribution of other cetacean species in the Gulf of California, Mexico. *Mar Biol* 141:591–601
- Jaquet N, Whitehead H (1996) Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. *Mar Ecol Prog Ser* 135: 1–9
- Jaquet N, Whitehead H, Lewis M (1996) Coherence between 19th century sperm whale distributions and satellite-derived pigments in the tropical Pacific. *Mar Ecol Prog Ser* 145:1–10
- Jefferson TA, Leatherwood S, Webber MA (1993) *Marine mammals of the world*. FAO, Rome
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends Ecol Evol* 19:101–108
- Jongman RHG, Braak CJFT, Tongeren OFRV (eds) (1995) *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge
- Kasamatsu F, Ensor P, Joyce GG, Kimura N (2000a) Distribution of minke whales in the Bellingshausen and Amundsen Seas (60°W–120°W), with special reference to environmental/physiographic variables. *Fish Oceanogr* 9:214–223
- Kasamatsu F, Matsuoka K, Hakamada T (2000b) Interspecific relationships in density among the whale community in the Antarctic. *Polar Biol* 23:466–473
- Kaschner K (2004) *Modelling and mapping of resource overlap between marine mammals and fisheries on a global scale*. PhD dissertation, University of British Columbia, Vancouver
- Kaschner K, Watson R, Trites AW, Pauly D (2006) Mapping worldwide distributions of marine mammals using a Relative Environmental Suitability (RES) model. *Mar Ecol Prog Ser* (in press)

- Kass RE, Raftery AE (1995) Bayes factors. *J Am Stat Assoc* 90: 773–795
- Keitt T, Bjørnstad O, Dixon P, Citron-Pousty S (2002) Accounting for spatial pattern when modeling organism–environment interactions. *Ecography* 25:616–625
- Kenney RD, Winn HE (1986) Cetacean high-use habitats of the northeast United States continental shelf. *Fish Bull (Wash DC)* 84:345–357
- Koblinsky CJ, Smith NR (eds) (2001) Observing the oceans in the 21st century: a strategy for global observations. GODAE Project Office, Bureau of Meteorology, Melbourne, Australia
- Legendre P (1993) Spatial autocorrelation—trouble or new paradigm? *Ecology* 74:1659–1673
- Lennon JJ (2000) Red-shifts and red herrings in geographical ecology. *Ecography* 23:101–113
- Logerwell EA, Smith PE (2001) Mesoscale eddies and survival of late stage Pacific sardine (*Sardinops sagax*) larvae. *Fish Oceanogr* 10:13–25
- Ma Z, Redmond RL (1995) Tau coefficients for accuracy assessment of classification of remote sensing data. *Photogramm Eng Remote Sens* 61:435–439
- MacLeod K, Simmonds MP, Murray E (2003) Summer distribution and relative abundance of cetacean populations off north-west Scotland. *J Mar Biol Assoc UK* 83:1187–1192
- Manly B (1991) Randomization and Monte Carlo methods in biology. Chapman & Hall, New York
- Marsh H, Sinclair DF (1989) Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. *J Wildl Manage* 53:1017–1024
- Mate BR, Lagerquist BA, Calambokidis J (1999) Movements of North Pacific blue whales during the feeding season off southern California and their southern fall migration. *Mar Mamm Sci* 15:1246–1257
- Mayo C, Marx M (1990) Surface foraging behavior of the North Atlantic right whale and associated zooplankton characteristics. *Can J Zool* 68:2214–2220
- McGillicuddy DJ Jr, Anderson LA, Doney SC, Maltrud ME (2003) Eddy-driven sources and sinks of nutrients in the upper ocean: results from a 0.1° resolution model of the North Atlantic. *Global Biogeochem Cycles* 17:1035–1047
- Mellinger DK, Stafford KM, Fox CG (2004) Seasonal occurrence of sperm whales (*Physeter macrocephalus*) sounds in the Gulf of Alaska, 1999–2001. *Mar Mamm Sci* 20: 48–62
- Michaelsen J, Schimel DS, Friedl MA, Davis FW, Dubayah RC (1994) Regression tree analysis of satellite and terrain data to guide vegetation sampling and surveys. *J Veg Sci* 5: 673–686
- Moore JK, Doney SC, Kleypas JA, Glover DM, Fung IY (2002) An intermediate complexity marine ecosystem model for the global domain. *Deep-Sea Res II* 49:403–462
- Moore SE, DeMaster DP, Dayton PK (2000) Cetacean habitat selection in the Alaskan Arctic during summer and autumn. *Arctic* 53:432–447
