

Modelling and Mapping Resource Overlap between Marine Mammals and Fisheries on a Global Scale

by

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Biologie Diplom, Albert-Ludwigs-Universität, Freiburg, Germany, 1998

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES

(Department of Zoology)

We accept this thesis as conforming

to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

September 2004

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Abstract

Potential competition for food resources between marine mammals and fisheries has been an issue of much debate in recent years. Given the almost cosmopolitan distributions of many marine mammal species, investigations conducted at small geographic scales may, however, result in a distorted perception of the extent of the problem. Unfortunately, the complexity of marine food webs and the lack of reliable data about marine mammal diets, abundances, food intake rates etc., currently preclude the assessment of competition at adequately large scales. In contrast, the investigation of global resource overlap between marine mammals and fisheries (i.e., the extent to which both players exploit the same type of food resources in the same areas) may, however, be easier to achieve and provide some useful insights in this context.

Information about the occurrence of species is a crucial pre-requisite to assess resource overlap and also to address other marine mammal conservation issues. However, the delineation of ranges of marine mammals is challenging, due to the vastness of the ocean environment and the difficulties associated with surveying most species. Consequently, existing maps of large-scale distributions are mostly limited to subjective outlines of maximum range extents, with little additional information about heterogeneous patterns of occurrence within these ranges.

I developed a new, more objective approach to map global geographic ranges and the relative environmental suitability (RES) for 115 marine mammal species. This habitat suitability model is a rule-based environmental envelope model that can utilize not only quantitative data, but also alternative, non-quantitative and more readily available information about species habitat preferences (such as expert knowledge). As a first step, I assigned each species to broad-scale ecological niche categories with respect to depth, sea surface temperature and ice edge association based on synopses of published qualitative and quantitative habitat preference information. Within a global grid with 0.5 degree latitude by 0.5 degree longitude cell dimensions, I then generated an index of the relative environmental suitability (RES) of each cell for a given species by relating quantified habitat preferences to locally averaged environmental conditions in a GIS modeling framework.

RES predictions closely matched published distributions for most species, suggesting that this rule-based approach for delineating range extents represents a useful, less subjective alternative to existing sketched distributional outlines. In addition, raster-based predictions provided information about heterogeneous patterns of the relative suitability of the environment and potential core habitat for each species throughout its range.

I validated RES model outputs for four species (northern fur seals, harbor porpoises, sperm whales and Antarctic minke whales) from a broad taxonomic and geographic range using 'at-sea' sightings from

dedicated surveys. Observed relative encounter rates and species-specific predicted environmental suitability were significantly and positively correlated for all species. In comparison, observed encounter rates were positively correlated with < 3 % of 1000 simulated random data sets of species occurrence.

To validate the RES predictions for data-deficient species such as beaked whales (Ziphiidae, Cetacea), I developed a different evaluation approach using stranding records as an alternative type of test data. Ziphiids represent one of the least known families of mammals, primarily known from strandings, along with only a few known 'at-sea' records for each species. Using a global data set of residual ocean currents, I developed a simulation model of ziphiid strandings and used this to generate relative probabilities of strandings along all coastlines. Predictions were generated based on two different input distributions: species-specific RES predictions and uniform distributions based on published information, which served as the null model. Large-scale patterns of simulated strandings based on RES predictions produced significant correlations with observed strandings for five times as many species (10 of 21 ziphiid species) as those generated based on the null model (2/21), suggesting that RES predictions represent an improvement over existing simple outlines.

The extensive validation provided support that RES predictions capture patterns of species occurrence sufficiently enough to be used as the basis for large-scale investigations of marine mammal-fisheries interactions. I therefore used the model to assess the importance of spatial aspects for the investigation of overlap between marine mammals and fisheries in terms of food resource exploitation.

To assess spatially-explicit resource overlap, I first estimated global annual food intake (specified by food types) for each species based on a basic food consumption model. This model required information about global population abundances, sex-specific mean weights, standardized diet compositions, and weight-specific feeding rates, which was obtained through the compilation, screening and processing of more than 2000 publications. By linking species-specific RES predictions with estimated consumption for each species, I generated spatially-explicit food consumption rates (expressed as food intake per km² per year). Superimposing geographically disaggregated fisheries catches (generated by a similar model) allowed me to calculate overlap between catches and consumption with respect to both the composition of food types and areas where food / catches were taken.

The model indicated that, in the 1990s, average consumption by all marine mammal species combined was several times higher than total fisheries catches during the same time period. However, effective spatial overlap and exploitation of the same food types was relatively low, suggesting that actual competition between fisheries and marine mammals may be much lower than proposed. I predicted the highest resource overlap in the temperate to subpolar shelf regions of both hemispheres, though overlap is more pronounced in the North. Overall, < 15 % of all fisheries catches and < 1% of all estimated marine mammal food consumption stem from areas of high predicted overlap. Nevertheless, overlap between

marine mammals and fisheries may be an issue of concern on smaller scales (especially for species with small feeding distributions) that requires more detailed, local investigations.

I propose that mapping of suitable habitat for marine mammals using the new RES model is useful for evaluating current assumptions and knowledge about species' occurrences, especially for data-poor species. Generated hypotheses about suitable habitat and species' occurrences may help to focus research efforts on smaller geographic scales, and usefully supplement other, statistical habitat suitability models. Furthermore, the mapping of food consumption rates and geographical 'hotspots' of marine mammal-fisheries interactions will help to identify potential areas of highest conflict and may aid the development of management approaches at appropriate scales.

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Acknowledgements

This thesis was conducted as part of the ‘Sea Around Us’ Project with funding provided by the Pew Charitable Trusts of Philadelphia, USA as well as National Science and Engineering Research Council of Canada. I am very grateful for additional support that I received through a ‘DAAD’ scholarship, a ‘Li Tze Fong’ Graduate Fellowship and a Partial University Graduate Fellowship from the University of British Columbia and for the funding provided by the Humane Society of the United States during the last months of this thesis.

I am indebted to my supervisors, Daniel Pauly and Andrew Trites as well as to my Committee members, Reg Watson, Villy Christensen and Brian Klingenberg for their support and patience with me and for helping me to wrap up the actual writing part of this thesis in an insanely short period of time. I would particularly like to thank Daniel, for being one of the most inspiring supervisors I can imagine, and for teaching me to how to ‘think big’. I would also like to thank him for recruiting me for the ‘Sea Around Us’ project, an experience I have greatly enjoyed and from which I have benefited immensely. I am more than grateful to Reg Watson, whose incredible faith in my modeling abilities, though generally by far exceeding the real state of affairs, continued to pushed me beyond what I thought I could do and without whom I couldn’t have done this thesis.

Many thanks to everybody in the Marine Mammal Research Unit and the Fisheries Centre for making this a wonderful place to work in. I would like to thank Ben Wilson for sharing so many of those late nights and weekends at the office with me and for his great feedback on everything I did – his input has made me a better scientist. I am equally thankful to Ed Gregr, for our regular ‘Socrates’ walks during which we discussed effort issues and other geeky modeling questions. My thanks also to Madlen Denoth, Anna Hall, Andrea Hunter, Soenke Jansen, Ruth Joy, Arliss Winship, who helped with the development of the statistical approach. In addition, I am grateful to Fritz Denoth, Alicia De Praeter, Saeko Kumagai, Jason Ladell, Gunna Weingartner and Kate Willis for their help with the data entry.

I am greatly indebted to Cherry Allison and the Secretariat of the International Whaling Commission for providing us with the IWC catch and sighting data sets used for the validation of the RES model and would also like thank Phil Hammond, SMRU for giving me access to the SCANS data set used for the same purposes and Peter Olesiuk for providing the northern fur seal data. Thank you also to Angela D’Amico and colleagues, who – through Colin MacLeod – gave me access to the global database of beaked whale strandings and sightings, compiled by them

I am eternally grateful for the wonders of modern technology and the inventors of the internet which allowed me to work on this PhD project while effectively splitting my time between Vancouver and Hamburg, Germany due to the maintenance demands of a transatlantic relationship. In Hamburg, I am particularly indebted to everybody at the Bundesanstalt für Fischereiforschung (BFA) and Gerd Hubold, for providing me with workspace and never-ending logistical support when the wondrous internet wasn’t being co-operative. I

would like to particularly thank Soenke Jansen for generously allowing me to share his always immaculately tidy office, and for forgiving me for the considerable amount of chaos I generally introduced into it, and his patience with the many, many distractions – strictly professional, of course – that came along with my presence.

So many people have helped in numerous little ways, mainly by being there for me at the right times and for picking me up when this thesis felt like it was never going to end, all of whom I want to thank:

Gunna and Madlen for our regular ‘Germanische Weiberklub’-meetings and Gunna for dragging me out of the office on weekends to go ski-touring or hiking. Sheila for sharing my joy for singing and for being who she is to me, always giving me what I needed most whenever I needed it most, a kick in the butt, a helping hand or a great loving hug. The Enga family, for providing me with a second home away from home, for all your love and support – I couldn’t have done this without you. Kate, my eternal heroine and role-model when it comes to sticking to deadlines, for being there for me in my darkest, most doubtful hours and pulling me through by showing me again how to walk one step at a time. My dearest Ayesha, for putting things into perspective (‘World fisheries crisis’ – such a quaint little subject...). Colette for moving to Vancouver, even if it was way too late! Volker Deecke, my longest office-mate, Doppelkopf-partner and friend, for his considerable insight into the female psyche that was very apparent from the selection of numerous cheer-up gifts he gave me and for – by lending us his gorgeous wonderful house during the final month of this undertaking – turning what should have been the most awful period of my PhD into a time that has seen me more relaxed and more tanned (!) than I have been in a couple of years. Mary-Ann for great coffee breaks and for sacrificing the better part of her birthday to help me during the manic rush to print this thing.

My friends at in Germany for keeping me in their hearts and in their thoughts during these past six years and for all the effort you, Fee, Andreas, Krischan, Monika, Hermensche, Sandra, Daggy, Bero and all the others made to see me during my always too short sojourns in good old Germany.

My family for being what you are to me, for all your constant, never-ending love, patience and support and my dearest and most beloved niece, Lina, for reminding me what is really important in life.

And finally, Frank, mein Macker und geliebtester Held, for believing in me, as only you believe in me and for selflessly giving up a lot to walk with me for the last year of this incredibly long journey, thereby adding infinitely more happiness to it – and also, after 5 years of transatlantic relationship, for still being there when this finally ended – we made it!

Pamela, you can have my desk now....☺

1. General Introduction¹

1.1. MARINE MAMMAL-FISHERIES INTERACTIONS

The anthropogenic impact on marine ecosystems, through fisheries or other human activities, is of major concern. World fisheries are in decline (Watson & Pauly 2001, Pauly et al. 2002, Hilborn et al. 2003) and the last decades have seen massive collapses in fisheries (Swissenwine & Rosenberg 1993, Pauly et al. 2002). Moreover, there has been a severe depletion of marine top predators (Christensen et al. 2003, Myers & Worm 2003) and a worrisome trend to target lower and lower trophic levels that has been termed ‘fishing-down-the-food-web’ (Pauly et al. 1998a), all of which have contributed to the crisis that world fisheries are in today. The focus of fisheries management on single stock assessments has been partially held responsible for this crisis, since this approach neglects important trophic interactions and other interdependences of species in marine ecosystems (Christensen & Pauly 1997, Link 2002, Pauly et al. 2002). Consequently, there has been an increasing demand for ecosystem-based fisheries management that considers the direct and indirect effects of fisheries on all components of marine food webs, including those on predators of commercially targeted fish species (Christensen 1996, Constable 2001).

Such predator species include marine mammals, many of which are affected and frequently threatened by fisheries and other human activities (Northridge 1991, Northridge 2002). Marine mammals are a heterogeneous group of species that belong to one of four taxonomic groups of mammals (Suborder *Pinnipedia* – seals and sealions, Suborder *Mysticeti* – baleen whales, Suborder *Odontoceti* – dolphins and porpoises and Order *Sirenia* – dugongs and manatees) – the majority of which have evolved independently adaptations for an aquatic lifestyle (Rice 1998). Of the 128 currently recognised species, 115 live predominately in the oceans (Rice 1998, Bannister et al. 2001, Dalebout et al. 2002). In the past, the main anthropogenic threats to marine mammals were large-scale whaling (Clapham & Baker 2002) and sealing operations (Gales & Burton 1989, Knox 1994, Rodriguez & Bastida 1998). These focussed initially on the waters of northern Europe and Asia, but soon extended all the way to Antarctica, and reduced numerous populations to small fractions of their former abundances (Perry et al. 1999) or extirpated them completely, as with the now extinct Atlantic grey whale (Mitchell & Mead 1977) or the Caribbean monk seal (Kenyon 1977, Gilmartin & Forcada 2002). Today, humans adversely impact marine mammals mainly through incidental entanglement in fishing gear (Northridge 1991, Harwood et al. 1999, Northridge 2002, Kaschner 2003) and in some cases ship strikes (Clapham et al. 1999, Fujiwara & Caswell 2001). Moreover, marine mammal species, just like other components of marine ecosystems,

¹ Parts of this chapter have been submitted as Kaschner, K. & Pauly, D (2004). Competition between marine mammals and fisheries: Food for thought. Report to the Humane Society of the United States.

are affected by chemical (Mossner & Ballschmiter 1997, Borrell & Reijnders 1999, Coombs 2004) and acoustical pollution (Johnston & Woodley 1998, Jepson et al. 2003). These impacts and the effects of climate change are likely to increase in the future (Harwood 2001), but even today some populations or species have been brought close to the point of extinction by human activities, such as the vaquita (D'Agrosa et al. 2000), the Mediterranean (Aguilar 1998, Ridoux 2001, Gucu et al. 2004) and Hawaiian monk seals (Carretta et al. 2002) and western North Atlantic right whales (Perry et al. 1999, COSEWIC 2003).

There are, however, also situations in which some marine mammals could potentially adversely impact humans, although this is primarily restricted to interactions with fishing operations. Controversial cases include the damaging of gear (e.g., harbour seals vs. fish farms) (Johnston 1997, Fertl 2002), devaluation of catch through depredation (killer whales vs. long line fisheries in Alaska) (Dahlheim 1988, Fertl 2002) or indirectly, through costs incurred by gear modifications that are required to reduce anthropogenic impacts on marine mammal species (e.g., dolphin-excluder devices, pingers) (Harwood 1999, Palka 2000, Read 2000, Culik et al. 2001).

In recent years, as the fisheries crisis has developed from a set of regional problems to a global concern (Pauly et al. 2002, Pauly et al. 2003) and the animal protein that millions of people depend upon is in increasingly shorter supply, competition between marine mammals and fisheries for available marine food resources has often been mentioned as another issue of concern (Beddington et al. 1985, Harwood & Croxall 1988, Plagányi & Butterworth 2002). This is understandable as many marine mammal species, in common with humans and many other apex predators, such as piscivorous fish, operate near or at the top of the marine food web (Pauly et al. 1998a). However, in comparison to fish, marine mammals are much more conspicuous and most species are relatively large, indicating that they must consume large quantities of food. Moreover, at least some species – notably various species of fur seals (Torres 1987, Wickens & York 1997) and some of the northern hemisphere phocid species (Angliss & Lodge 2002, Lucas & Daoust 2002, Waring et al. 2002) - have recovered from previous levels of high exploitation and their populations are increasing, although population levels of most species are still far below their pre-exploitation abundance (Torres 1987, Wickens & York 1997, Perry et al. 1999).

For these reasons – and given the growing need to find scapegoats for the collapse of fisheries – marine mammals lend themselves quite easily as culprits for the problems various fisheries are facing (Holt 2004). Thus, the voices of countries and corporations with large fishing interests, requesting “holistic management” that includes “the utilization of marine mammals such as whales...to increase catch from the oceans” (Anonymous 2001), have been growing louder. As a consequence, much political pressure has been applied in recent years in various international fora concerned with the management of global marine resources to begin to address the issue of competition between marine mammals and fisheries on a global scale (van Zile 2000, FAO 2001, Holt 2004).

1.2. COMPETITION FOR FOOD AND RESOURCE OVERLAP

1.2.1. Definitions of competition and resource overlap

From an ecological perspective, competition has been defined as a situation where the simultaneous presence of two resource consumers is mutually disadvantageous (Chase & Leibold 2003). A rarely acknowledged, but implicit assumption is that the removal of one of the players would translate into direct benefits for the other consumer. In the context of the proposed competition between marine mammals and fisheries, competition occurs when both marine mammals and fisheries consume the same types of food in the same general geographical areas (and water depths). More importantly though, competition occurs only if the removal of either marine mammals or fisheries results in a direct increase of food available to the other (Cooke 2002, IWC 2003).

Within the same theoretical framework of niche ecology, resource or niche overlap describes a more neutral form of species interaction. Resource overlap represents the extent to which two consumers overlap in the exploitation of the same resource in the same area but without the assumption that the presence of either consumer has any effect on the other (Chase & Leibold 2003). Although not identical to competition, the extent of niche similarity that is described by resource overlap is widely recognized as being a useful indicator for potential competition (Hurlbert 1978, Wan-Xiong et al. 2003). At the same time, measurements of resource overlap are less data-demanding than the assessment of competition since trophic linkages are not considered. Consequently, until more adequate models can be developed, the assessment of resource overlap between marine mammals and fisheries can provide some useful insights into the extent of potential competition and has been the focus of most studies addressing this issue to date.

1.2.2. Objectives of the study

The main objective of my study was to investigate the extent of resource overlap between marine mammals and fisheries on a global scale taking differences in spatial occurrence and food types taken by either groups into account. To assess this issue, I addressed the following questions:

- Is it possible to develop a generic model to predict marine mammal distributions based on the available information?
- Can such a model adequately capture patterns of species occurrence, even for data-deficient species?
- Is it possible to investigate global resource overlap by linking such a model to a simple food consumption model?

- Are there any indications that resource overlap is great enough to provide some support for the notion that competition between marine mammals and fisheries may be a global problem?

In the following, I present a brief overview of existing models that have been applied to similar questions to put the questions asked and the models developed here into context.

1.2.3. Measuring competition and resource overlap

There are many approaches that have been used to qualitatively and quantitatively assess the ecological role of marine mammals and the extent of their trophic competition or overlap with fisheries (e.g., Harwood & Croxall 1988, Sigurjónsson & Víkingsson 1992, Bowen 1997, Trites et al. 1997, Hammill & Stenson 2000, Thomson et al. 2000, Yodzis 2001, Boyd 2002). To address this question, various approaches have been applied to the problem of modelling marine mammal food consumption and the potential effects of this intake on fisheries yields (reviewed in detail by Cooke 2002, Harwood & McLaren 2002, IWC 2003). Existing approaches range from simple static surplus yield models to very sophisticated trophodynamic ecosystem models that consider, among other things, interactions between multiple species changing over time and in space (Bogstad et al. 1997, ICES 1997, Bogstad et al. 2000, Christensen & Walters 2000, Livingston & Jurado-Molina 2000). All input parameters of any of these models are greatly affected by uncertainties that stem from the difficulties of studying any aspects of marine mammal biology in the wild (Tjelmeland 2001, Harwood & McLaren 2002, IWC 2003). Consequently, experts agree that there is as yet no model that is sufficiently detailed and meets the stringent scientific requirements to allow a reliable investigation of the effects, positive or negative, that the reduction of marine mammal populations might have on net fisheries catches (Harwood & McLaren 2002, IWC 2003).

1.2.3.1. Surplus yield models

Surplus yield models are simple food consumption models that – in their simplest form – calculate the quantity of prey taken by marine mammal species by simply estimating the amount of food consumed by one animal of a specific species based on its estimated mean weight, multiplying this amount by the total estimated number of animals of this species and then summing this estimate of food intake for all or major subgroups of marine mammal species. In some cases, information about the diet composition of the marine mammal in question is also incorporated. Estimates of marine mammal food consumption thus derived generally amount to quantities several times greater than the catches of fisheries taken in the same geographic area (e.g., Kenney et al. 1997, Sigurjónsson & Víkingsson 1997, McLaren et al. 2002, Tamura 2003). Gross estimates of the total amount of fish consumed by marine mammals, by themselves, provide little or no information about the net ‘gain’ in fisheries catches that might result from a reduction in numbers of any marine mammal population. It is, nevertheless, often assumed or implied that a

reduction in the predator population will translate directly into a corresponding increase in prey, and that this increase would then be available for fisheries to exploit (reviewed in Harwood & McLaren 2002).

Simplistic surplus yield models are regarded as inadequate to investigate the issue of potential competition since they largely ignore important issues of uncertainty associated with all input parameters and the effects of food web interactions (Harwood & McLaren 2002, IWC 2003). Most importantly, these models completely ignore the complex range of dynamic factors that determine how the removal of large, high-level predators affects ecosystems (Parsons 1992). However, generated outputs from such models may allow an assessment of resource overlap with fisheries, if spatial aspects and dietary considerations are incorporated as done in this study.

1.2.3.2. Minimum realistic models

Minimum realistic models are expansions of surplus yield models that incorporate predator mortality directly into models of the dynamics of targeted prey species. Such models can consider some prey species interactions and may also be spatially-explicit (Harwood & McLaren 2002). Incorporating additional trophic linkages can lead to counter-intuitive results of predicted responses of prey stocks in relation to changes in predator abundance, where prey biomass may actually decrease if predator abundance decreases. This may be the case if predators do not only consume the prey species itself, but also the prey species' competitors and /or its predators – thereby actually reducing the net predation on the prey (Parsons 1992, Punt & Butterworth 1995, Cooke 2002). This so-called 'beneficial predation' or 'meso-predator release' is a common feature in ecosystems and counterintuitive results of removing high-level predators from ecosystems have been well demonstrated (Parsons 1992, Punt & Butterworth 1995, Caddy & Rodhouse 1998, Yodzis 1998, Crooks & Soulé 1999, Pauly et al. 2000, Yodzis 2001, Bjørge et al. 2002, Okey et al. 2004).

Examples of minimum realistic models include MULTSPEC, a spatially-explicit, mixed static-flow and dynamic modelling approach developed to assess the impacts of consumption of herring, capelin and cod by two marine mammal predators (minke whales and harp seals) (Bogstad et al. 1997). Other minimum realistic models are modified versions of the multi-species virtual population analysis (Livingston & Jurado-Molina 2000). The United Nations Environment Programme recommended the use of minimum realistic models to investigate proposals for marine mammal culls (UNEP 1999), although some authors have cautioned against the usefulness of such models in the context of investigating competitive interactions between marine mammals and fisheries (Yodzis 1998, 2000, 2001).

1.2.3.3. Food web and mass-balance models

The most complex models used to assess effects of marine mammal food consumption are static or dynamic representations of food webs that model energy flows in ecosystems. Examples of such models include Ecopath with Ecosim (EwE) (Christensen & Walters 2000, Pauly et al. 2000) which combines a static mass-balance model with a dynamic component and allows the expression of biomass flux rates among food web

components as a function of time, varying biomass and harvest rates (Christensen et al. 2000). Investigations of marine mammal-fisheries interactions based on EwE models include e.g., a Bering Sea model used to examine some possible explanations for the ecosystem changes that occurred in the Bering Sea between the 1950s and 1980s (Trites et al. 1999). Moreover, EwE has recently been used to investigate the effects of different functional responses on estimates of minke whale food intake (Mackinson et al. 2003). Other types of trophodynamic food web models include approaches where population dynamics are deduced from bioenergetics, such as a model developed by Yodzis (1998) to assess the effects of Cape fur seal culls on the ecosystem.

Current existing ecosystem models, though useful for generating hypotheses about possible impacts of fisheries on marine ecosystems, are also generally considered to be inadequate for providing reliable answers to guide management decisions concerning the effects of competitive interactions due to high input parameter uncertainties (IWC 2003).

1.2.2.5. Importance of scale and scope

Most existing complex models studying food consumption and competitive interactions of marine mammals and fisheries focus on relatively small geographic areas (e.g., Stenson & Perry 2001, Bjørge et al. 2002, García-Tiscar et al. 2003). However, except for a few species that haul out on land during reproductive seasons, or have very small coastal ranges, marine mammals are not restricted in their distribution by the distance to the nearest landmass or the climatic conditions that largely influence the locations of fishing grounds and major human settlements. Conversely, many species occur predominately in geographic areas still largely inaccessible and/or rarely frequented by humans, such as the ice-breeding seals of the northern and southern hemispheres or many of the dolphin or whale species occurring in tropical offshore waters. As a result, the perception of the extent of the problem in terms of resource overlap and potential competition between fisheries and most marine mammal species is distorted by models that are restricted to areas that represent only a small part of a species' distributional range.

The few models that encompass larger areas and higher taxonomic groupings represent the other end of the scale in terms of model complexity (Hinga 1979, Trites et al. 1997, Young 1999, Tamura 2003). Many of these highly simplified, large-scale models have failed to adequately specify their results by prey type (Hinga 1979, Tamura 2003), thus ignoring a key factor that will determine the extent of resource overlap and potential competition. Furthermore, the spatial and temporal resolution of marine mammal food consumption of most large-scale models is very coarse, with total food intake being only specified by ocean basin (Young 1999, Tamura 2003) or FAO statistical areas (Trites et al. 1997). Such models implicitly assume homogenous geographic species distributions and feeding patterns.

The development of a large-scale model investigating resource overlap that considers important spatial aspects of marine mammal food intake and fisheries catches would enable the assessment of the extent to

which marine mammal foraging overlaps with areas of fishing activities. The spatial co-occurrences of fisheries and marine mammals may be indicative of the degree of likely competition. Unfortunately, the data needed for such models, that is information about marine mammal species occurrence (as well as the geographic origin of fisheries catches), is generally considered to be unavailable at larger scales. However, the application of habitat suitability modelling approaches may hold some promise.

1.3. HABITAT SUITABILITY MODELLING AND MARINE MAMMAL DISTRIBUTIONS

Habitat suitability modelling allows the objective and quantitative delineation of maximum range extents of species, in addition to providing information about patterns of occurrence of species throughout their range (Guisan & Zimmermann 2000). This is generally achieved by predicting potential habitat in unsurveyed areas based on the relationships between species' presence and the environmental parameters observed in surveyed areas (e.g., Fera & Peterson 2002, Hamazaki 2002, Johnson et al. 2004). The advantages of using models to map species occurrence is that generated results are reproducible and underlying assumptions are clearly defined and modifiable.

Existing habitat suitability modelling approaches range from highly specific empirical models to broader mechanistic models that sacrifice predictive precision for general applicability and focus on the investigation of processes (reviewed in Guisan & Zimmermann 2000). While empirical models strive to describe a species' realized niche or actual habitat based on location point-data, mechanistic models often start off by parameterizing the fundamental niche (i.e., a species' potential habitat) (Guisan & Zimmermann 2000). All habitat suitability models use resource response curves that describe the distribution of a species in relation to a specific environmental parameter (Austin 2002, Boyce et al. 2002). However, assumptions and shape of such curves vary widely between different approaches (Guisan & Zimmermann 2000). Most commonly used habitat prediction approaches are empirical models that include regression models such as generalized linear models (GLMs) and general additive models (GAMs) (Guisan et al. 2002) as well as classification and ordination techniques (Guisan & Zimmermann 2000). These empirical approaches tend to be applied only to relatively small geographic areas. Large-scale distributions of species may be more adequately described using mechanistic, rule-based modelling approaches, such as environmental envelope models (Shao & Halpin 1995, Guisan & Zimmermann 2000), genetic algorithms (e.g., GARP Stockwell & Noble 1992, Peterson 2001) or ecological niche factor analysis (e.g., ENFA Hirzel et al. 2002). These models require fewer data points and can handle the problems of missing absence data (Hirzel et al. 2002, Engler et al. 2004) as they rely more on conceptual frameworks and non-quantitative general information about species occurrences in relation to their environment (Store & Jokimäki 2003).

Habitat suitability modelling in general is still a nascent field with most efforts having focused on the application of such models to terrestrial systems and non-mobile organisms (e.g., Peterson & Navarro-

Sigüenza 1999, Moisen & Frescino 2002, Zaniewski et al. 2002, Store & Jokimäki 2003). Although a number of studies have investigated a wide range of environmental correlates of marine mammal species occurrence (Davis et al. 2002, Baumgartner et al. 2003, Lea & Dubroca 2003, Trukhin 2003, Hastie et al. 2004), there are only a few attempts to predict marine mammal species occurrence (Moses & Finn 1997, Hedley et al. 1999, Gregr & Trites 2001, Hamazaki 2002). Most of these habitat suitability models cover only small areas representing only a fraction of a species total distributional ranges.

However, objective models that describe large-scale occurrence patterns of marine mammals are lacking and existing information is limited to subjective outlines of maximum ranges (e.g., Ridgway & Harrison 1981a, b, Jefferson et al. 1993, Reijnders et al. 1993). For many marine mammal species, the vastness of their distributions in the ocean environment and the difficult accessibility of large proportions of it, contributes to a prevailing lack of comprehensive data sets, such as are needed for the applications of GLMs, GAMs or other empirical model types. It has been suggested, however, that the distribution and spatial dynamics of large marine organisms in relation to the physical environment may be more productively investigated by testing hypotheses in relation to well defined conceptual models than by direct correlation with measurements of oceanographic parameters (Schneider 1997). Moreover, a comparison of the performance of different habitat suitability models showed that more sophisticated statistical models do not necessarily perform better than simpler approaches when faced with real data, especially if data quality was poor (Moisen & Frescino 2002). When focusing on a global scale, the simpler environmental envelope type models that sacrifice ‘detail for generality’ (Gaston 1994) may therefore represent a more suitable option.

1.4. THESIS OVERVIEW

This thesis focuses on the investigation of the extent of overlap in food resource exploitation between 115 marine mammal species and fisheries on a global scale. Although resource overlap cannot be equated with food competition and *vice versa*, results from my study may provide insights into the severity of potential impacts of competitive interactions between marine mammals and fisheries. I have investigated resource overlap by developing a new rule-based spatial modelling approach to predict large-scale distributions of marine mammal species that relies on non-quantitative information generally not exploited by other habitat prediction models. The model was tested extensively and then used, in conjunction with other data and a simple food consumption model, to generate spatially-explicit food consumption estimates for all marine mammal species. These were compared with spatially-explicit fisheries catches to assess the degree of spatial and dietary overlap between the two. Input parameters for the rule-based models were obtained by synthesizing available information on marine mammal distributions, diets, abundances and other parameters extracted from more than 3000 publications that I standardized and compiled in a global marine mammal database.

My thesis consists of five chapters: Following the overview about marine mammal food consumption and habitat suitability models in the General Introduction, I present a relative environmental suitability (RES) model used to map global distributions of 115 species of marine mammals (Chapter 2). This environmental envelope model mainly relied on alternative types of habitat preference information such as expert knowledge and general species descriptions, which is more readily available than comprehensive sightings data sets for many species. Within a GIS modelling framework I sought to predict the relative suitability of the environment for each species by relating known habitat preferences to local environmental conditions in a global grid of 0.5 degree latitude by 0.5 degree longitude cells. Predicted distributions are presented together with results of a validation approach using large-scale sightings data sets. For further validation I used a stranding simulation model to test the validity of the RES predictions for data-deficient marine mammal species such as the beaked whales (Chapter 3). In Chapter 4, I combined the species-specific RES maps with global estimates of species abundance for the 1990s, and used a basic food consumption model to generate spatially-explicit estimates of marine mammal food intake (expressed in proportions of nine different food types) for four major species groups (mysticetes, pinnipeds, large odontocetes and small cetaceans). I then investigated the extent to which marine mammals exploited the same food resources as fisheries in the same areas during an average year of the 1990s. This was achieved by comparing food consumption densities with fishing rates during the same time period that were generated by a similar rule-based approach and were expressed as proportions of the same nine food types. Finally, I discuss all of the findings in the context of related habitat suitability and marine mammal-fisheries interaction studies and provide suggestions for future improvements and applications of the RES model (Chapter 5).

Except for the concluding chapter (Chapter 5), all chapters are self-contained and have been written up as scientific papers or reports that have been already published, are currently in review or have been submitted for review. Consequently there is a degree of necessary repetition between chapters. I am the senior author on all papers presented in this thesis and have been primarily responsible for the development of the RES and the resource overlap model, the collection, compilation and synthesis of input parameter information and validation data sets, the validation approach itself, the statistical analysis conducted and the preparation of all manuscripts. However, several co-authors have contributed significantly to all chapters and their respective contributions are briefly outlined in the following:

Reg Watson, Andrew W. Trites and Daniel Pauly (all based at the Fisheries Centre, UBC, Canada) are co-authors of the second chapter. Reg Watson was instrumental for the development of the RES mapping approach, since I programmed the model as a module of a custom-made GIS package, SimMap, developed by him and Norman Hall. He, moreover, provided most of the rasterized environmental data.

Chapter 3 presents work carried out in collaboration with Reg Watson, Colin MacLeod (University of Aberdeen, UK) and Daniel Pauly, all of whom are co-authors. Reg Watson programmed the initial

stranding simulation model that was then further developed by me. Colin MacLeod gave me access to the global beaked whale strandings and sightings database and provided expert knowledge on ziphiids.

The assessment of global resource overlap between marine mammals and fisheries presented in Chapter 4 is co-authored with Reg Watson, Andrew W. Trites, Villy Christensen (Fisheries Centre, UBC, Canada) and Daniel Pauly as co-authors. I, again, programmed the spatially-explicit food consumption and resource overlap model as modules of the SimMap programme. Reg Watson provided the spatially disaggregated fisheries data for the 1990s that I used in the overlap analysis. Villy Christensen helped with the modification of the resource overlap index.

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2. Mapping world-wide distributions of marine mammal species using a Relative Environmental Suitability (RES) model²

2.1. INTRODUCTION

A number of marine mammal species are currently threatened by a variety of anthropogenic factors, ranging from bycatch and ship-strikes to pollution, global warming and potential food competition (Perrin et al. 2002). Limited information about where these species occur and which areas may be critically important to them is an obstacle to developing efficient management strategies to reduce such impacts. However, delineating geographic ranges of marine mammals is hampered by difficulties in defining distributional limits of these elusive and often highly mobile animals. Due to the vastness of the marine environment, even designated and costly surveys usually cover only a small fraction of the distributional ranges of most species, and often yield little more than a snapshot, both in time and space, of a given species' occurrence and geographic range (e.g., Kasamatsu et al. 2000, Hammond et al. 2002, Waring et al. 2002). The comparatively low densities of many marine mammal species further means that it is often difficult to distinguish between insufficient effort to detect a species in a given area and its actual absence. Conversely, a concentration of sightings may only reflect the concentration of effort rather than a concentration of animals (Kenney & Winn 1986).

As a consequence of the inherent difficulties of surveying marine mammals, the description of the geographic ranges is based on the professional judgment of experts and the synopsis of qualitative information (e.g., Ridgway & Harrison 1981a, b, 1985, 1989, Ridgway & Harrison 1994, Ridgway & Harrison 1999, Perrin et al. 2002). Distributional ranges published to date therefore mainly consist of rough sketches on maps outlining the proposed maximum range of species' occurrence – often supplemented by relatively large regions covered by question marks, indicating areas of likely occurrence. These maps are greatly confounded by the uncertainty in the degree of interpolation applied to the occurrence data (Gaston 1994), and there is considerable variation amongst range extents proposed by different authors for the same species (Jefferson et al. 1993, Reijnders et al. 1993). Alternative approaches to mapping species distributions have been to summarize documented stranding or sighting locations on maps as point data (e.g., Perrin et al. 1994, Jefferson & Schiro 1997, Ballance & Pitman 1998), or to map relative sighting or catch rates in raster maps (Kasamatsu & Joyce 1995). However, none of these approaches delineate species distributions based on an explicit algorithm that captures

² Chapter as manuscript in review: Kaschner, K., Watson, R., Trites, A.W. & Pauly, D. Mapping world-wide distributions of marine mammal species using a Relative Environmental Suitability (RES) model. *Marine Ecology Progress Series*. This chapter was also presented as Document SC/56/E30 at the Environmental Concerns Sub-Committee of the Scientific Committee of the International Whaling Commission (2004).

patterns of species' occurrences using a rule-based approach or statistical models, as recommended by Gaston (1994).

In recent years, advances in geographic information systems and computational power have allowed the development of habitat suitability models that provide quantitative alternatives to delineating maximum range extents. Habitat suitability modelling has been widely applied in terrestrial systems and a wide range of land-based species (Peterson & Navarro-Sigüenza 1999, Zaniwski et al. 2002, Store & Jokimäki 2003). There are, however, comparatively few such models that concentrate on the marine environment and specifically marine mammals. To date, existing efforts have dealt with only a few species in some restricted areas (Moses & Finn 1997, Hedley et al. 1999, Gregr & Trites 2001, Hamazaki 2002), and few authors have attempted to validate their models (Hedley et al. 1999, Gregr & Trites 2001, Hamazaki 2002).

Most of the existing habitat suitability models use empirical statistical models, such as general linear models (GLMs) or general additive models (GAMs) based on point data such as sighting or catch data sets. These models then investigate the relationships between observed species occurrence and the underlying environmental parameters that – either directly or indirectly – determine a species' presence in a known area to predict occurrence in other, unsurveyed areas (Moses & Finn 1997, Gregr & Trites 2001, Hamazaki 2002).

A shortage of sightings data sets has prevented the application of such models to predict patterns of occurrences or maximum range extents for the lesser-known species in more inaccessible or understudied regions of the world oceans. For the most part there is little likelihood of sufficient data being collected in the foreseeable future although recent modelling advances, such the development of ecological niche factor analysis (ENFA), may reduce the amount of data needed (Hirzel et al. 2002, Engler et al. 2004). Nevertheless, we already know quite a bit about the general habitat preferences of most marine mammal species available in the form of qualitative descriptions, mapped outlines, geographically fragmented quantitative observations, and large-scale historical catch data sets. I propose that this type of data may represent an alternative and underutilized resource, which can form the basis for the development of other types of habitat suitability models such as environmental envelope models. Envelope models have frequently been used in the past to predict large-scale terrestrial plant distributions (e.g., Shao & Halpin 1995, Guisan & Zimmermann 2000) but have not yet been applied to describe marine mammal range extents.

The objective of the study was to develop a generic quantitative approach to predict the average annual geographical ranges of all marine mammal species during the late twentieth century using basic descriptive data that were available for almost all species. I also wanted to gain insight into the potential relative environmental suitability (RES) of a given area for a species throughout this range. Unlike most existing habitat suitability models that rely on the statistical analysis of point data as input, I sought to

generate predictions based on the synthesis of existing and often general qualitative observations about spatial and temporal relationships between basic environmental conditions and a given species' presence. The resulting maps I produced represent a visualization of the complex relationships between some basic environmental parameters that may describe potentially suitable habitat or main aspects of a species' fundamental ecological niche, as defined by Hutchinson (1957). I tested and evaluated the model predictions using marine mammal sightings and catch data to establish the extent to which this approach may be able to capture actual patterns of species' occurrence. Finally, I explored the merits and limitations of the model as a useful supplement to existing habitat suitability modelling approaches.

2.2. MATERIAL & METHODS

2.2.1. Model structure, definitions, scope & resolution

I derived the geographic ranges for 115 marine mammal species and predicted the relative suitability of the environment for each of them throughout this range. RES predictions were based on the synthesis of the existing, often qualitative observations about the relationship between a species' presence and some basic environmental conditions. Species were assigned to broad ecological niche or habitat preference categories, which were then related to locally averaged environmental parameters in a global grid system with 0.5 degree latitude by 0.5 degree longitude cell dimensions (see Fig. 2.1 for model flow chart; note that this grid resolution was selected for the model input and outputs to be compatible with other data and maps generated by the *Sea Around Us Project*). Consequently, model outputs represented a spatially explicit index of suitability of a given location for a given species in terms of this species' preference with respect to the incorporated environmental parameters. Objective geographic ranges of species can then be determined based on predictions of low or non-suitability of areas for a given species to occur in.

Following Gaston (1994), I defined geographic range as the area between the known outer-most limits of a species' regular or periodic occurrence. While this definition is inclusive of all areas covered during annual migrations, dispersal of juveniles etc. – it specifically excludes extralimital sightings, which are sometimes difficult to distinguish from the core range (Gaston 1994). I chose to use the term 'environmental suitability' rather than 'habitat suitability' to describe the heterogeneous patterns I generated for each species, as the model often more closely describes a species fundamental rather than its realized niche (Hall et al. 1997).

General patterns of occurrence of larger, long-living animals, such as marine mammals, are unlikely to be affected by environmental heterogeneity over small temporal and spatial scales (Turner et al. 1995, Jaquet 1996). This may be particularly true for species living in the marine environment, as pelagic systems show greater continuity in environmental conditions over evolutionary time than terrestrial environments (Platt & Sathyendranath 1992). I chose to model at a global geographic scope to accommodate the wide-

ranging annual movements and cosmopolitan occurrence of numerous marine mammal species. To match the geographic scope, I used long-term averages of temporally varying environmental input parameters to minimize the impacts of inter-annual variation.