- Moore SE, Waite JM, Friday NA, Honkalehto T (2002) Cetacean distribution and relative abundance on the central-eastern and the southeastern Bering Sea shelf with reference to oceanographic domains. *Prog Oceanogr* 55: 249–261
- Moser HG, Smith PE (1993) Larval fish assemblages and oceanic boundaries. *Bull Mar Sci* 53:283–289
- Moses E, Finn JT (1997) Using geographic information systems to predict North Atlantic right whale (*Eubalaena glacialis*) habitat. *J Northwest Atl Fish Soc* 22:37–46
- Mullin KD, Hoggard W, Roden CL, Lohoefer RR, Rogers CM (1994) Cetaceans on the upper continental shelf in the north-central Gulf of Mexico. *Fish Bull (Wash DC)* 92: 773–786
- Murase H, Matsuoka K, Ichii T, Nishiwaki S (2002) Relationship between the distribution of euphausiids and baleen whales in the Antarctic (35E–145W). *Polar Biol* 25:135–145
- Murison LD, Gaskin DE (1989) The distribution of right whales and zooplankton in the Bay of Fundy, Canada. *Can J Zool* 67:1411–1420
- Murphy EJ, Morris DJ, Watkins JL, Priddle J (1988) Scales of interactions between Antarctic krill and the environment. In: Sahrhage D (ed) Antarctic Ocean resources variability. Springer-Verlag, Berlin, p 120–130
- Naud MJ, Long B, Brêthes JC, Sears R (2003) Influences of underwater bottom topography and geomorphology on minke whale (*Balaenoptera acutorostrata*) distribution in the Mingan Islands (Canada). *J Mar Biol Assoc UK* 83: 889–896
- Neter J, Kutner MH, Nachtsheim CJ, Wasserman W (1996) Applied linear statistical models. Irwin, Chicago, IL
- Okamura H (2003) A line transect method to estimate abundance of long-diving animals. *Fish Sci* 69:1176–1181
- Oksanen J, Minchin PR (2002) Continuum theory revisited: What shape are species responses along ecological gradients? *Ecol Model* 157:119–129
- Oswald JN, Barlow J, Norris TF (2003) Acoustic identification of nine delphinid species in the eastern tropical Pacific Ocean. *Mar Mamm Sci* 19:20–37
- Pearce J, Ferrier S (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol Model* 133:225–245
- Piatt JF, Methven DA (1992) Threshold foraging behavior of baleen whales. *Mar Ecol Prog Ser* 84:205–210
- Pontius RG (2000) Quantification error versus location error in comparison of categorical maps. *Photogramm Eng Remote Sens* 66:1011–1016
- Qian SS, Stow CA, Borsuk M (2003) On Bayesian inference using Monte Carlo simulation. *Ecol Model* 159:269–277
- Raum-Suryan KL, Harvey JT (1998) Distribution and abundance of and habitat use by harbor porpoise, *Phocoena phocoena*, off the northern San Juan Islands, Washington. *Fish Bull (Wash DC)* 96:808–822
- Reid JB, Evans PGH, Northridge SP (2003) Atlas of cetacean distribution in north-west European waters. Joint Nature Conservation Committee, Peterborough
- Reilly SB (1990) Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. *Mar Ecol Prog Ser* 66:1–11
- Reilly SB, Fiedler PC (1994) Interannual variability of dolphin habitats in the eastern tropical Pacific. I. Research vessel surveys 1986–1990. *Fish Bull (Wash DC)* 92:434–450
- Ribic CA, Ainley DG, Fraser WR (1991) Habitat selection by marine mammals in the marginal ice zone. *Antarct Sci* 3: 181–186
- Robinson AR, Lermusiaux PFJ (2002) Data assimilation for modeling and predicting coupled physical–biological interactions in the sea. In: Robinson AR, McCarthy JJ, Rothschild BJ (eds) The sea. John Wiley & Sons, New York, p 475–536
- Rowley C, Barron C, Smedstad LC, Rhodes R (2002) Real-time ocean data assimilation and prediction with Global NCOM. In: Proceedings of the Oceans. IEEE/MTS, Biloxi, MS, p 775–780
- Runge JA, Franks PJS, Gentleman WC, Megrey BA, Rose KA, Werner FE, Zakardjian B (2004) Diagnosis and prediction of variability in secondary production and fish recruitment processes: developments in physical–biological modeling. In: Robinson AR, Brink K (eds) The sea, Vol 13. The glo-

- bal coastal ocean: multi-scale interdisciplinary processes. Harvard University Press, Cambridge, MA, p 413–473
- Schick RS, Urban DL (2000) Spatial components of bowhead whale (*Balaena mysticetus*) distribution in the Alaskan Beaufort Sea. *Can J Fish Aquat Sci* 57:2193–2200