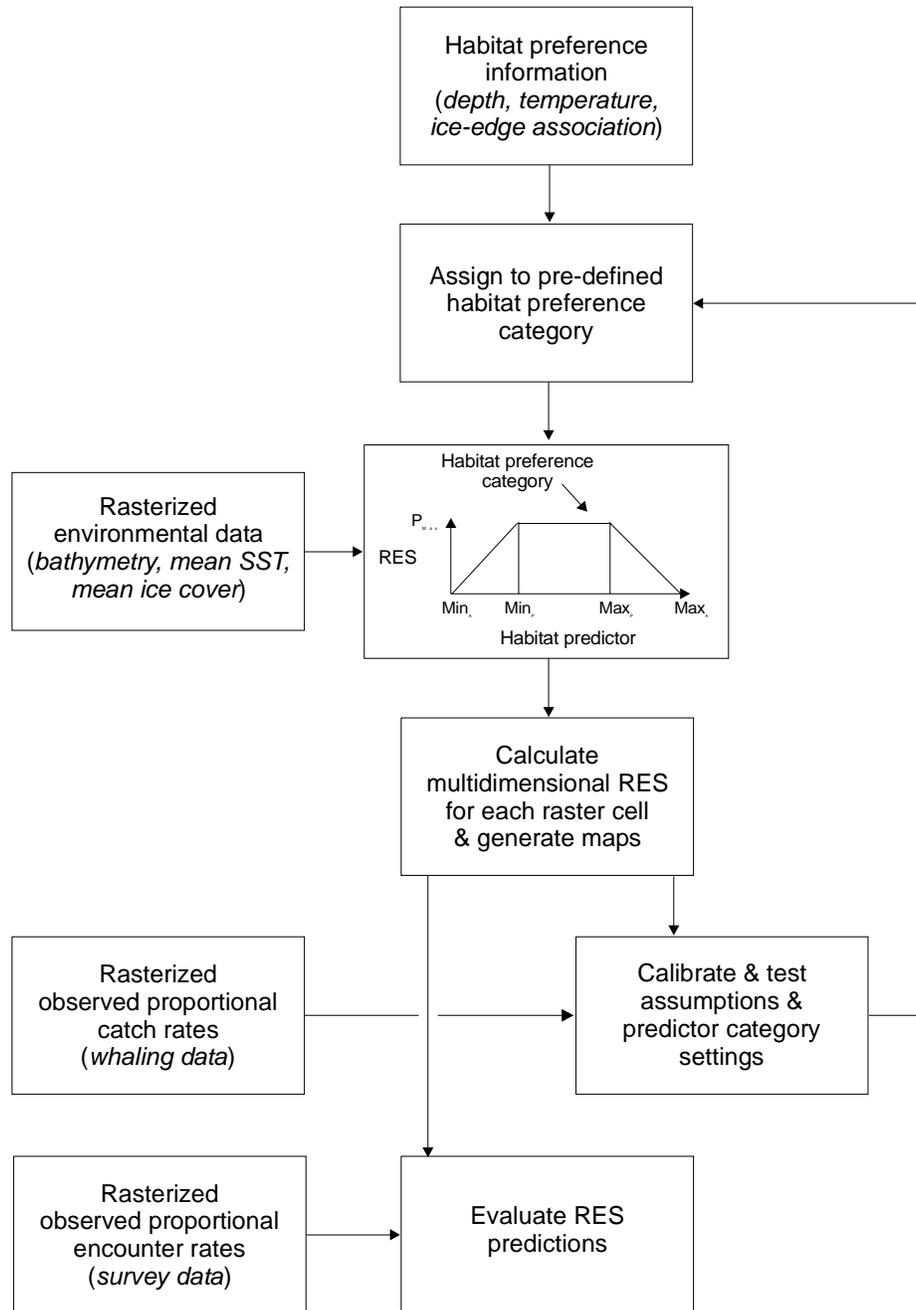


Figure 2.1.

Relative Environmental Suitability (RES) prediction model – flow chart of model structure and evaluation approach used for individual marine mammal species. Also shows trapezoidal resource selection function describing the habitat preference categories used in the model.

2.2.2. Independent variables

Selection of environmental proxies that served as independent variables in the model was based on the availability of data at appropriate scales. Moreover, predictors were chosen based on the availability of matching habitat preference information that were obtainable for all or at least the majority of all species. All environmental data were interpolated and rasterized using a custom GIS software package (SimMap) and stored as attributes of individual grid cells in the global raster (Watson et al. 2004) (Fig. 2.2 A-C).

2.2.2.1 Bottom depth

Strong correlations between bathymetry and patterns in inter- or intraspecific species occurrences have been noted for many species of cetaceans and pinnipeds in different regions and ocean basins (Payne & Heinemann 1993, Moore et al. 2000, Baumgartner et al. 2001, Hamazaki 2002), making seafloor elevation an ideal candidate as an environmental proxy for a generic habitat suitability model.

Bathymetric data were taken from the ETOP02 dataset available on the U.S. National Geophysical Data Center's 'Global Relief' CD (www.ngdc.noaa.gov/products/ngdc_products.html) which provides elevation in 2-minute intervals for all points on Earth (Fig. 2.2 A).

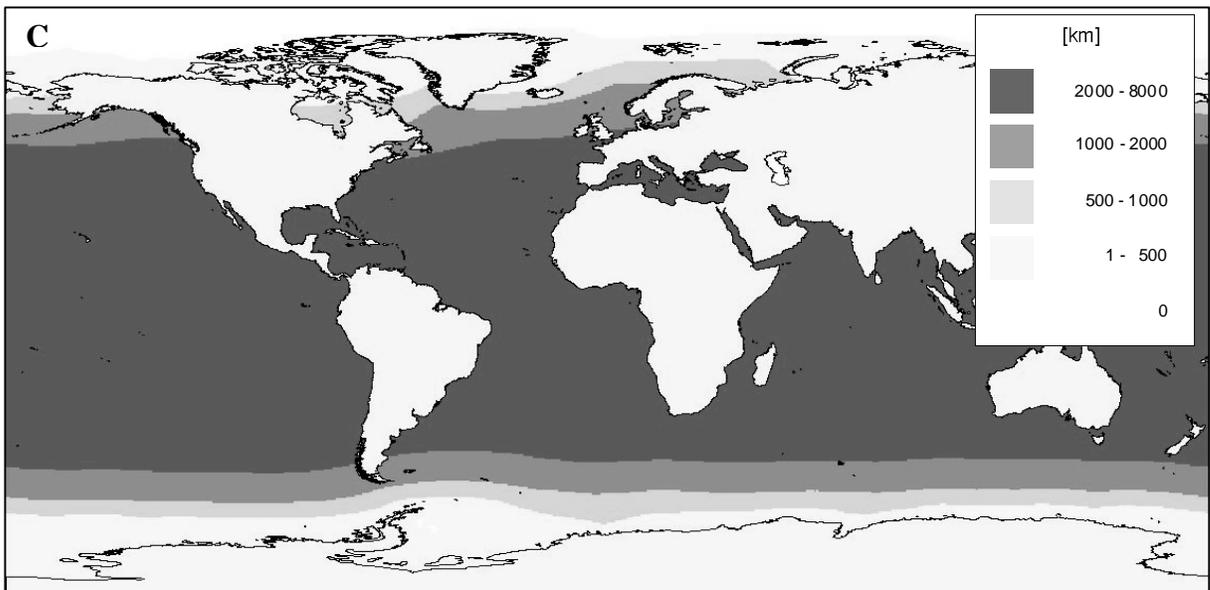
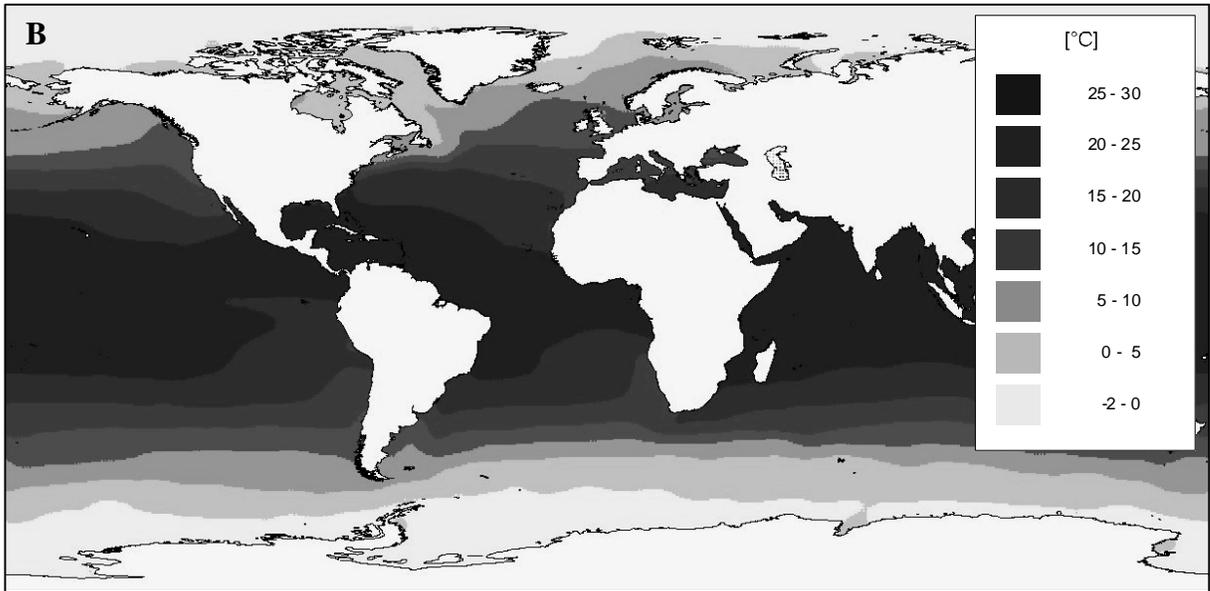
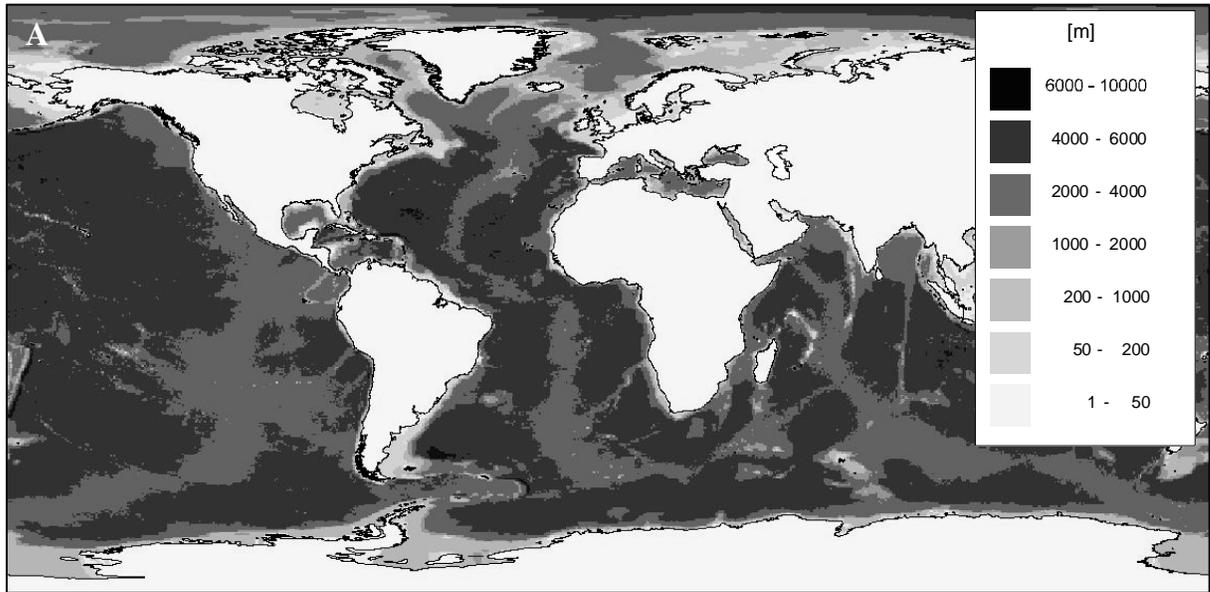
2.2.2.2. Mean annual sea surface temperature (SST)

In addition to temporally fixed parameters, such as bathymetry, marine mammal distributions are influenced by a host of variable environmental factors, such as water temperature. Changes in sea surface temperature may be indicative of oceanographic processes that ultimately determine marine mammal occurrence across a number of different temporal scales (Au & Perryman 1985) and significant correlations with sea surface temperatures have been demonstrated in different areas and for a variety of different marine mammals species (e.g., Davis et al. 1998, Baumgartner et al. 2001, Hamazaki 2002). Surface temperature may not serve as a good predictor for all marine mammals, given the substantial foraging depths of some species (Jaquet 1996). However, I nevertheless chose to use SST as a proxy, because of the general availability of observations or quantitative measurements of surface temperature conditions associated with marine mammal occurrences. Moreover, SST most commonly serves as a reference point for climatic conditions, such as 'sub-polar' and 'tropical', commonly used to describe qualitatively the temperature preferences of various species.

Global annual sea surface temperature data, averaged over the past fifty years, were extracted from the NOAA World Ocean Atlas 1998 CD (NOAA/NODC 1998) (Fig. 2.2 B).

Figure 2.2. A-C. (next page)

Distribution of model predictors: (A) bathymetry in meters; (B) annual average sea surface temperature in °C; (C) mean annual distance to the ice edge in km.



2.2.2.3. Mean annual distance to ice edge

The shifting edge of the pack ice is a highly productive zone (Brierley et al. 2002, Hewitt & Lipsky 2002) and represents important feeding grounds for many species of marine mammals (Murase et al. 2002). A number of studies have shown that sea ice concentration and ice cover, in combination with depth, play a key role in ecological niche partitioning for many species (Ribic et al. 1991, Moore & DeMaster 1997). I chose to include the distance to the ice edge as an additional predictor in the model, as the distribution of species in the polar zones may not be captured sufficiently using only SST. Although ice extent is strongly spatially correlated with SST, the actual edge of the sea ice does not directly coincide with any single isotherm throughout the year (Fig. 2.2 B & C). Moreover, the ability of different marine mammal species to venture into the pack-ice varies substantially.

Spatial information about the average monthly ice extent (1979-1999) – defined by the border of minimum 50 % sea ice coverage – was obtained from US National Snow & Ice Data Center web site (http://nsidc.org/data/smmr_ssmi_ancillary/trends.html#gis). I smoothed the ice edge border to correct some obvious misclassification and/or re-projection errors. After rasterizing the ice extent data, I calculated monthly distances from the nearest ice edge cell for each cell in the raster and computed annual average distance based on these monthly distances (Fig. 2.2 C).

2.2.2.4. Distance to land

Some pinniped species – specifically the eared seals (otariids) – appear to be restricted to areas fairly close to their terrestrial resting sites – haulouts and rookeries (Costa 1991, Boyd 1998). The maximum distances away from these land sites are determined by a combination of species-specific life history and physiological factors, such as the maximum nursing intervals based on the ability of pups to fast (Bonner 1984) and maximum swimming speed of adults (Ponganis et al. 1992). Global data sets identifying pinniped rookery sites do not exist. However, distance from landmasses in general was deemed to be an appropriate proxy in the context of this model, and served as an additional predictor particularly to model the distribution of some of the pinniped species (see Appendix 2 for specific species). For each cell, distance to land was calculated in the same manner as distance to the ice edge.

2.2.3. Dependent variables

2.2.3.1. Marine mammal species

The model encompassed 115 species of marine mammals that live predominantly in the marine environment, but did not consider exclusively freshwater cetacean or pinniped species or sirenians, sea otters or the polar bear. Taxonomically, I largely followed Rice (1998); except for right whales, for which, I recognized three separate species as supported by most recent findings (Bannister et al. 2001, Rosenbaum et al. 2000). In addition, I included a recently described additional species, Perrin's beaked whale (*Mesoplodon perrini*; Dalebout et al. 2002). A subset of 20 marine mammal species that I will

focus on in the following is listed in Table 2.1 together with information about general distributions. The complete species list is provided in Appendix 1.

Table 2.1. Names, taxonomy and general distributions of the 20 selected marine mammal species included in the RES model for which I show predictions (Fig. 2.4) (for all other species see Appendix 1).

Common name	Scientific name	Suborder	Distribution
North Atlantic right whale	<i>Eubalaena glacialis</i>	Mysticeti	N Atlantic
Antarctic minke whale	<i>Balaenoptera bonaerensis</i>	Mysticeti	S hemisphere
Gray whale	<i>Eschrichtius robustus</i>	Mysticeti	N Pacific
Hourglass dolphin	<i>Lagenorhynchus cruciger</i>	Odontoceti	S hemisphere
Northern right whale dolphin	<i>Lissodelphis borealis</i>	Odontoceti	N Pacific
Irrawaddy dolphin	<i>Orcaella brevirostris</i>	Odontoceti	Indo-Pacific
Indian hump-backed dolphin	<i>Sousa plumbea</i>	Odontoceti	W Indian O.
Clymene dolphin	<i>Stenella clymene</i>	Odontoceti	Atlantic
Narwhal	<i>Monodon monoceros</i>	Odontoceti	Circumpolar N hemisphere
South African & Australian fur seal	<i>Arctocephalus pusillus</i>	Pinnipedia	S African & S Australian waters
Guadalupe fur seal	<i>Arctocephalus townsendi</i>	Pinnipedia	NE Pacific
Australian sea lion	<i>Neophoca cinerea</i>	Pinnipedia	SE Indian O., S & SW Australia
South (American) sea lion	<i>Otaria flavescens</i>	Pinnipedia	S American waters
Hooker's or New Zealand sea lion	<i>Phocarctos hookeri</i>	Pinnipedia	New Zealand waters, SW Pacific
Galapagos sea lion	<i>Zalophus wollebaeki</i>	Pinnipedia	Galapagos Islands, E Pacific
Hooded seal	<i>Cystophora cristata</i>	Pinnipedia	N Atlantic
Ribbon seal	<i>Histiophoca fasciata</i>	Pinnipedia	N Pacific
Mediterranean monk seal	<i>Monachus monachus</i>	Pinnipedia	Mediterranean & NE Atlantic
Hawaiian monk seal	<i>Monachus schauinslandi</i>	Pinnipedia	Hawaiian waters, NE Pacific
Ross seal	<i>Ommatophoca rossii</i>	Pinnipedia	Circumpolar S hemisphere

2.2.3.2. Definition of habitat preference categories

I defined habitat categories to represent broad predictor ranges, which roughly describe real marine physical/ecological niches inhabited by different marine mammal species. While ecologically meaningful bottom-depth and ice edge-association niches are variable in width and were defined accordingly, SST categories were described by regular 5° C steps, based on the average intra-annual variation of 5-10° C in most areas of the world (Angel 1992). Quantitative definitions and corresponding qualitative descriptions of potential niches of the resulting 17 bottom depth ranges, 27 broad temperature ranges and 12 ice edge association categories are shown in Table 2.2. I described habitat preference categories by means of an assumed trapezoidal probability distribution that I defined as a resource selection function (RSF) (Fig. 2.1), although I recognize that all the independent variables represent indirect ecological gradients rather than actual resource gradients (Guisan & Zimmermann 2000). The RSF represented the simplest and broadly appropriate option in view of the absence of data that could be used to derive generic functional responses of marine mammal occurrence and environmental gradients. The selected shape of the RSF meant that I assumed the relative environmental suitability be uniformly highest throughout a species' preferred parameter range (Min_P to Max_P in Fig. 2.1). Beyond this range, I assumed that suitability would decrease linearly towards the minimum or maximum thresholds for a species (Min_A or Max_A in Fig. 2.1). Probabilities were set to zero outside the absolute minimum or maximum values.

2.2.3.3. Marine mammal habitat preferences

I compiled published information about species-specific habitat preferences with respect to their known association with the ice edge, as well as preferred bottom depth and temperature ranges in a database. Where appropriate, additional information about maximum likely distance from landmasses was also collected, based on information about maximum foraging trip lengths. Selected sources of information included more than a thousand primary and secondary references, all screened for relevant information on habitat preferences. Data extracted from these sources ranged from statistically significant results of quantitative investigations of correlations between species' occurrence and environmental predictors (e.g., Gregr & Trites 2001, Moore et al. 2002, Baumgartner et al. 2003, Cañadas et al. 2003), opportunistic observations (e.g., Carlström et al. 1997), maps of sightings or distribution outlines, to qualitative broad descriptions of habitat preferences such as "oceanic, subtropical species" (e.g., Jefferson et al. 1993). I assigned a level of confidence to each record to reflect the origin, reliability and detail of the data, with quantitative investigations of environmental factors and species' occurrence ranking highest and qualitative descriptions ranking lowest. Data were entered with high spatial and temporal resolution to allow for future analyses at different geographic and seasonal scales.

Table 2.2. Quantitative and qualitative definitions of habitat preference categories.

Environmental parameter	Minimum	Preferred minimum	Preferred maximum	Maximum	Habitat category description
Depth preferences [m]	0	-1	-8000	-8000	all depths (uniform distribution)
	0	-1	-50	-200	mainly estuarine to edge of cont. shelf
	0	-1	-50	-500	mainly estuarine to beyond shelf break
	0	-10	-100	-1000	mainly coast.-up. cont. shelf to up. cont. slope
	0	-10	-200	-2000	mainly coast.-cont. shelf to end of cont. slope
	0	-10	-200	-6000	mainly coast.-cont. shelf to deep waters
	0	-10	-1000	-6000	mainly coast.-up. cont. slope to deep waters
	0	-10	-2000	-6000	mainly coast.-cont. slope to deep waters
	0	-10	-2000	-8000	mainly coast.-cont. slope to v. deep waters
	0	-10	-4000	-8000	mainly coast.-abyssal plains to v. deep waters
	0	-200	-1000	-6000	mainly up. cont. slope to deep waters
	0	-200	-2000	-6000	mainly cont. slope to deep waters
	0	-200	-2000	-8000	mainly cont. slope to v. deep waters
	0	-200	-4000	-8000	mainly cont. slope-abyssal plains to v. deep waters
	0	-1000	-2000	-8000	mainly low. cont. slope to v. deep waters
0	-1000	-4000	-8000	mainly low. cont. slope-abyssal plains to v. deep waters	
0	-2000	-6000	-8000	mainly abyssal plains to v. deep waters	
Temperature preferences [mean ann. SST in °C]	-2	-2	35	35	all temperatures (uniform distribution)
	-2	0	0	5	polar only
	-2	0	5	10	polar-subpolar
	-2	0	10	15	polar-c. temperate
	-2	0	15	20	polar-w. temperate
	-2	0	20	25	polar-subtropical
	-2	0	25	30	polar-tropical
	-2	0	30	35	polar-full tropical
	0	5	5	10	subpolar only
	0	5	10	15	subpolar-c. temperate
	0	5	15	20	subpolar-w. temperate
	0	5	20	25	subpolar-subtropical
	0	5	25	30	subpolar-tropical
	0	5	30	35	subpolar-full tropical
	5	10	10	15	c. temperate only
	5	10	15	20	c. temperate-w. temperate
	5	10	20	25	c. temperate-subtropical
	5	10	25	30	c. temperate-tropical
	5	10	30	35	c. temperate-full tropical
	10	15	15	20	w. temperate only
10	15	20	25	w. temperate-subtropical	
10	15	25	30	w. temperate-tropical	
10	15	30	35	w. temperate-full tropical	
15	20	20	25	subtropical only	
15	20	25	30	subtropical-tropical	
15	20	30	35	subtropical-full tropical	
20	25	25	30	tropical only	
20	25	30	35	full tropical only	
Ice edge association preferences [mean annual distance from ice edge in km]	-1	0	8000	8000	no association w. ice edge (uniform distribution)
	-1	0	500	2000	mainly restricted to fast & deep pack-ice
	-1	0	500	8000	mainly in fast & deep pack-ice, but also elsewhere
	0	1	500	2000	mainly around edge of pack-ice
	0	1	500	8000	mainly around edge of pack-ice, but also elsewhere
	0	1	2000	8000	mainly around edge of pack-ice & max. ice extent, but also elsewhere
	0	1	8000	8000	reg. but not pref. around edge of the pack-ice
	0	500	2000	8000	mainly in areas of max. ice extent, but also elsewhere
	0	500	8000	8000	reg. but not pref. in areas of max. ice extent
	500	1000	2000	8000	no association w. ice edge, but seasonally close to max. ice extent
500	1000	8000	8000	no association w. ice edge, but pref. close to areas of max. ice extent	

I assigned each species to habitat preference categories for depth, temperature and ice edge association (and in some case distance to land) based on the most reliable information available (see Table 2.3 for the 20 species listed in Table 2.1; see Appendix 2 for all other species). If the available information was inconclusive, or different conclusions could be drawn from the data, the species was assigned to multiple alternative habitat categories representing different hypotheses. ‘Distance from land’ preferences were used as an additional constraining factor for all species marked by an asterisk in Table 2.3 & Appendix 2. For three species (vaquita, Galapagos fur seal, Juan Fernandez fur seal), the general temperature categories were adjusted to reflect the apparent extreme narrowness of their niche.

2.2.3.4. Area restrictions

Contemporary distributions of marine mammals and other species are – at least in part – the result of their evolutionary history. Present occurrences and restrictions to certain areas therefore reflect a species center of origin, and its ability to disperse, as influenced by its ecological requirements and competitors (LeDuc 2002, Martin & Reeves 2002). To capture the results of this evolutionary process, restrictions of non-cosmopolitan species to large ocean basins (i.e., North Atlantic or southern hemisphere) were used as a rough first geographical constraint in the RES model.

If generated RES predictions did not reflect documented species’ absences from certain areas, further geographical restrictions were imposed (Table 2.3). It should be noted, however, that such restrictions were only imposed when known areas of non-occurrence were conceivably results of the constraints clearly definable, such as “marginal” ocean basins (e.g., Red, Mediterranean or Baltic Seas). Area constraints were also imposed when RES predictions showed signs of bi- or multi-modality, meaning that areas of high suitability were separated by long stretches of less suitable habitat. I attempted to minimize introductions of such additional constraints so as not to impede the assessment of the ability of the RES model to describe, on its own, patterns of species’ presence and absence.

Table 2.3. Habitat preferences in terms of depth, mean annual sea surface temperature and distance to the edge of sea ice for selected marine mammal species. Superscripts denote the particular habitat preference type about which the reference provided information: ¹ = depth preferences, ² = temperature preferences, ³ = distance to edge of sea ice. For species marked by *, distance from land was used as an additional constraining factor, limiting species to waters < 500 km (*) or < 1000 km (**) from land (for all other species see Appendix 2).

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
North Atlantic right whale	mainly coast.-cont. shelf to deep wat.	subpolar-tropical	no assoc. with ice edge, but season. close to areas of max. ice extent	N Atlantic - (Med., Black S., Hudson's Bay & Strait, Baltic)	Baumgartner et al, 2003 ¹ ; Evans, 1980 ¹ ; Gaskin, 1991 ² ; Jefferson et al, 1993 ³ ; Kenney, 2002 ² ; Knowlton et al, 1992 ¹ ; Mitchell et al, 1983 ² ; Woodley & Gaskin, 1996 ¹
Antarctic minke whale	mainly cont. slope to v. deep wat.	polar-tropical	mainly around edge of pack-ice, but also elsewhere	S hemisphere	Kasamatsu et al, 2000 ¹ ; Murase et al, 2002 ^{1,3} ; Perrin & Brownell, 2002 ^{1,3} ; Ribic et al, 1991 ² ; Rice, 1998 ^{2,3}
Gray whale	mainly estuar. to beyond shelf break	subpolar-subtropical	reg. but not pref. around edge of the pack-ice	N Pacific	Deecke, 2003 ^{1,2} ; Gardner & Chavez-Rosales, 2000 ² ; Jones & Swartz, 2002 ^{1,2,3} ; Moore & DeMaster, 1997 ^{1,3} ; Moore, 2000 ³ ; Rugh et al, 1999 ³ ; Weller et al, 2002 ^{1,2}
Hourglass dolphin	mainly low. cont. slope-abyss. plains to v. deep wat.	polar-warm temperate	mainly in areas of max. ice extent, but also elsewhere	S hemisphere	Gaskin, 1972 ² ; Goodall, 2002 ^{1,2} ; Goodall, 1997 ^{1,2,3} ; Jefferson et al, 1993 ^{1,3} ; Kasamatsu et al, 1988 ² ; Kasamatsu & Joyce, 1995 ³
Northern right whale dolphin	mainly low. cont. slope-abyss. plains to v. deep wat.	subpolar-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	N Pacific - (Lat: < 10°N)	Bjørge et al, 1991 ^{1,2} ; Forney & Barlow, 1998 ¹ ; Jefferson & Newcomer, 1993 ¹ ; Jefferson et al, 1993 ¹ ; Jefferson et al, 1994 ³ ; Rice, 1998 ³ ; Smith et al, 1986 ²
Irrawaddy dolphin	mainly estuar. to end of cont. shelf	full-on tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Lon: > 156°E & < 80°E)	Arnold, 2002 ^{1,2} ; Freeland & Bayliss, 1989 ¹ ; Mörzner Bruyns, 1971 ² ; Parra et al, 2002 ^{1,2} ; Rice, 1998 ³ ; Stacey, 1996 ^{1,2}
Indian hump-backed dolphin	mainly estuar. to end of cont. shelf	subtropical-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Med., Black S.; Lon > 90°E & < 14°E)	Findlay et al, 1992 ¹ ; Jefferson et al, 1993 ² ; Jefferson & Karczmarski, 2001 ¹ ; Karczmarski et al, 2000 ¹ ; Rice, 1998 ³ ; Ross, 2002 ^{1,2}
Clymene dolphin	mainly cont. slope-abyss. plains to v. deep wat.	full tropical only	no assoc. with ice edge, nowhere near ice at any time of the year	Atlantic - (Lon: > 15°E & > 70°W)	Davis et al, 1998 ^{1,2} ; Mullin et al, 1994a ^{1,2} ; Perrin et al, 1981 ¹ ; Rice, 1998 ³
Narwhal	mainly up. cont. slope to deep wat.	polar only	mainly restricted to fast & deep pack-ice	N hemisphere	Dietz & Heide-Jørgensen, 1995 ¹ ; Heide-Jørgensen, 2002 ^{1,3} ; Heide-Jørgensen et al, 2003 ¹ ; Jefferson et al, 1993 ² ; Martin et al, 1994 ¹ ; Rice, 1998 ³

Table 2.3. (cont.)

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
Guadalupe fur seal*	mainly low. cont. slope to v. deep wat.	warm temperate-tropical	no assoc. with ice edge, nowhere near ice at any time of the year	NE Pacific - (Lat: < 10°N & Lon: > 150°W)	Belcher & Lee, 2002 ² ; Lander et al, 2000 ¹ ; Reijnders et al, 1993 ² ; Rice, 1998 ³
South African & Australian fur seal*	mainly coast.-up. cont. shelf to up. cont. slope	warm temperate-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	S hemisphere - (Lon: > 160°E & > 20°W)	Arnould & Hindell, 2001 ¹ ; Reijnders et al, 1993 ² ; Rice, 1998 ³ ; Thomas & Schulein, 1988 ¹
Australian sea lion	mainly coast.-up. cont. shelf to up. cont. slope	warm temperate-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	S hemisphere - (Lon: > 155°E & < 75°E)	Costa, 1991 ¹ ; Gales et al, 1994 ² ; Jefferson et al, 1993 ¹ ; Ling, 2002 ² ; Rice, 1998 ³
South (American) sea lion*	mainly estuar. to end of cont. shelf	polar-subtropical	no assoc. with ice edge, but season. close to areas of max. ice extent	S hemisphere - (Lat: > 60°S & Lon: < 40°W & > 120°W)	Campagna et al, 2001 ¹ ; Jefferson et al, 1993 ² ; Reijnders et al, 1993 ² ; Rice, 1998 ³ ; Thompson et al, 1998 ¹ ; Werner & Campagna, 1995 ¹
Hooker's or New Zealand sea lion	mainly coast.-cont. shelf to end of cont. slope	subpolar-cold temperate	reg. but not pref. in areas of max. ice extent	W Pacific - (Lat: > 0°N)	Costa & Gales, 2000 ¹ ; Crocker et al, 2001 ¹ ; Gales, 2002 ^{1,2} ; Jefferson et al, 1993 ² ; Rice, 1998 ^{1,3}
Galapagos sea lion*	mainly coast.-cont. shelf to deep wat.	full tropical only	no assoc. with ice edge, nowhere near ice at any time of the year	E Pacific - (Lat: > 10°N & Lon: > 100°W)	Dellinger & Trillmich, 1999 ² ; Heath, 2002 ¹ ; Jefferson et al, 1993 ¹ ; Rice, 1998 ³
Hooded seal	mainly low. cont. slope to v. deep wat.	polar-cold temperate	mainly around edge of pack-ice, but also elsewhere	N Atlantic	Folkow & Blix, 1995 ^{1,3} ; Folkow et al, 1996 ^{1,3} ; Folkow & Blix, 1999 ¹ ; Kovacs & Lavigne, 1986 ^{1,2,3} ; Reijnders et al, Fedoseev, 2002 ^{1,2} ; Jefferson et al, 1993 ^{1,2} ; Mizuno et al, 2002 ^{1,2} ; Reijnders et al, 1993 ¹ ; Rice, 1998 ³
Ribbon seal	mainly coast.-cont. slope to deep wat.	polar-subpolar	mainly in areas of max. ice extent, but also elsewhere	N Pacific	Fedoseev, 2002 ^{1,2} ; Jefferson et al, 1993 ^{1,2} ; Mizuno et al, 2002 ^{1,2} ; Reijnders et al, 1993 ¹ ; Rice, 1998 ³
Hawaiian monk seal*	mainly coast.-cont. shelf to deep wat.	subtropical-tropical	no assoc. with ice edge, nowhere near ice at any time of the year	NE Pacific - (Lat: < 10°N & Lon: < 140°W)	Gilmartin & Forcada, 2002 ¹ ; Parrish et al, 2000 ¹ ; Parrish et al, 2002 ¹ ; Reijnders et al, 1993 ^{2,3} ; Schmelzer, 2000 ²
Mediterranean monk seal	mainly coast.-up. cont. shelf to up. cont. slope	subtropical only	no assoc. with ice edge, nowhere near ice at any time of the year	N hemisphere - (Pacific, Indian O.; Lon: > 20°W)	Duguy, 1975 ¹ ; Kenyon, 1981 ¹ ; Reijnders et al, 1993 ^{1,2,3}
Ross seal	mainly coast.-cont. slope to deep wat.	polar only	mainly restricted to fast & deep pack-ice	S hemisphere	Bengtson & Steward, 1997 ¹ ; Bester et al, 1995 ³ ; Jefferson et al, 1993 ² ; Knox, 1994 ³ ; Rice, 1998 ³ ; Spletstoeser et al, 2000 ¹ ; Thomas, 2002 ³

2.2.3.5. Model algorithm

In the global raster, I predicted the species-specific relative environmental suitability of each individual grid cell based on its physical attributes and how well these matched the species' habitat preferences, assuming the trapezoidal resource selection function described above. Using:

$$RES_c = RES_{c_D} * RES_{c_T} * RES_{c_I} * RES_{c_{Dis}} \dots\dots\dots 1)$$

I computed a categorical index of the overall relative environmental suitability for each cell c – ranging between 0 to 1 – as a joint probability based on the RES of each cell c for depth (D), SST (T), distance from the ice edge (I) and, in some cases, from land (Dis), respectively. A multiplicative approach was chosen to allow each predictor to serve as an effective “knock-out” criterion (i.e., if a cell's average depth exceeded the absolute maximum of a species' absolute depth range, the overall RES should be zero, even if annual SST temperature and distance to ice edge of the cell were within the species preferred or overall habitat range).

Multiple hypotheses about species distributions were generated using different combinations of predictor category settings if a species had been assigned to multiple, equally plausible, options of habitat preference categories based on available data. I then selected the hypothesis considered to represent the best model fit through an iterative process and by qualitative comparison of outputs with all available information about the species' distribution and occurrence patterns within its range.

2.2.4. Model testing – input parameter settings

I used the long-term data set of commercial whaling records to validate both the choice in habitat preference category for specific species as well as the shape of the selected RSF. The data set contained commercial catches of member states of the International Whaling Commission (IWC) between 1800-2001 and was compiled by the Bureau of International Whaling Statistics (BIWS) and the Museum of Natural History, London, UK (IWC/BWIS 2001). Whaling operations did not adhere to any of the particular sampling schemes that dedicated surveys follow. Consequently, whaling effort distribution and catch per unit effort (CPUE) were likely strongly biased. Nevertheless, long-term catch data sets may still serve as good indicators of annual average species distribution and may thus provide some quantitative insight into general patterns of occurrence (Whitehead & Jaquet 1996, Gregr 2000). To test the input parameter selections, I analysed whaling data following a similar approach as chosen by Kasamatsu et al. (2000) and Cañadas et al. (2002). As a first step, I assigned all catches recorded with reliable, accurate positions to the corresponding cell in the global raster, thus obtaining information about mean depth, temperature and distance to ice edge associated with each catch position. In the absence of specific effort information, I then derived a relative index of CPUE per individual raster cell by assuming that whalers would have caught any species of whale where and whenever they encountered it. CPUE was thus

calculated as a proportional catch rate based on the proportion of total catch in each cell that consisted of the specific species in question. I subsequently computed average CPUE across all cells within a specific environmental stratum, defined to correspond to breakpoints in the habitat categories, and plotted these as histograms to compare with predictor probability distributions.

I included measures of uncertainty associated with mean encounter rates obtained for each stratum. In a spatial context, two types of biases in effort distributions may affect the level of confidence in CPUE values. Customary standard error calculation only captures the extent of variability of CPUE within one environmental stratum – reflected by the standard deviation – and the proportion of effort spent in each stratum in comparison to the total effort across all strata as reflected by \sqrt{n} or $\sqrt{n/\sum n}$. This approach fails, however, to address the problem of non-representative effort distribution with respect to total available habitat. Generally, the amount of area covered by effort in each strata is not equally representative of the total habitat available in a particular stratum when compared across all environmental strata and for all predictor variables (Compare Fig. 2.3 A & B). This sampling bias will be more pronounced in opportunistic data sets obtained through non-dedicated surveys or whaling operations. Nonetheless, it should be noted that most of the dedicated marine mammal surveys, generally designed for abundance estimation purposes, are rarely stratified with respect to more than one environmental parameter (if at all). To account for these biases in effort distribution, I modified standard error calculations by weighting errors by the proportion of total available habitat that was covered by effort within each environmental stratum.

Finally, to assess the overall importance of effort considerations in the context of habitat suitability modelling, I also generated histograms of catch frequency distributions, based on the cumulative catches reported from all cells within a specific environmental stratum.