- Schneider D, Piatt JF (1986) Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. *Mar Ecol Prog Ser* 32:237–246
- Schneider K, Dawson S, Visser I, Childerhouse S (1998) Reactions of bottlenose dolphins to tagging attempts using a remotely-deployed suction-cup tag. *Mar Mamm Sci* 14:316–324
- Selzer LA, Payne PM (1988) The distribution of white-sided (*Lagenorhynchus acutus*) and common dolphins (*Delphinus delphis*) vs. environmental features of the continental shelf of the northeastern United States. *Mar Mamm Sci* 4: 141–153
- Smith RC, Dustan P, Au D, Baker KS, Dunlap EA (1986) Distribution of cetaceans and sea-surface chlorophyll concentrations in the California Current. *Mar Biol* 91:385–402
- Sokal RR, Rohlf FJ (1995) *Biometry*. WH Freeman, New York
- Spitz YH, Newberger PA, Allen JS (2003) Ecosystem response to upwelling off the Oregon coast: behavior of three nitrogen-based models. *J Geophys Res* 108(7):1–22
- Stafford KM, Fox CG, Clark DS (1998) Long-range acoustic detection and localization of blue whale calls in the northeast Pacific Ocean. *J Acoust Soc Am* 104:3616–3625
- Stammer D, Chassignet E (2000) Ocean state estimation and prediction in support of oceanographic research. *Oceanography* 13:51–56
- Steele JH (1978) Some comments on plankton patches. In: Steele JH (ed) *Spatial pattern in plankton communities*. Plenum, New York, p 1–20
- Torres LG, Rosel PE, D'Agrosa C, Read AJ (2003) Improving management of overlapping bottlenose dolphin ecotypes through spatial analysis and genetics. *Mar Mamm Sci* 19: 502–514
- Tynan CT, Ainley DG, Barth JA, Cowles TJ, Pierce SD, Spear LB (2005) Cetacean distributions relative to ocean processes in the northern California Current System. *Deep-Sea Res II* 52:145–167
- Waring GT, Fairfield CP, Ruhsam CM, Sano M (1993) Sperm whales associated with Gulf Stream features off the northeastern USA shelf. *Fish Oceanogr* 2:101–105
- Waring GT, Hamazaki T, Sheehan D, Wood G, Baker S (2001) Characterization of beaked whale (Ziphiidae) and sperm whale (*Physeter macrocephalus*) summer habitat in shelf-edge and deeper waters off the northeast US. *Mar Mamm Sci* 17:703–717
- Watkins WA, Tyack P (1991) Reaction of sperm whales (*Physeter catodon*) to tagging with implanted sonar transponder and radio tags. *Mar Mamm Sci* 7:409–413
- Watkins WA, Daher MA, Reppucci GM, George JE, Martin DL, DiMarzio NA, Gannon DF (2000) Seasonality and distribution of whale calls in the North Pacific. *Oceanography* 13:62–67
- Weber LH, El-Sayed SZ, Hampton I (1986) The variance spectra of phytoplankton, krill and water temperature in the Antarctic Ocean south of Africa. *Deep-Sea Res I* 33: 1327–1343
- Werner FE, Quinlan JA, Lough RG, Lynch DR (2001) Spatially-explicit individual based modeling of marine populations: a review of the advances in the 1990s. *Sarsia* 86: 411–421
- Wiens JA (1989) Spatial scaling in ecology. *Funct Ecol* 3: 385–397
- Wintle BA, McCarthy MA, Volinsky CT, Kavanagh RP (2003) The use of Bayesian model averaging to better represent uncertainty in ecological models. *Conserv Biol* 17: 1579–1590
- Wood SN (2003) Thin plate regression splines. *J R Stat Soc B Met* 65:95–114
- Wood SN, Augustin NH (2003) GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. *Ecol Model* 157: 157–177
- Woodley TH, Gaskin DE (1996) Environmental characteristics of North Atlantic right and fin whale habitat in the lower Bay of Fundy, Canada. *Can J Zool* 74:75–84
- Wunsch C (1996) *The ocean circulation inverse problem*. Cambridge University Press, Cambridge
- Yen PPW, Huettmann F, Cooke F (2004a) A large-scale model for the at-sea distribution and abundance of marbled murrelets (*Brachyramphus marmoratus*) during the breeding season in coastal British Columbia, Canada. *Ecol Model* 171:395–413
- Yen PPW, Sydeman WJ, Hyrenbach KD (2004b) Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. *J Mar Syst* 50:79–99

*Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany*

*Submitted: April 26, 2005; Accepted: October 27, 2005  
Proofs received from author(s): February 23, 2006*