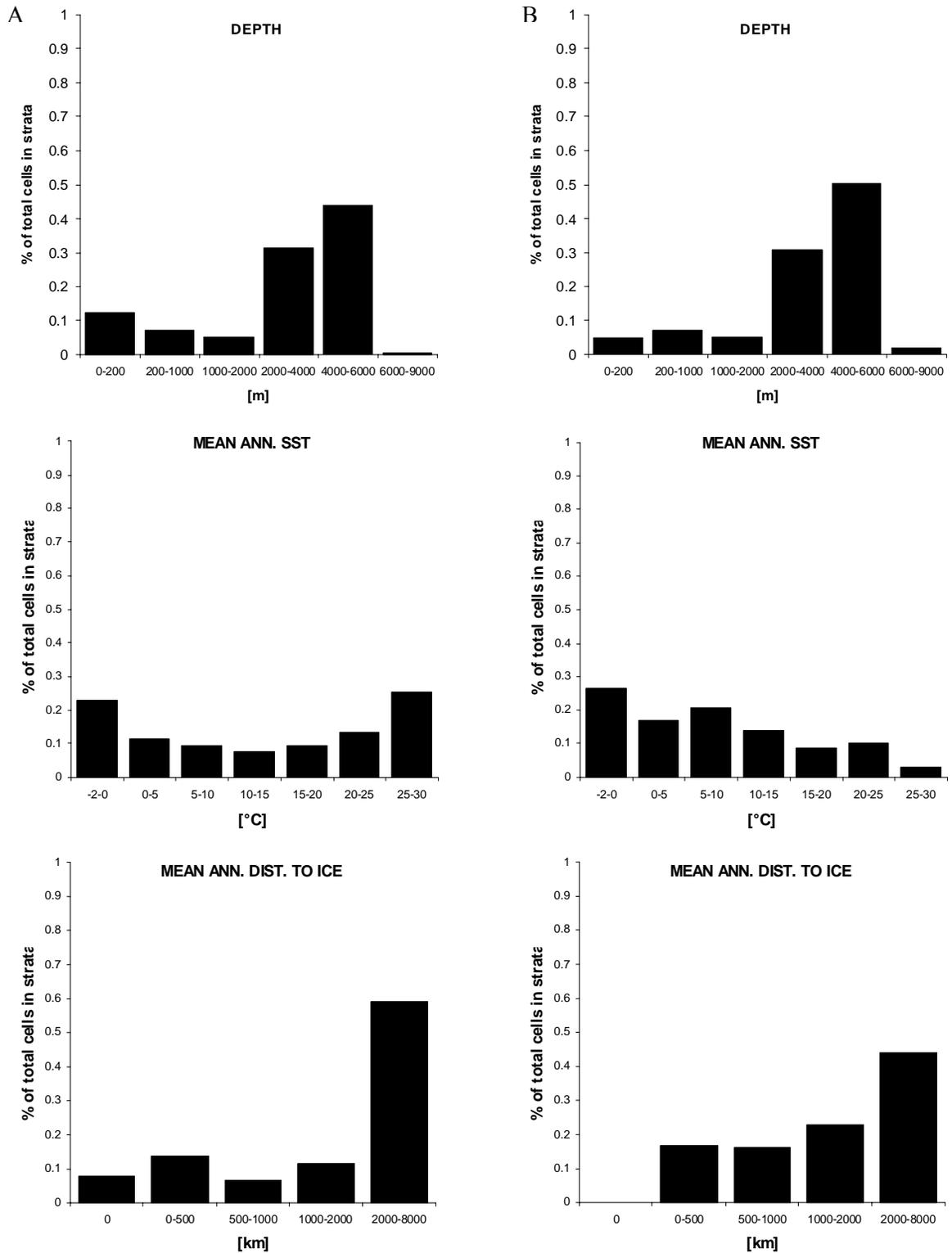


Figure 2.3. A–C.

Frequency distribution of (A) globally available habitat (left column) and (B) amount of habitat covered by whaling effort (right column) as % of cells per available environmental strata for depth, mean annual sea surface temperature (SST) and mean annual distance to ice edge.

2.2.5. Model evaluation – RES model outputs

I evaluated the generated RES predictions by testing the extent to which these may be representative of actual species' occurrence for a number of marine mammal species found in different parts of the world's oceans using sightings and catch data collected during dedicated surveys. Species for which I was able to obtain data sets suitable for testing RES predictions included harbour porpoises, northern fur seals, sperm whales and Antarctic minke whales. I selected species to cover a wide taxonomic, geographic and ecological range to test the robustness of the generic RES approach. In addition, I chose test data sets that varied widely in geographic and temporal scope to assess at which temporal or spatial scale RES predictions may prove to be insufficient to capture patterns of species' occurrences. To minimize risks of circularity, I tried to ascertain that test data had not been used to contribute directly or indirectly towards any of the studies or species reviews used to select input parameter settings. Test data sets included (1) the SCANS data collected during a dedicated line-transect survey in the North Sea and adjacent waters in the summer of 1994, (2) a long-term catch/sighting data set of northern fur seals collected during annual dedicated sampling surveys in the north-eastern Pacific that were conducted as a collaboration of US and Canadian federal fisheries agencies between 1958-1974 and (3) the long-term IWC-DESS data set collected during the IDCR-SOWER line-transect surveys in the Antarctic conducted annually over the past two and a half decades (Table 2.4).

Similar to the treatment of whaling data, species-specific catch/sighting frequencies were obtained by binning records from each data set by raster cells, using only those records with sufficient spatial and taxonomic accuracy (i.e., catch or sightings positions of reliably identified species reported to, at least, the nearest half degree lat/long). I used the minke whale sightings reported in the IWC-DESS database to test the predictions for the Antarctic minke whales, although its closely related sister species, the Dwarf minke whale, occurs sympatrically in some areas and the two species are not distinguished in the data set.

To convert the different types of spatial effort information available for the different test data sets to the same raster format (e.g., regularly recorded absence/presence or on-effort/off-effort transect or leg-starting-points), I developed two different types of effort proxies. The first, used for the northern fur seal and IWC-DESS survey data sets, was based on an approach similar to that applied to the IWC whaling data (i.e., I assumed that, on average, the total number of on-effort, reliable sighting records reported for one cell was representative of the effort spent surveying a cell). Species-specific relative encounter rates or SPUE (sightings per unit of effort) per raster cell were then calculated as the proportion of total sightings in a cell consisting of reports of the given species. I used an alternative approach in the case of the much smaller SCANS data set because the total number of animals sighted in one cell did not appear representative of the number of transects per cell, given a visual comparison of plotted sightings data with a map of survey transects (Hammond et al. 2002). Instead, using only the ship-based data, I derived a categorical effort proxy based on the number of leg-starting-points per cell provided in the available

effort data files. Relative encounter rates of harbour porpoises per cell were then calculated relative to this proxy.

For each test data set, I compared species-specific SPUEs with the corresponding RES model output for that species by averaging encounter rates over all cells covered by any effort that fell into a specific RES class. Using a bootstrap simulation routine, I generated 1000 random data sets, similar in terms of means, ranges and distribution shapes to the observed data sets. I then used Spearman's non-parametric rank correlation test (Zar 1996, JMP 2000) to compare average observed and randomly generated encounter rates with predicted corresponding RES classes. To assess the performance of the model compared to random distributions, I obtained a simulated p-value by recording the number of times the relationship between random data sets and RES classes was as strong or stronger than that found between the observed encounter rates and the model predictions.

Table 2.4. Sighting and catch data sets used for RES model testing.

	IWC-BIWS catch data	IDCR-DESS/SOWER sighting data	SCANS survey data	Northern fur seal distribution data
Agency/Source	International Whaling Commission, UK; Bureau of International Whaling Statistics, Norway; Natural History Museum of London, UK	IWC Member State collaboration / International Whaling Commission	EU collaboration / Sea Mammal Research Unit	Arctic Unit, Canada & NOAA, USA collaboration
Time period	1800-1999	1978-2001	June/July 1994	1958-1974
Ocean basin	World	Antarctica (S of 60° S)	ASCOBANS area & adjacent waters	Northeastern Pacific
Survey focal species	Large whales	Minke whales	Harbour porpoise	Northern fur seal
No. of marine mammal species reported	~ 20	~ 50	~ 5	1
No. of sighting/catch records	~ 2 000 000	~35000	1940	~ 18000
Used for testing of	RES assumptions & input parameter settings: minke whales, blue whale, humpback whale	RES model output: minke whales, sperm whale	RES model output: harbour porpoise	RES model output: northern fur seal

2.3. RESULTS

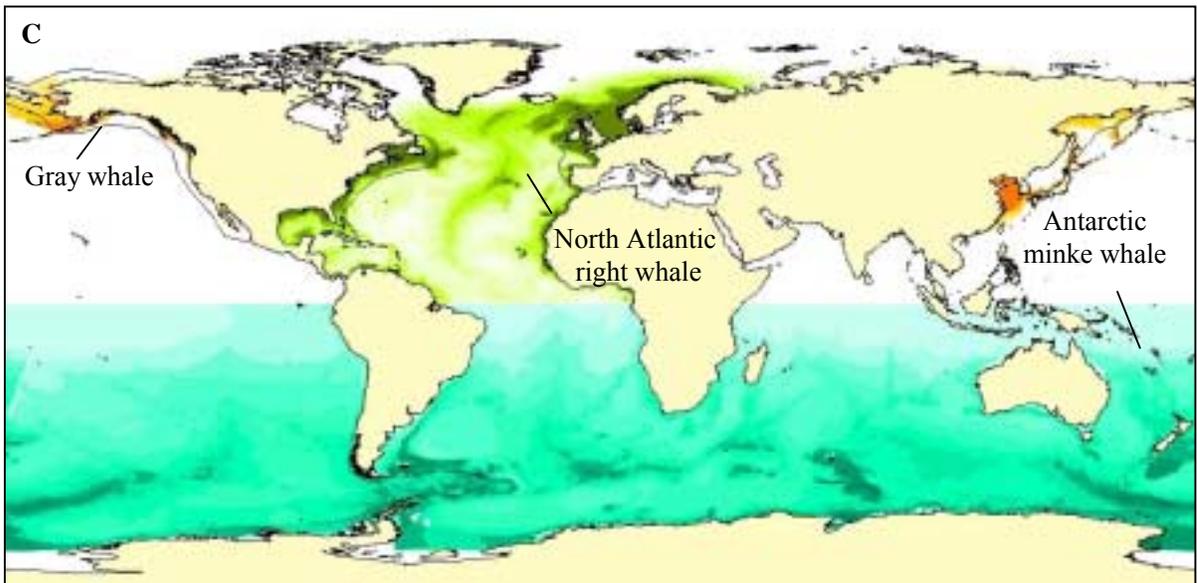
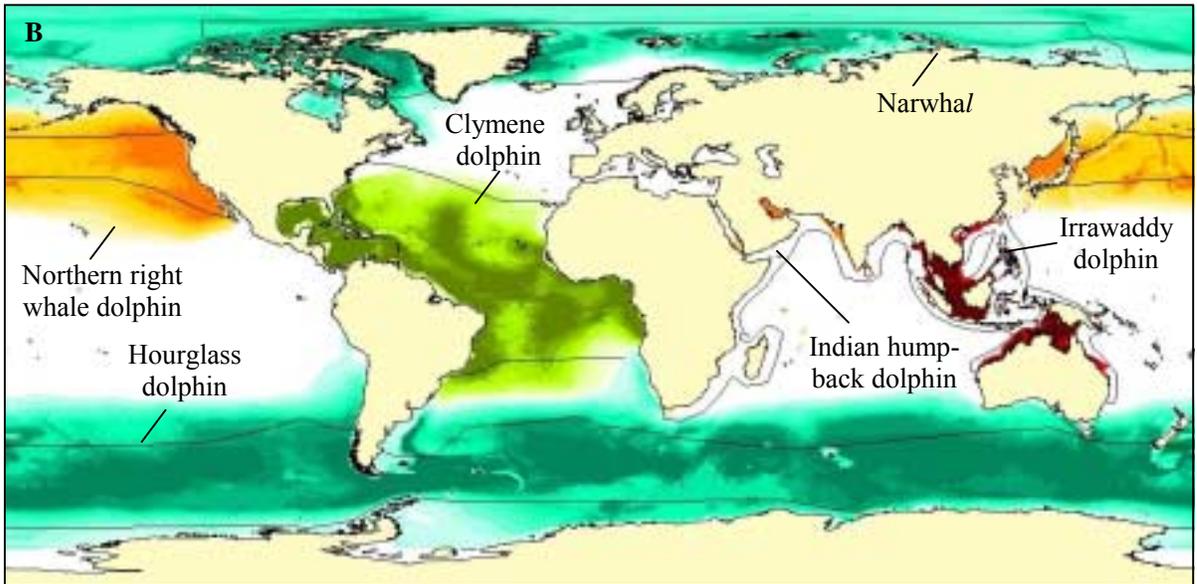
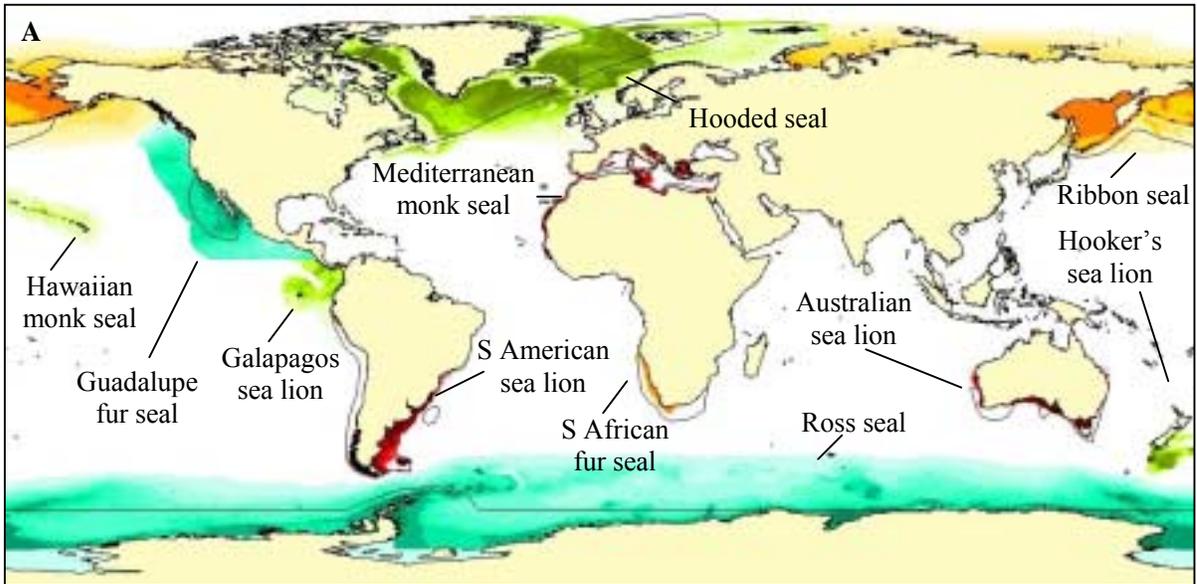
2.3.1. Relative environmental suitability predictions

RES modelling allows for potential habitat to be visualized on a large-scale while maintaining a high resolution of detail. Model results represent specific hypotheses about general heterogeneous occurrence patterns throughout a species' range. Examples of RES predictions for 11 pinniped, 6 toothed and 3 baleen whale species are shown in Fig. 2.4. A–C. These examples were selected to demonstrate the applicability of the modelling approach over a wide geographic and taxonomic range of species (compare Table 2.1 and Appendix 1) and to illustrate the diversity of generated model outputs for species occupying different environmental niches. Where they existed, I included published outlines of maximum range extents (e.g., Jefferson et al. 1993, Reijnders et al. 1993) for comparison. The predicted distributions for all other species can be viewed in Appendix 3 or online at www.seararoundus.org/distribution/search.aspx (Watson et al. in press).

Generally, maximum extents of RES predictions for species closely matched published distributional outlines (Fig. 2.4). RES outputs for many species also captured distinct areas of known non-occurrence well, without the need to introduce any geographic constraints. Examples of this are the predicted absence of hooded seals from Hudson's Bay, the restriction of gray whales to the north-eastern Bering Sea and the non-occurrence of Irrawaddy dolphins in southern Australia.

Figure 2.4. A–C (next page)

Examples of RES model outputs: Predicted relative environmental suitability in each raster cell (ranging from less suitable (light) to very suitable (dark)) based on habitat preference information for (A) eleven pinniped, (B) six odontocete and (C) three mysticete species. Outlines of proposed maximum range extent (Jefferson et al, 1993) are included for comparison. Note that, when viewed on a global scale, RES predictions for many coastal species are difficult to see in narrower shelf areas, such as along the western coast of South America and east coast of Africa and apparent absences from certain areas may just be artefacts of viewing scale. RES predictions of narwhal distribution in Sea of Okhotsk are masked to some extent by those for the northern right whale dolphin. RES maps for all marine mammal species can be viewed in Appendix 3 or online at www.seararoundus.org/distribution/search.aspx.



Though I only included a few very basic environmental parameters in the model, the complexity of the relationships between these parameters lead to distinctly different patterns of suitable habitat for species with slightly different habitat preferences. This is illustrated, for instance, by the predictions for hooded and harp seal *Pagophilus groenlandica* in the North Atlantic (Fig. 2.4 & Appendix 3; Section 8.3.20). Though published maximum range extents of the two species overlap to a large degree, the small difference in model parameterization resulted in substantially different RES predictions for the two species. The extent of possible spatial niche separation between harp and hooded seals that was achieved by these subtle differences in habitat preferences was interesting to see, given the similarity in physical size of the two species (Reijnders et al. 1993) and dietary preferences (Pauly et al. 1998), which is likely to result in some degree of interspecific competition.

RES predictions for different large whale species in polar waters represent similar examples for ecological niche separations based on small differences in habitat preferences (e.g., compare Fig. 2.4 for Antarctic minke whale with blue whale *Balaenoptera musculus*, Appendix 3, Section 8.1.6). For these species, it has also been proposed that niche partitioning may have evolved to reduce food competition (Kasamatsu & Joyce 1995).

2.3.2. Model validation

2.3.2.1. Evaluation of RES input parameter choices

Results from the analysis of whaling data to evaluate the input parameter choices illustrated the importance of considering effort in the context of habitat suitability modelling. Without considering effort, total catches by environmental strata generally diverged from the habitat preference categories I had assigned each species to, based on the syntheses of available, non-point data (Fig. 2.5). In contrast, the histograms of species-specific average CPUE by environmental strata mostly provided good support for the selected categories, indicating that whaling data distributions do indeed reflect the general perception of a species' habitat preference. The fit of assigned habitat preference categories with the observed distribution of average CPUE was particularly good in case of depth preferences. For this environmental parameter, the RSF matched the CPUE histogram quite closely (see examples in Fig. 5), providing support for the selected trapezoidal shape of the probability distribution used to describe habitat preference categories. Fit of selected habitat preference categories with whaling data was also satisfactory for the mean annual distance to ice parameter settings, but generally not as good for the mean annual SST settings (both not shown). Sub-optimal fit for SST and ice are probably due the large concentration of the whaling effort in the summer months, which introduced a strong seasonal bias (IWC 2001b).

In general, these comparisons provided a useful feedback mechanism to identify discrepancies between whaling data distributions and assigned habitat preference categories. Decisions about changes in parameterization of the model for a given species were then made by carefully weighting known biases of

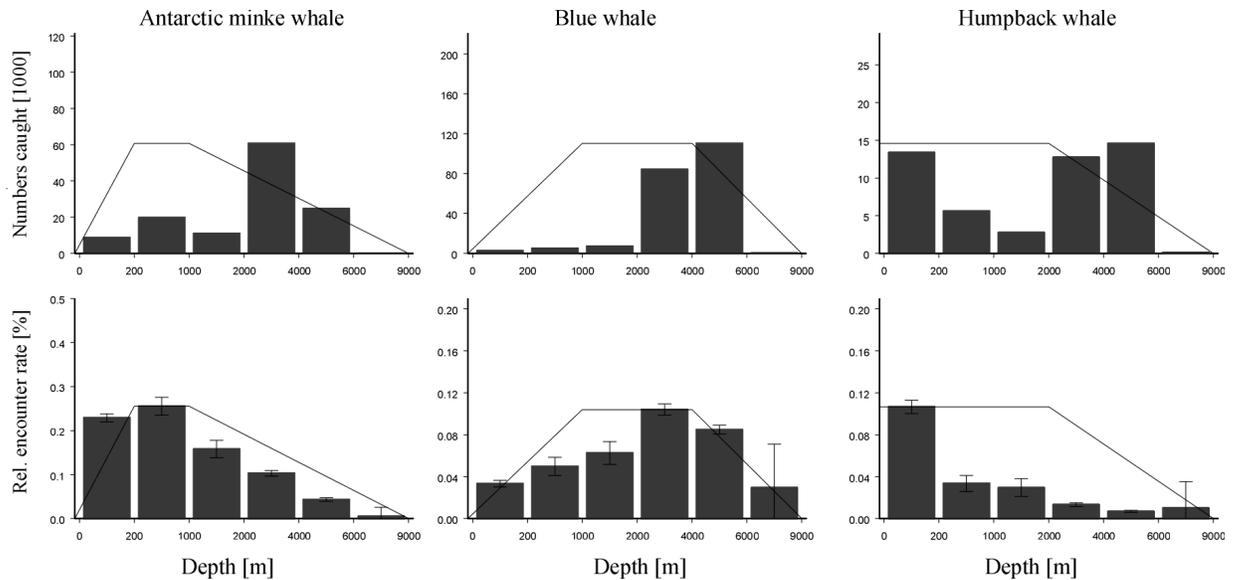


Figure 2.5.

Frequency distribution of IWC-BWIS whaling data set (1800-2001) plotted against depth strata to illustrate the importance of effort considerations when using point data for habitat suitability modelling and the extent to which the catch data supported the choice of habitat preference category for each species. Top graphs show the total number of catches reported in cells falling into the specified depth stratum, bottom graphs show the same data after effort corrections using average relative encounter rates per stratum. Lines represent the resource selection function describing the depth preference category that the species was assigned to based on available information (Table 2.3 and Appendix 2). Information about depth at catch locations was obtained by assigning records to corresponding 0.5 latitude/longitude cells in a global raster with associated environmental data. Only records with adequate geographic accuracy and unequivocal species identification were used. Standard errors of relative encounter rates shown in the graphs have been modified to reflect two types of effort biases: the heterogeneous distribution of effort coverage across all strata and the different proportions of total available habitat that was covered by whaling within each stratum. Note that frequency distributions were scaled to touch highest bar for better visualization of fit of the habitat preference range.

all available data for that species, re-running the model for all possible combinations of predictor setting and selecting what was regarded to be the most parsimonious hypothesis for each species.

2.3.2.2. Validation of RES results

Relative environmental suitability modelling captured a significant amount of the variability in observed species' occurrences – corrected for effort – in all test cases (Table 2.5). Average species' encounter rates were correlated positively with predicted suitability of the environment for each species based on Spearman's non-parametric test of rank correlation. While the positive correlations detected were relatively weak, particularly in the case of Antarctic minke whale, in each case < 3 % of the random datasets produced results more strongly correlated with observed encounter rates than the RES predictions (Table 2.5). Model predictions were fairly robust across a large range of temporal and spatial

Table 2.5. Statistical results of model testing for four different species including relevant information about test data sets to illustrate robustness of RES model over a wide range of temporal and spatial scales. Relationships between RES categories and average observed proportional encounter rates were tested using non-parametric rank correlation analysis. Simulated p-values represent the percentage of random data sets, generated using bootstrap simulation, that were more strongly correlated with observed data than RES predictions for given species. Note that generic “minke whale” sightings were used to test RES predictions for Antarctic minke whales.

Common name	Survey area	Size of survey area (effort cells) [1000 km ²]	Time period covered by survey	No. of reported encounters	Spearman's non-parametric rank correlation analysis of RES vs mean SPUE		Comparison with random data sets Simulated p-value
					rho	p	
Northern fur seal	Northeastern Pacific	2011	~ 20 years	10254	0.54	< 0.0001	0
Harbour porpoise	Greater North Sea	741	~ 1 month	1265	0.57	< 0.0001	0.027
Sperm whale	South of S 60	5489	~ 20 years	951	0.42	< 0.0001	0
Antarctic minke whale	South of S 60	5489	~ 20 years	12288	0.28	0.01	0.014

scales, as significant correlations were found even between RES predictions for harbour porpoise and observed relative encounter rates from the comparatively small-scale and short-term SCANS data.

2.4. DISCUSSION

2.4.1. Relative Environmental Suitability predictions

The model represents a new, more objective approach for mapping large-scale distributions of marine species. RES model performance is convincing when compared to existing information about species' distributions, available in the form of descriptions of occurrences (see e.g., Rice 1998), or existing sketched outlines of distributional ranges (Jefferson et al. 1993). The fact that the RES maximum range extents closely match existing outlines may not be surprising, as the information about habitat preferences and the basic environmental parameter that drives the model is likely to have been considered and incorporated to some extent by the experts who drew these outlines. Moreover, there is some circularity operating here, since I sometimes used such outlines to infer temperature and/or ice edge category settings for species. However, the hand-drawn outlines vary considerably between different sources for the same species owing to differences in underlying assumptions or subjective – and to some extent arbitrary – decisions made by the expert who drew them. In contrast, within the RES model framework, assumptions and input parameter settings are clearly defined, thus making results reproducible and testable.

By sacrificing “detail for generality” (Levins 1966, Gaston 1994), the model was able to accommodate the frequently poor quality of available data. Consequently, the principle strength of the model lies in its

greater objectivity and generic applicability. Using RES modelling, I can thus investigate different hypotheses about large-scale distributions over a broad range of species by visualizing some of the multi-dimensional relationships of environmental factors that indirectly determine the effective boundaries of range extents. Even more importantly though, RES predictions provide some information about the environmental heterogeneity described by the complex interactions between environmental parameters that – in part – ultimately determine the occurrence of a species throughout its maximum range.

In most cases, the predicted relative environmental suitability corresponded closely to the present ecological niche of a species. In some cases, predictions approximated a species' habitat including its historical range extension prior to human-induced depletion. For some species, however, the results diverge substantially from known distributional ranges, suggesting that other factors may play a more important role in determining some distributions. In general, RES predictions should be viewed as hypotheses about some major aspects of a species' spatial fundamental niche.

2.4.2. RES predictions: limitations and biases

The predictions generated by the model are affected by various biases, operating on a number of different levels. Some biases are inherent to the present implementation of the approach, such as the absence of factors known to influence species occurrence (notably seasonality), the definition and shape of resource selection function or the model algorithm. Other biases are associated with the dependent and independent variables I use.

2.4.2.1. Other factors influencing species occurrence

In most cases, the realized niche of a species is likely to be influenced by many more factors other than the three basic environmental parameters I considered in the model, though the role these play will differ between species. Investigations of environmental correlates of species occurrence have identified a host of other parameters, such as warm core rings for sperm whales (Jaquet & Whitehead 1996), zones of confluence of cyclone-anticyclone eddy pairs for a number of cetacean species occurring in the northern Gulf of Mexico (Griffin 1999, Davis et al. 2002) or the depth of the bottom mixed layer for North Atlantic right whales (Baumgartner et al. 2003). Consequently, it can be expected that the incorporation of factors such as these would lead to more heterogeneous patterns of species' occurrence than implied by the model results.

Moreover, dynamic ecological factors that are not easily quantifiable, such as intra- and inter-specific competition and other behavioral interactions, greatly influence occurrence of species, especially on smaller geographic and temporal scales (Austin 2002). As a result, the spatial overlap in occurrence between different species may be, in reality, smaller than that implied by the predictions. Examples are the competitive exclusion or behavioral niche separation of species, that can be found between Pacific harbour seals (*Phoca vitulina*) (Appendix 3; Section 8.3.22) and spotted seals (*Phoca largha*) (Appendix

3; Section 8.3.21) in the North Pacific (Rice 1998) or New Zealand fur seals (*Arctocephalus forsteri*) (Appendix 3; Section 8.3.9) and the Australian sea lions (*Neophoca cinerea*) (Fig. 2.4) along the southern Australian coastline (Ling 1992).

Some of the most obvious discrepancies between RES predictions and known regional occurrences of species are easily explained by past or present anthropogenic impacts, such as whaling, sealing or fisheries bycatch. An example of the importance of this human-related factor is the stark contrast between the predicted distribution of the North Atlantic right whales (Fig. 2.4), and today's well-known absence of this species from European waters (Perry et al. 1999), likely due to the extreme reduction of its north-eastern stock by whalers in the past century (Brownell et al. 1983).

Another very important factor that impacts the results is the lack of consideration of short-term and long-term temporal variation of model parameters. Based on the long-term annual averages of environmental data, RES predictions describe the general distribution of a species averaged over the course of a whole year at any time from 1950 to 2000. Assigned habitat preference categories thus represent a compromise selected to capture as much of a 'typical' distributions of a species as possible but ignore, therefore, much of the effects of seasonality, environmental regime shifts, such as global warming, and range depletion or expansion associated with population trends. Seasonal changes in habitat preferences are well documented for many of the baleen whales (Kasuya & Miyashita 1997, MacLeod et al. 2004), and may be associated with annual migrations or other seasonal movements from feeding to breeding grounds, where parameters other than those determining food availability may be important, such as predator avoidance (Corkeron & Connor 1999, Pitman et al. 2001). It has also been suggested that habitat preferences of species may have changed over long temporal scales, especially in highly depleted, long-lived species such as the North Pacific right whale (*Eubalaena japonicus*) (Tynan et al. 2001). Such changes would explain the observed discrepancies between today's known occurrences of this species in limited regions of North Pacific and the wide-ranging presence throughout this ocean basin predicted by the RES model (Appendix 3; Section 8.1.2), which is supported by historical records (Scarff 1983).

RES model predictions and actual species occurrences also diverge noticeably in areas with great inter-annual or seasonal fluctuations in environmental conditions, such as some areas along the east coast of the United States, where inter- and inter-annual variation in SST exceeds 10°C (Angel 1992, NOAA/NODC 1998) and zones of high predicted environmental suitability will shift considerably throughout a year. RES predictions of species migrating along this coast, for instance, would greatly benefit from incorporating seasonality in the model. This would allow narrower temperature preference categories to be selected, which would improve predictions of species such as the northwestern stock of North Atlantic right whales. These feed in the Gulf of Maine and Newfoundland area and overwinter along the Florida coast, but rarely venture into the Gulf of Mexico (Jefferson & Schiro 1997, Kenney 2001) (unlike suggested by the predictions in Fig. 2.4).

2.4.2.2. *Biases of dependent and independent variables*

Even under the assumption that the RES model incorporates the most important aspects of a species' niche, the results are affected by a number of biases associated with the input parameters and model algorithm that can help explain some of the discrepancies between the predictions and known species occurrences.

First, the model algorithm and the assumed habitat preference categories described by the shape of the resource selection function are likely overly simplistic. A linear relationship between all three environmental parameters is improbable, as is the assumption that their role is equally important with respect to influencing distributions across all species (as implied by the unweighted model algorithm, Equation 1). Likewise, the assumed unimodal shape of the RSF is unlikely to always describe adequately the presences of species along environmental gradients, even though symmetrical, unimodal RSFs were found to be most common during a comprehensive investigation of the shape of RSF of terrestrial plant species (Oksanen & Minchin 2002). It is questionable, whether these findings can be directly applied to the marine environment and mammal species, given that functional responses may in fact be strongly bimodal for some species that undertake long annual migrations between feeding and breeding grounds. Nevertheless, the trapezoidal shape represents the most parsimonious and broadly applicable choice in absence of detailed investigations of RSFs for most marine mammal species.

Other discrepancies between model predictions and known occurrences may be due to a lack of consideration of geographical differences in sea floor topography, which are not reflected in the quantitative definitions of the habitat preference categories. For instance, marine mammals are often found in high densities along the highly productive shelf edge, which represents an important transition zone between the different shelf and slope species communities. However, the shelf edge is typically much deeper (~500 m) in Antarctic waters than in other parts of the world, as the weight of the ice has caused the continental plate to sink in these areas (Knox 1994a). Consequently, the definition of 200 m bottom depth as the cut-off point for the preferred range for the shelf-edge habitat preference categories (Table 2.2) resulted in predicted absences of many species in areas of the Antarctic where these species are known to occur regularly in high numbers (e.g., compare Hedley et al. (1999), IWC (2001a) with RES predictions for baleen whales; Appendix 3; Section 8.1)

The environmental parameters used as predictors in the model were themselves affected by biases which include direct measurement errors associated with the samples and problems introduced through interpolation and rasterization processes. Biases are reviewed in detail by the data providers (e.g., http://nsidc.org/data/smmr_ssmi_ancillary/trends.html#gis; NOAA/NODC 1998). Of particular relevance to the RES model are some interpolation related biases. As interpolation is sensitive to variation in the density of the point data, the long-term averages of SST measurements, in particular, will have been

affected, as oceanographic sampling stations were much scarcer during the earlier decades of the last century than at present (NOAA/NODC 1998). Averaged over only the past twenty years, ice edge data may be less affected by this bias. However, the smoothing of ice edges, undertaken to eliminate some nonsensical results in the computation of ice edge distances, created its own set of problems. Predicted false absences or presences of species such as the harbour porpoise (Appendix 3; Section 8.2.46) in the Baltic and Sea of Azov, or the beluga (*Delphinapterus leucas*) (Appendix 3; Section 8.2.42) in the St. Lawrence are – at least partially – explainable based on effects of this *ad hoc* smoothing. Other problems may be related to the use of 50 % ice coverage data to define the edge of ice, which made the distinction between fast-ice and pack-ice species impossible in the context of the model (Compare e.g., Wedell seals (*Leptonychotes weddellii*) and Ross seals; Fig. 2.4 & Appendix 3; Section 8.3.27). Further artifacts of using this type of presence/absence ice data are areas of false predicted absences in Antarctic waters or false predicted presences very close to the North Pole for species not usually known to actually enter the pack-ice, such as the blue whale (Appendix 3; Section 8.1.6). In the future, some ice data biases may be reduced by the use of sea ice concentration data instead, which would allow the setting of more flexible thresholds to define the edge of pack ice.

Unlike the independent variables, the information forming the basis for the dependent variables is less likely to be affected by interpolation issues due to its mainly qualitative nature. However, both quantitative and qualitative information about habitat preferences is probably influenced to some extent by unequal distribution of survey effort in the marine environment, which much greater in the northern hemisphere and mostly concentrated along the continental shelves, relatively close to land.

2.4.3. RES model validation: Results, limitations and biases

2.4.3.1. Evaluation of input parameters and assumptions

The whaling data provided a helpful feedback mechanism to optimize input parameter model settings and investigate the validity of some of the model assumptions, especially the selection of the habitat preference category for a given species, and the trapezoidal shape of the RSF. The fit of CPUE histograms and selected habitat preference category settings was generally best for bottom depth across almost all species and provided support for the validity of the shape of the RSF used here. Corresponding histograms for temperature and ice distance matched the distribution of whaling data less well. While a species' depth preferences are often consistent throughout its latitudinal range extent, temperature ranges and distance to ice edge will naturally vary depending on where, throughout its range, an animal is captured or sighted. Whaling effort was concentrated in the polar waters of both hemispheres during summer months (IWC 2001b), thereby only covering a part of the distributions of most species targeted. To describe a species' complete range extents including all migratory movements, temperature and ice distance categories often had to be defined much broader than would have been indicated by whaling data

alone. In these cases, the discrepancies between CPUE plots and selected habitat preference category generally did not result in a re-consideration of selected model settings. Nevertheless, the visualization of catch data distributions and the subsequent evaluation process of input parameter settings proved to be a useful exercise that helped identify problems and inconsistencies.

2.4.3.2. Investigation of assumptions on effort

The impact of sampling schemes and effort biases on statistical habitat suitability model outputs is recognized and often stressed, yet little work has so far been done to investigate these effects quantitatively. Hirzel & Guisan (2002) used a virtual population model and simulation tools to investigate optimal sampling strategies for habitat suitability modelling and found that regular and equal-stratified sampling schemes provided most robust and accurate results. It is difficult to assess the extent to which these findings are transferable to the marine environment and to highly mobile organisms such as marine mammals, where the development of optimal sampling strategies needs further investigation. In the meantime, it is rarely acknowledged that survey designs optimized for abundance estimation may not be equally suitable for obtaining data for habitat suitability modelling (e.g., Kasamatsu et al. 2000). Even if effects of skewed effort distributions are acknowledged as a potential bias for marine mammal habitat predictions (Gregar & Trites 2001), such effects are rarely further investigated. In this context, comparisons of general knowledge on ecological niche preferences with frequency distributions point data and their effort-corrected derivatives across environmental strata for different environmental parameters will be helpful. The analysis performed here to test input parameter settings and model assumptions represents a useful starting point to visualize the extent of sampling biases in multiple dimensions (Fig. 2.3 and Fig. 2.5).

2.4.3.3. Evaluation of RES predictions

Statistical tests of RES model results indicated that the generic approach has some merit to adequately describe suitable habitat, as significant amounts of the variability in average species occurrence were captured for all species tested. Model performance contrasted with the simulated random data sets that rarely showed stronger relationships with the observed data than the predictions. Nevertheless, relationships between predicted and observed data were quite weak, particularly in the case of Antarctic minke whales. This species occurs sympatrically with its sister species, the Dwarf minke whale, in some parts of the area covered by the IDCR-SOWER surveys, and the pool of generic ‘minke whale’ observations therefore likely represents sightings of both species (IWC 2001a, Matsuoka et al. 2003). Consequently, the relationship between predictions for either minke whale species and the generic sightings is likely to be weaker than for the other tested species since both species appear to prefer slightly different habitat (Perrin & Brownell 2002).

2.4.3.4. Data independence & effort biases

The statistical testing of both the predictions and model assumptions will have been impacted by a number of biases. First, given the broad nature of the habitat preference input parameters and the type of information they were based on, I cannot be certain that the test data sets were indeed completely independent. Consequently, there is a risk of circularity, if the test data had somehow formed the basis of one of the broad ‘expert knowledge’ statements that was fed into the model. However, the process of abstraction from point data to these general statements in and of itself would probably ensure a certain degree of data independence. Furthermore, I argue that even if test data did serve as the basis for one of the broad statements used for input, such as “coastal, subtropical species”, testing the extent to which such broad statements may actually suffice to describe species’ occurrence when applied in a GIS modelling framework would be a worthwhile exercise. Nevertheless, I tried to minimize potential circularity by excluding all references that were directly based on these data from the pool of input sources for habitat preferences for the particular species tested (e.g., Kasamatsu et al. 2000, Hammond et al. 2002).

Other biases affecting the validation analysis have been introduced by relying on proxies of CPUE or SPUE such as the proportional encounter rates used here, as they are based on some major assumptions, ignore temporal components of effort distributions and do not represent real absence data. In case of the IWC whaling data, the assumption of an equal catch probability for all species, which forms the basis for the proportional catch rate, is quite unrealistic, since whaling operations tended to target specific species in specific areas at specific times (e.g., Perry et al. 1999). Similarly, deriving proportional catch rates by binning catches by grid cells across all years and seasons ignores the temporal aspects of effort distributions, therefore masking effects of the well-known serial depletion of the large whale species (Pike 1968, Clark & Lamberson 1982). Also masked by this are the effects of unequal time spent in different environmental strata and the progressive expansion of whaling grounds which will result in some distortion as well (Walters 2003). While the problems associated with differential catchabilities are more difficult to address, the effects of serial depletions could be investigated through the computation and comparison of decadal or annual proportional catch rates for species. Likewise, effects of temporally or seasonally skewed effort distribution and expansion of whaling grounds can be studied by generating proportional catch rates on smaller temporal scales. Initial tests of this showed, however, that the number of ‘effort days’ spent in each environmental stratum was strongly and positively correlated with the total number of ‘effort cells’, indicating that the amount of area that whalers covered was directly related to the time they spent there.

The lack of real absence data does not preclude the application and validation of habitat suitability models if pseudo-absence data can be generated (Robertson et al. 2001, Hirzel et al. 2002, Engler et al. 2004). Here, the proportional encounter rates used include adequate pseudo-absence data, as many encounter

rates for a given species were frequently zero in cells where only other species had been caught. Nevertheless, it would be advisable to use direct measures of effort on a per cell basis to test RES predictions in the future to reduce or eliminate impacts of all these effort proxy biases.

2.4.3.5. Spatial autocorrelation

The spatial autocorrelation of predictor variables and test data and the resulting lack of independence of grid cells is always a problem when testing predictions generated by habitat suitability models (Burrough & McDonnell 1998). While acknowledging the impact that this will have on the results, I have not attempted to correct for effects of spatial autocorrelation. However, spatial autocorrelation is unlikely to have impacted results to an extent that invalidates the generated hypotheses, although the lack of independence may have affected the relative strength of the relationships (GREGG and TRITES 2001).

2.4.3.6. Generic applicability and robustness of RES model

Statistical tests of RES predictions were only performed for a small proportion of species included in the model. However, for other species qualitative comparison with maps of plotted point data from different regions (e.g., Kasuya 1986, Kasamatsu & Joyce 1995, Heide-Jørgensen et al. 2003) as well as with predictions generated by smaller scale habitat models (e.g., Gregg & Trites 2001, Hamazaki 2002) provide some confidence in the general applicability of the approach. Moreover, the taxonomic diversity of the species that were tested and the broad range of the test data sets, both in terms of geographic origin as well as survey area covered and survey durations are noteworthy in this context. For instance, contrary to the long-term average occurrence patterns that may be inferred from the IWC and North Pacific data sets, both of which span several decades, the test data set for the harbour porpoise represents only a month long snapshot of species' occurrence observed during a single year in a relatively small area. This result suggested a remarkable robustness of RES model across a broad range of temporal and spatial scales. Furthermore, it suggested that the long-term averages of the basic environmental predictors play a substantial role in determining not only the fundamental, but also the realized ecological niche of a species, regardless of short-term and small-scale variability of these predictors, and of other factors that determine habitat use. I found the extent to which the delineation of marine species' distributions and patterns of occurrence could be quantitatively described using so few basic parameters remarkable, although further tests of RES predictions for others species and areas are required when suitable data sets can be obtained.

2.4.4. Comparison with other habitat suitability modelling approaches

Despite the apparent robustness of the RES modelling approach to perform well at different scales, care should be taken when interpreting model outputs. Environmental envelop models, such as the RES model, cannot predict the real probability of species' occurrences in a specific place on a specific day or month of a given year. It should therefore not be viewed as an alternative to empirical habitat prediction

approaches that are based on specific sighting data sets and directly predict species presence (e.g., Moses & Finn 1997, Hedley et al. 1999, Gregr & Trites 2001, Hamazaki 2002). Instead, RES modelling can usefully supplement such small-scale studies, by providing some general boundaries of species' distribution and by identifying potential focal areas.

Habitat suitability modelling is still a nascent field, and to date most efforts have focused on terrestrial systems and non-mobile organisms (e.g., Moisen & Frescino 2002, Zaniwski et al. 2002). At this stage, it is difficult to assess the advantages and disadvantages of different methodological approaches in different contexts. It is noteworthy, however, that more sophisticated statistical models do not necessarily perform better than simpler approaches when faced with real data, especially if quality of the underlying data was poor, as shown by comparing different statistical habitat suitability modelling approaches (Moisen & Frescino 2002).

I compared the statistical results of the evaluation with those obtained by others when validating predictions of other habitat suitability approaches, such as general linear models. I recognize that the differences in scale, questions asked and the associated conceptual frameworks of these different approaches may make the usefulness of a direct comparison somewhat questionable, particularly since the underlying assumptions of the parametric test statistics used by others are different than those for Spearman's rho. However, most statistics are similar enough to allow a meaningful comparison (Zar 1996) and a comparison may illustrate the extent of limitations of many currently existing models. For instance, Spearman's rho values from the analysis were comparable to the logistic regression coefficients of tests of predicted whale habitat around Vancouver Island that were generated by GLMs (based on comparison with reported logistic coefficients of determination presented in Table 2.2 in Gregr & Trites 2001). More importantly, even when comparing predictions generated by GLMs which had been developed based on "perfect" data sets in a virtual population simulation with test data, reported values of Pearson's r only ranged between 0.6 and 0.7, depending on the underlying sampling scheme and sample size (Hirzel & Guisan 2002). This indicates that even empirical habitat suitability models developed based on perfect data explain only roughly half of the observed variance in the test data. Thus, the RES approach performed surprisingly well in comparison.

2.4.5. Future work and applications

RES predictions would be greatly improved by incorporating seasonality, especially for the many marine mammal species that undergo large annual migrations from winter feeding to summer breeding grounds. This would require using seasonally averaged temperature and sea ice data as well as considerations of seasonal difference in habitat preferences of individual species. Predictions for species occurring in the pack- or fast-ice or in close vicinity of the ice edge may be improved if long-term sea ice concentrations were used instead of the 50% ice coverage data. In addition, it may be worthwhile to investigate what

other environmental and/or biological factors could be fruitfully added to the model. In some cases, the exclusion of known areas of human-caused local extinctions would improve predictions about effectively utilized habitat.

Further validation of the model, for other species and using diverse data sets, would be useful. Testing should be conducted using direct measurements of effort in the form of sighting rates per km per raster cell instead of the proportional encounter rates used here. Although direct field tests of the predictions would be desirable for validation, the logistical and financial effort involved may exceed limits of realistic feasibility, given the scale at which the model operates.

In the future, RES modelling may serve as a useful tool to address both basic ecological questions as well as management and conservation related issues in situations where the paucity of data precludes the use of other more data intensive habitat modelling approaches.

The vastness and remoteness of the ocean environment contributes to a prevailing lack of comprehensive point data sets needed for statistically investigating patterns of species occurrence. Relying on more readily available types of data, such as general descriptions, RES modelling will therefore be particularly useful to study basic niche similarities and overlap between different species or groups of species in the marine environment. Here, its application may also be a worthwhile first step to investigate potential large-scale species' occurrence, including historical distributions of heavily depleted species (e.g., gray whales in the North Atlantic; Mitchell & Mead 1977), calving grounds of endangered baleen whale species (yet unknown for species such as the North Pacific right whale; Gaskin 1991) or changes in species distributions due to environmental regime shifts.

Similar to a proposed application of ecological niche factor analysis (Engler et al. 2004), RES modelling – though based on a somewhat different approach – may also be helpful to predict suitable habitat of rare and endangered species, such as for beaked whales species that have few if any 'at-sea' records (D'Amico et al. 2003).

Most importantly, the extent to which RES generated hypotheses describe actual observed patterns in species occurrence allows more specific questions to be asked about the role that other factors play in determining actual distributions. Moreover, the comparison of RES predictions with outputs of point-data based statistical models will help identify discrepancies that may be symptomatic for underlying sampling biases and related issues, but can also highlight the problems of misapplications of such models using non-effort corrected data.

In a management context, RES predictions represent cost-efficient starting points to focus future research and survey efforts. In particular, this is practical when dealing with one of the many data-poor marine mammal species in the lesser-studied regions of the world. As already demonstrated on small geographic scales, habitat prediction models may be usefully applied to design marine reserves that would minimize

anthropogenic impacts on endangered species of marine mammals (Mullin et al. 1994b, Moses & Finn 1997, Hooker et al. 1999). By generating global spatially explicit indices of biodiversity and species richness, or visualizing potential geographic hotspots of high conflict with fisheries or other human operations, RES modelling may be equally useful when attempting to delineate efficient marine protected areas or critical habitat on larger temporal and geographic scales.

2.5. CHAPTER SUMMARY

I developed a large-scale habitat suitability modelling approach to map global distributions of 115 species of marine mammals. Predictions were generated by first assigning each species to broad-scale categories of habitat preferences with respect to depth, sea surface temperature and ice edge association based on synopses of published qualitative and quantitative habitat preference information. Using a global grid with 0.5 degree lat/long cell dimensions, I generated an index of the relative environmental suitability (RES) of each cell for a given species by relating quantified habitat preferences to locally averaged environmental conditions in a GIS modelling framework. RES predictions closely matched published maximum range extents for most species, suggesting that the model-based approach for identifying habitat represents a useful, more objective alternative to existing sketched distributional outlines. In addition, raster-based predictions provided more detailed information about heterogeneous patterns of potentially suitable habitat for species throughout their range. I validated RES model outputs for four species (northern fur seal, harbour porpoise, sperm whale and Antarctic minke whale) from a broad taxonomic and geographic range using 'at-sea' sightings from dedicated surveys. Observed relative encounter rates and species-specific predicted environmental suitability were significantly and positively correlated for all species. In comparison, observed encounter rates were positively correlated with < 3 % of 1000 simulated random data sets.

Mapping of suitable habitat for marine mammals using this environmental envelope model is helpful for evaluating current assumptions and knowledge about species' occurrences, especially for data-poor species. Moreover, RES modelling may help to focus research efforts on smaller geographic scales and usefully supplement other, statistical, habitat suitability models.

2.6. LITERATURE CITED

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3. Mapping worldwide distributions of data-deficient marine mammals: a test using stranding data for beaked whales³

3.1. INTRODUCTION

The beaked whales, family Ziphiidae, represent one of the least studied and most elusive taxonomic group of mammal species. Often most information about these large odontocete species stems from a handful of widely scattered stranding records and some of the 21 currently recognized species (Rice 1998, Dalebout et al. 2002, van Helden et al. 2002) have yet to be seen alive and are recognised based on skeletal remains of a few stranded individuals alone (van Helden et al. 2002) (Table 3.1). Because of their inconspicuous behaviour and apparent restriction to deep offshore waters (Mead 1989a), most beaked whales are difficult to detect and identify at sea. Combined with potentially very large species' ranges (Jefferson et al. 1993) and the logistical difficulties of surveying their habitat, these factors result in a dearth of knowledge about most ziphiid species, which greatly hampers the delineation of species ranges. This information, however, is a basic pre-requisite for any attempts to minimize anthropogenic impacts on these species, such as the potential effects of sonar exercises that have been proposed as a cause for recent mass strandings of ziphiids (Jepson et al. 2003).

To date, there are only a few existing and often disjointed outlines of maximum range extents for beaked whales that use existing sighting, and sometimes stranding records, as anchor points to construct simple polygons (Mead 1989a, Jefferson et al. 1993, MacLeod 2000). Such outlines vary considerably between authors (compare e.g., Jefferson et al. 1993, MacLeod 2000) and, moreover, implicitly suggest a uniform probability of occurrence of a species throughout the enclosed area. Some experts, aware of the temporal and spatial biases associated with the underlying data, hesitate to deduce anything about a species' distribution from sightings or strandings. Instead it is often preferred to simply compile and plot exact positions of records (Balcomb 1989). This approach, however, leaves it up to the sometimes less informed readers to draw their own conclusions about a species potential distributional ranges and thus under-utilizes the available ancillary expert knowledge about unequal survey effort distributions, seasonal differences and irregularities such as extralimital sightings.

Shortcomings of both approaches are subjectivity and some unrealistic implicit assumptions about species occurrence. In contrast, the application of GIS mapping and spatial modelling techniques to predict marine mammal habitat offers a more objective approach, generating reproducible results with clear and modifiable underlying assumptions (e.g., Gregr & Trites 2001, Hamazaki 2002). However, most common

³ Chapter submitted as manuscript: K. Kaschner, R. Watson, C. MacLeod, D. Pauly. Mapping worldwide distributions of data-deficient marine mammals: a test using stranding data for beaked whales.

habitat suitability modelling approaches require large amounts of effort-corrected sighting data, frequently lacking for many marine mammal species.

I have developed a generic environmental envelope model to predict global marine mammal distributions that mainly relies on the synthesis of non-quantitative habitat preference information (Chapter 2). This type of information is more readily available for most species than results from statistical investigations of sightings data and the determination of environmental correlates for species occurrence. I propose that this non-quantitative ‘expert knowledge’ may represent a currently under-utilized source of information that can be usefully applied within a knowledge-based habitat suitability modelling framework.

Validation of the relative environmental suitability (RES) model using large-scale, long-term sighting data sets indicated that the predictions appear to capture a significant amount of the observed variability in occurrence for several of the better known species (Chapter 2). However, the validation results were biased to some extent by the lack of complete independence of test data sets, which is impossible to guarantee using the RES approach. Moreover, sufficiently large ‘at-sea’ sightings data sets to test RES predictions are largely unavailable for many of the data-poor marine mammal species, such as the beaked whales. Information about stranding locations of these species is more frequently available and has been used to make inferences about maximum range extents (MacLeod 2000). It is, however, generally believed that dead and even living animals may have drifted or swum for considerable distances before washing up on shore, and surface currents have been documented to play an important role in determining stranding locations (Maigret 1979, Duguay & Wisdorff 1988, Brabyn & MacLean 1992, Anderson et al. 1999). Using sea surface currents as a link, stranding records may thus be used to test hypotheses about ‘at-sea’ species occurrence, while at the same time being more independent than sightings as they are less likely to have formed the basis for the habitat preference information used in the RES model.

The goal of this study was the development of a test of the RES model predictions for data-deficient marine mammal species, based on non-quantitative habitat preference information, using available stranding data sets. I sought to simplistically simulate the stranding process of a beaked whale dying offshore using a two-dimensional hydrodynamic model to compare relative stranding frequencies generated based on the predicted RES maps and a null model as starting point distributions for drifting carcasses. If the obtained large-scale relative stranding density patterns thus generated match observed patterns of long-term stranding data sets, I argue that this would allow us to draw some conclusions about the quality of the starting point distributions. The stranding simulation would therefore provide a potential validation for RES modelling predictions and allows us to evaluate the usefulness of the approach for data-deficient species such as most beaked whales.

Table 3.1. Ziphiid species list and general distributional area of individual species as well as documented reliable stranding and ‘at-sea’ records (sightings, bycatch & offshore whaling). Records with tentative species identification and/or approximate positions are shown in parentheses.

Scientific name	Common name	General distributional area / ocean basin	Number of stranding records	Earliest stranding record	Latest stranding record	Number of 'at-sea' records	Earliest 'at-sea' record	Latest 'at-sea' record
<i>Mesoplodon bidens</i>	Sowerby's beaked whale	N. Atlantic	133 (2)	1800	2002	15	1828	1998
<i>Mesoplodon bowdoini</i>	Andrews' beaked whale	S. hemisphere	32 (1)	1904	2000	-	-	-
<i>Mesoplodon carlhubbsi</i>	Hubb's beaked whale	N. Pacific	36	1944	1997	-	-	-
<i>Mesoplodon densirostris</i>	Blainville's beaked whale	World	98 (2)	1839	2000	26 (1)	1963	2001
<i>Mesoplodon europaeus</i>	Gervais' beaked whale	Atlantic	93	1889	2002	1	1998	1998
<i>Mesoplodon ginkgodens</i>	Ginkgo-toothed beaked whale	World	20	1935	1994	3	1960	1989
<i>Mesoplodon grayi</i>	Gray's beaked whale	S. hemisphere	37 (1)	1895	1995	5	1974	1999
<i>Mesoplodon hectori</i>	Hector's beaked whale	S. hemisphere	25	1866	1999	1	1999	1999
<i>Mesoplodon layardii</i>	Strap-toothed whale	S. hemisphere	75 (1)	1866	1997	2	1967	1967
<i>Mesoplodon mirus</i>	True's beaked whale	Atlantic & Indian Ocean	41	1899	1999	1	1993	1993
<i>Mesoplodon peruvianus</i>	Pygmy beaked whale	Pacific	9	1955	1995	16 (3)	1976	1999
<i>Mesoplodon perrini</i>	Perrin's beaked whale	N. Pacific	5	1975	1997	1	1976	1976
<i>Mesoplodon stejnegeri</i>	Stejneger's beaked whale	N. Pacific	124	1883	1999	12 (1)	1960	1988
<i>Mesoplodon traversii</i>	Spade-toothed beaked whale	S. hemisphere	3	1872	?	-	-	-
<i>Berardius arnuxii</i>	Arnoux's beaked whale	S. hemisphere	29	1840	1994	2	1992	1993
<i>Berardius bairdii</i>	Baird's beaked whale	N. Pacific	46	1920	1999	170 (1)	1919	1996
<i>Hyperoodon ampullatus</i>	Northern bottlenose whale	N. Atlantic	158 (4)	1742	2002	23 (48)	1867	2000
<i>Hyperoodon planifrons</i>	Southern bottlenose whale	S. hemisphere	21 (1)	1884	1992	42 (29)	1898	1994
<i>Indopacetus pacificus</i>	Longman's beaked whale	Pacific & Indian Ocean	4	1979	2002	(44)	1966	1996
<i>Tasmacetus shepherdii</i>	Shepherd's beaked whale	S. hemisphere	8	1933	1977	(1)	1964	1964
<i>Ziphius cavirostris</i>	Cuvier's beaked whale	World	349 (5)	1845	2002	65 (2)	1889	2001

3.2. MATERIAL & METHODS

3.2.1. Stranding/sighting records

Records on beaked whale occurrence were located from a number of sources including unpublished reports, published sources, unpublished datasets, contacts with local research groups and privately held records (D'Amico et al. 2003) (a full list of data and sources is available on request from C.D. MacLeod: c.d.macleod@abdn.ac.uk). Occurrence records included reports of strandings, sightings, bycatch and directed takes as well as some more obscure records such as skeletal parts found at fish markets etc. Records were categorized by type as either 'strandings' or 'at-sea' records, which included bycatch, sighting and whaling reports. All strandings were presumed to have been dead, unless other information was available. Levels of confidence were assigned to each record based on available accuracy of location and species information. Records with questionable species identification or location were excluded from the data set. A summary of compiled records is shown in Table 3.1. The number of records for each species represents the number of known stranding or 'at-sea' incidents, i.e., strandings or sightings of multiple animals at the same time were considered as a single record.

3.2.2. Prediction of relative environmental suitability

The methodological approach of the RES model is outlined in Fig. 3.1 and is discussed in detail in Chapter 2. Environmental parameters that were used in the RES model as predictive variables included bathymetry, average annual sea surface temperature and average annual distance from the sea ice edge, defined as the extent of the annual average 50 % ice coverage of a grid cell.

Bathymetric data were taken from the ETOPO2 dataset available on the U.S. National Geophysical Data Center's 'Global Relief' CD (www.ngdc.noaa.gov/products/ngdc_products.html) that provides elevation in 2-minute intervals for all points on Earth. Global annual sea surface temperature data were extracted from the NOAA World Ocean Atlas 1998 CD and averaged for the second half of the 20th century. Spatial information about the average monthly ice extent (1979-1999), – delineated by the border of a minimum 50 % sea ice concentration or coverage – was taken from US National Snow & Ice Data Center web site (http://nsidc.org/data/smmr_ssmi_ancillary/trends.html#gis). The ice edge border was smoothed to correct misclassification and/or re-projection errors.

All environmental data were rasterized using a custom GIS software package (SimMap) and interpolated averages stored as cell attributes in a global raster database with a 0.5 degree latitude by 0.5 degree longitude cell size (Watson et al. 2004). Monthly distances from the nearest ice edge cell were subsequently calculated for each cell in the raster and average annual distances were computed based on

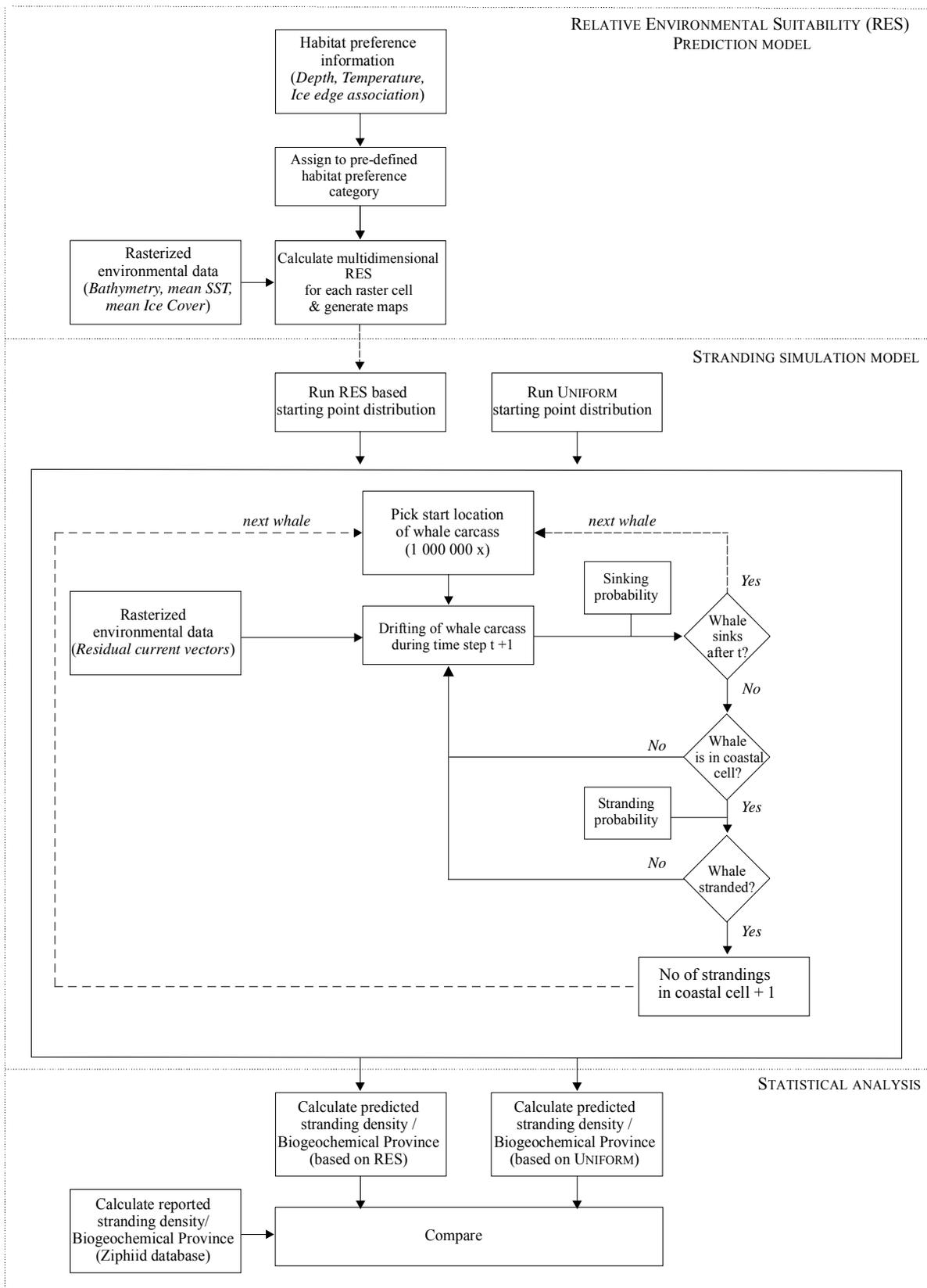


Figure 3.1.

Model flowchart of Relative Environmental Suitability (RES) model and stranding simulation model.

these monthly distances. Residual sea surface current vectors were provided by Arthur J. Mariano (University of Miami, pers. comm.) and are based upon global drifter data interpolated to 1 degree cells (Mariano et al. 1995).

Information about habitat preferences of ziphiids was extracted from the primary literature (e.g., Houston 1990, Reeves & Mitchell 1993, Herman et al. 1994, Kasuya & Miyashita 1997, Waring et al. 2001) and secondary sources (e.g., Mead 1989a, MacLeod 2000, Perrin et al. 2002). Information ranged from very broad qualitative general descriptions of habitat preferences, such as “deep-water, offshore” species (e.g., Jefferson et al. 1993, Kasuya 2002, Pitman 2002) to some quantitative studies investigating environmental correlations between ziphiid catch or sighting records (e.g., Smith et al. 1986, Waring et al. 2001, Hamazaki 2002). In addition, I obtained information about prevailing average environmental conditions associated with specific ziphiid sighting locations by assigning ‘at-sea’ records from the ziphiid database to the corresponding 0.5 degree raster cell. This should be regarded with some caution, however, since I was unable to correct sighting frequency per environmental stratum for effort due to the lack of available effort information. All habitat preference information was ranked based on the associated uncertainty (5 different categories) with investigation of statistically significant relationships between sighting and environmental correlates ranking highest and broad qualitative niche description ranking lowest.

I subsequently assigned species to ecologically relevant predefined predictor range categories (i.e., ‘habitat preferences’) using the most reliable information available. Predictor categories were chosen to represent input parameter ranges, defined to – collectively – describe real multi-dimensional marine physical/ecological niches inhabited by ziphiids (Table 3.2). Ecologically relevant depth and ice edge categories are irregular in width and were characterized accordingly. SST categories were defined in regular 5° C steps, based on the average inter-annual variation of 5-10° C in most areas of the world (Angel 1992).

Table 3.2. Qualitative description and corresponding quantitative definition of habitat preference categories for three predictor parameters (depth, mean sea surface temperature (SST), distance from edge of mean sea ice extent) used in the relative environmental suitability prediction model. Parameter values represent x coordinates of a trapezoidal probability distribution, that assumes maximum relative environmental suitability within a species-specific preferred range and tapers off on both sides towards the assumed minimum and maximum (see Fig. 3.2).

Environmental parameter	Minimum	Minimum of preferred range	Maximum of preferred range	Maximum	Description of habitat preference category
Depth [m]	0	-200	-2000	-8000	mainly continental slope
	0	-1000	-2000	-8000	mainly lower continental slope
	0	-1000	-4000	-8000	lower continental slope - deep offshore waters
	0	-2000	-6000	-8000	restricted to very deep offshore waters
Mean ann. SST [° C]	-2	0	15	20	polar - warm temperate
	-2	0	20	25	polar - subtropical
	-2	0	25	30	polar - tropical
	0	5	15	20	subpolar - warm temperate
	0	5	20	25	subpolar - subtropical
	5	10	20	25	cold temperate - subtropical
	5	10	30	30	cold temperate - full tropical
	10	15	20	25	warm temperate - subtropical
	10	15	30	30	warm temperate - full tropical
Distance from edge of mean sea ice extent [km]	0	1	500	8000	occur mainly around edge of pack-ice, but also elsewhere
	0	1	8000	8000	occur regularly but not preferentially around the edge of the pack-ice
	0	500	2000	8000	occur mainly in areas covered during maximum ice extent, but also elsewhere
	500	1000	8000	8000	no association with ice edge, but occur seasonally close to area of maximum ice extent
	1000	1500	8000	8000	no association with ice edge, do not occur anywhere near ice at any time of the year

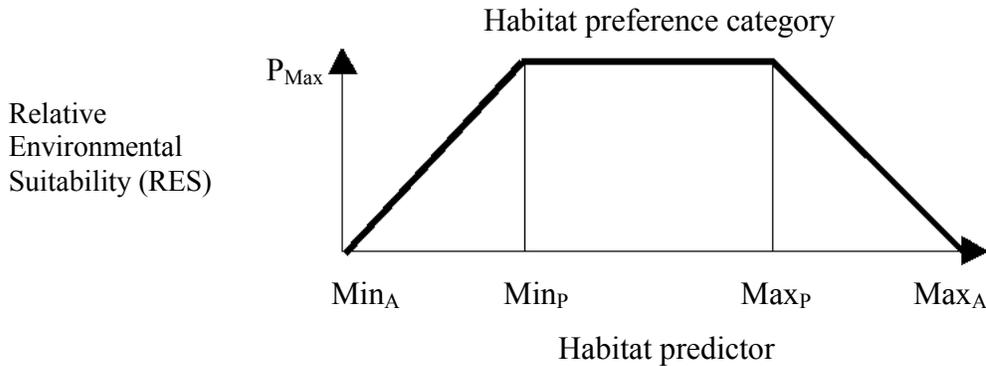


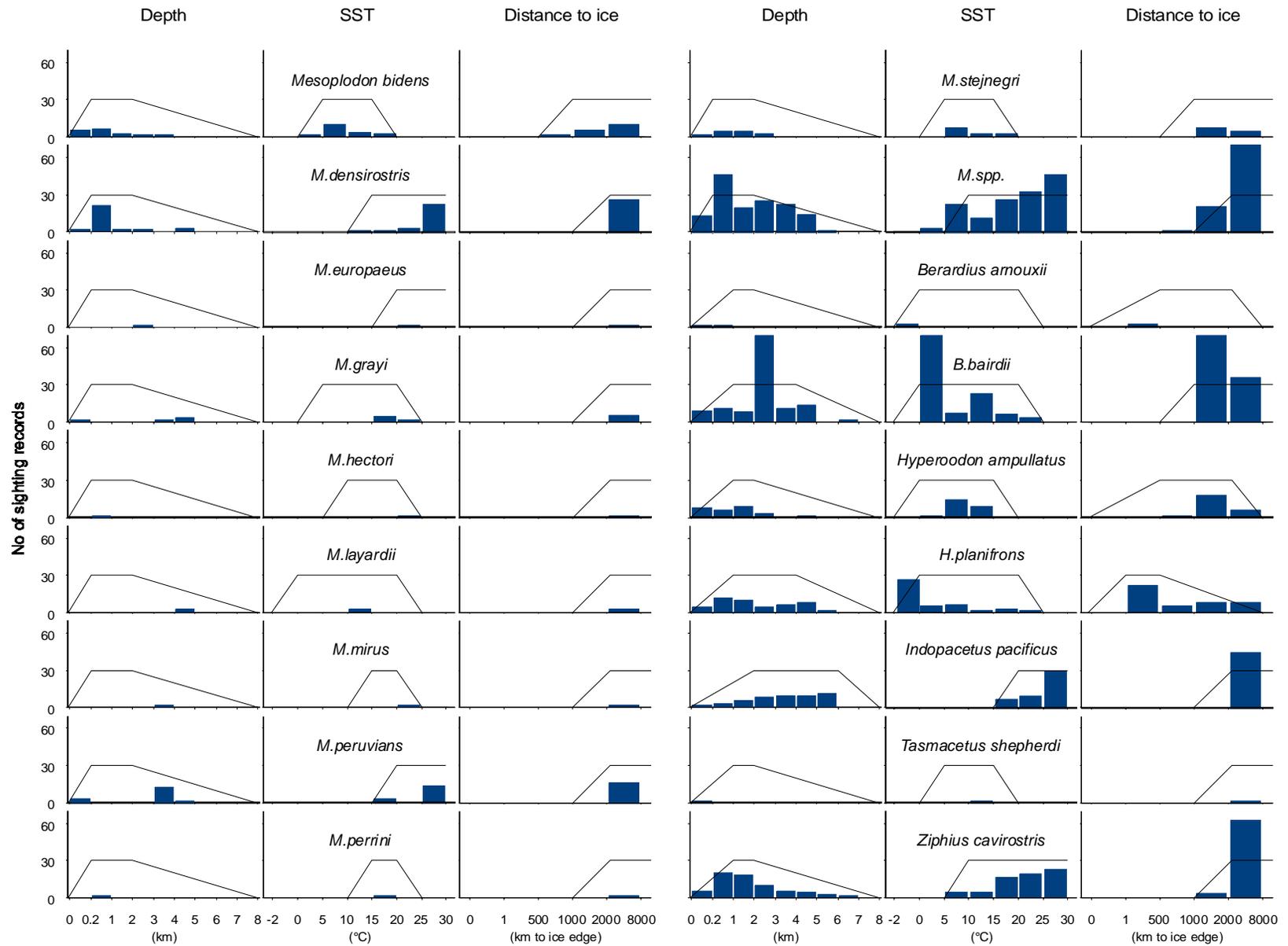
Figure 3.2.

Assumed trapezoidal probability distribution describing habitat preference categories. Relative environmental suitability is assumed to be highest between Min_P and Max_P (preferred range for a species) and tapers off towards the assumed minimum and maximum Min_A and Max_A .

Habitat preference categories were described as a trapezoidal probability distribution (Fig. 3.2). This distribution was selected as the simplest and most widely applicable option in view of the absence of sufficient data describing a specific relationship between ziphiid occurrence and environmental parameters. The degree to which the assumed predictor probability distribution was supported by the observed relationship between predictors and sighting frequencies for the 17 species with documented sighting records is illustrated in Fig. 3.3. It should be noted, however, that the lack of available effort introduced some serious biases into this analysis (Chapter 2).

Figure 3.3. (next page)

Frequency distribution of published sighting records of ziphiid species plotted against classes of environmental parameters that serve as predictors in the RES model (See Table 3.1 for common names). Information about average environmental conditions at sighting locations was obtained by assigning records to geographically corresponding 0.5 latitude/longitude cells in a global raster with associated environmental data. Only records with adequate geographic accuracy and unequivocal species identification were included, except for *Indopacetus pacificus* and *Tasmacetus shepherdi* where species identification for sighting records is only tentative. Please note that predictor class categorization for depth and mean distance to ice edge follows non-linear, but ecologically more meaningful intervals. Lines represent the quantitative habitat preference category to which each species was assigned based on sighting frequency distribution supplemented by qualitative descriptions and other available data. For species with few or no sighting records, habitat preferences were inferred from those of closely related species or genus (e.g., see *M.spp.* for distribution of combined *Mesoplodon* sightings).



In the few cases where specific or general information about species-specific depth preferences was non-existent, species were assigned to categories based on known preferences of closely related species, i.e. those generally observed within the genus (see *M. spp.* in Fig. 3.3). Similarly, if temperature and ice edge association information was missing, I inferred species-specific preferences from available information about maximum range extents (Jefferson et al. 1993, Rice 1998). Assigned habitat preference categories for all species are summarized in Table 3.3.

After excluding ocean basins with less than two reported sightings, I generated a surface map of environmental suitability for each specific species. This was achieved by calculating a relative environmental suitability index for each raster cell (ranging from 0 to 1) by relating assumed habitat preferences to the prevalent environmental conditions for each cell (see Chapter 2).

Table 3.3. Habitat preferences in terms of depth, mean annual sea surface temperature and distance to the edge of sea ice for beaked whale species. (See Table 3.1 for common names) Superscripts denote the particular habitat preference type about which the reference provided information: ¹ = depth preferences, ² = temperature preferences, ³ = distance to edge of sea ice.

Scientific name	Depth range preference	SST range preference	Distance to ice edge range preference	Sources
<i>Mesoplodon bidens</i>	mainly cont. slope	subpolar-w. temperate	no association, but season. in area of max. ice extent	Carlström et al, 1997 ¹ ; D'Amico et al, 2003 ^{1,2,3} ; Houston, 1990 ¹ ; Hooker & Baird, 1999 ^{1,2} ; MacLeod, 2000 ^{2,3} ; Waring et al, 2001 ¹
<i>M. bowdoini</i>	mainly cont. slope	c. temperate-subtropical	no association	Baker, 2001 ² ; Gaskin, 1968 ² ; Gaskin, 1971 ² ; Mead, 1989a ^{1,3} ; Pitman, 2002 ¹
<i>M. carlhubbsi</i>	mainly cont. slope	c. temperate-subtropical	no association	Houston, 1990 ^{2,3} ; MacLeod, pers comm ¹ ; Mead, 1989a ^{1,2}
<i>M. densirostris</i>	mainly cont. slope	w. temperate-tropical	no association	D'Amico et al 2003 ^{1,2,3} ; Houston, 1990 ^{1,2,3} ; Moore, 1966 ¹ ; Pitman, 2002 ² ; Ritter & Brederlau, 1999 ¹ ; Rosario-Delestro et al, 1999 ² ; Shallenberger, 1981 ¹
<i>M. europaeus</i>	mainly cont. slope	subtropical-tropical	no association	D'Amico et al, 2003 ^{1,2,3} ; Davis et al, 1998 ¹ ; Mead, 1989a ^{2,3} ; MacLeod, 2000 ² ; Pitman, 2002 ^{1,2} ; Rosario-Delestro et al, 1999 ² ; Waring et al, 2001 ¹
<i>M. ginkgodens</i>	mainly cont. slope	subtropical-full tropical	no association	Mead, 1989a ^{1,2,3} ; Miyakazi et al, 1987 ² ; Pitman, 2002 ¹
<i>M. grayi</i>	mainly cont. slope	subpolar-subtropical	no association	D'Amico et al, 2003 ^{1,2,3} ; Gaskin, 1971 ² ; Mead, 1989a ^{1,2,3} ; Pitman, 2002 ¹ ; Rice, 1998 ²
<i>M. hectori</i>	mainly cont. slope	c. temperate-subtropical	no association	D'Amico et al, 2003 ^{1,2,3} ; Mead, 1989a ^{1,2,3} ; Pitman, 2002 ¹ ; Rice, 1998 ²
<i>M. layardii</i>	mainly cont. slope	polar-subtropical	no association	D'Amico et al, 2003 ^{1,2,3} ; Guiler et al, 1987 ² ; Mead, 1989a ^{1,2,3} ; Pitman, 2002 ¹
<i>M. mirus</i>	mainly cont. slope	w. temperate-subtropical	no association	D'Amico et al, 2003 ^{1,2,3} ; Houston, 1990 ^{1,2,3} ; MacLeod, 2000 ² ; Mead, 1989a ^{1,2} ; Pitman, 2002 ^{1,2} ; Waring et al, 2001 ¹
<i>M. peruvianus</i>	mainly cont. slope	subtropical-tropical	no association	D'Amico et al, 2003 ^{1,2,3} ; Jefferson et al, 1993 ³ ; Mead, 1989a ¹ ; Pitman, 2002 ¹
<i>M. perrini</i>	mainly cont. slope	w. temperate-subtropical	no association	Dalebout et al, 2002 ¹ ; D'Amico et al, 2003 ^{1,2,3} ; Mead, 1998a ² ; Miyazaki et al, 1987 ² ; Pitman, 2002 ¹ ; Rice, 1998 ³
<i>M. stejnegeri</i>	mainly cont. slope	subpolar-w. temperate	no association, but season. in area of max. ice extent	D'Amico et al, 2003 ^{1,2,3} ; Houston, 1990 ² ; Loughlin et al, 1982 ¹ ; Loughlin & Perez, 1985 ^{2,3} ; Mead, 1989a ¹ ; Miyazaki et al, 1987 ² ; Pitman, 2002 ¹ ; Rice, 1998 ^{1,2}
<i>M. traversii</i>	mainly cont. slope	c. temperate-subtropical	no association	van Helden et al, 2002 ^{2,3} ; depth preference inferred from other species

Table 3.3. (cont.)

Scientific name	Depth range preference	SST range preference	Distance to ice edge range preference	Sources
<i>Berardius arnuxii</i>	mainly lower cont. slope	polar-subtropical	mainly pack-ice edge, but also elsewhere	Balcomb, 1989 ^{1,2,3} ; D'Amico et al, 2003 ^{1,2,3} ; Jefferson et al, 1993 ^{1,2} ; Hobson & Martin, 1996 ³ ; Ponganis & Kooyman, 1995 ¹
<i>B. bairdii</i>	lower cont. slope-offshore waters	polar-subtropical	no association, but season. in area of max. ice extent	D'Amico et al, 2003 ^{1,2,3} ; Fedoseev, 1984 ³ ; Jefferson et al, 1993 ¹ ; Kasuya et al, 1997 ¹ ; Kasuya, 2002 ^{1,2,3} ; Reeves & Mitchell, 1993 ^{1,2,3}
<i>Hyperoodon ampullatus</i>	mainly lower cont. slope	polar-w. temperate	mainly in max ice extent areas, but also elsewhere	Benjaminsen, 1972 ¹ ; Benjaminsen & Christensen, 1979 ^{1,2,3} ; D'Amico et al, 2003 ^{1,2,3} ; Hooker et al, 1999 ¹ ; Jefferson et al, 1993 ² ; Reeves et al, 1993 ^{1,3}
<i>H. planifrons</i>	lower cont. slope-offshore waters	polar-subtropical	mainly pack-ice edge, but also elsewhere	D'Amico et al, 2003 ^{1,2,3} ; Jefferson et al, 1993 ¹ ; Gowans, 2002 ¹ ; Kasamatsu & Joyce, 1995 ¹ ; Mead, 1989b ^{1,3} ; Rice, 1998 ³
<i>Indopacetus pacificus</i>	offshore waters	subtropical-full tropical	no association	D'Amico et al, 2003 ^{1,2,3} ; Mead, 1989 ^{1,2,3} ; Pitman, 2002 ²
<i>Tasmacetus shepherdi</i>	mainly lower cont. slope	subpolar-w. temperate	no association	D'Amico et al, 2003 ^{1,2,3} ; Gaskin, 1971 ² ; Jefferson et al, 1993 ^{1,2} ; Mead, 1989c ² ; Mead, 2002 ^{1,2} ; Rice, 1998 ³
<i>Ziphius cavirostris</i>	mainly lower cont. slope	c. temperate-full tropical	no association	D'Amico et al, 2003 ^{1,2,3} ; Dolar et al, 1997 ¹ ; Gannier, 2000 ¹ ; Heyning, 2002 ² ; Rice, 1998 ^{2,3} ; Waring et al, 2001 ¹

3.2.3. Stranding simulation

There is limited information about the processes that will culminate in the stranding of a whale carcass, which makes the development of a suitable simulation model difficult. Here, I briefly summarize the available knowledge about the stranding process, which provided the basis for the model I developed: Most cetaceans, with some exceptions such as right whales, will likely initially sink upon death (Schäfer 1962). In the open ocean, most whale carcasses probably sink beyond the aerobic layers into the deep-sea abyss, where they may be of considerable importance to sustain scavenging communities (Butman et al. 1995, Butman et al. 1996, Jelmert & Oppen-Berntsen 1996) and from which they may rarely re-surface. In the aerobic conditions found in shallower water depths, however, bacterial decomposition of the carcass will lead to the development of gases inside the body cavity (Schäfer 1962). Trapped inside by the blubber layer and a thick integument, these gases will result eventually in an increased buoyancy (Schäfer 1962). The bloated carcass probably floats back up to the surface within a time span ranging from a couple of days (Schäfer 1962) to some weeks (Moreno et al. 1993), depending on the species and environmental conditions. It will then start drifting with the surface currents until it reaches land or decomposition progresses to the point where the integument breaks and the gases escape and the carcass sinks again (Schäfer 1962). The only published information about sinking rates and associated floating times of cetaceans is supplied by Schäfer (1962) who very broadly talks about carcasses of small cetaceans floating for “a couple of weeks”. Ames et al. (2002), studying drifting of sea otter carcasses in California, provided the only available quantitative estimate of carcass floating times of any marine mammal species, which averaged around six weeks. Considering the small size of sea otters and the absence of a blubber layer, it seems likely that most other species would float for considerably longer time periods.

Here, I assumed the number of whales dying within each raster cell to be directly proportional to the species-specific environmental suitability of a cell in the stranding simulation model, although the actual occurrence of a species likely depends on a host of other factors not considered in the RES model. A basic underlying assumption of the stranding simulation model was that there would be more animals in a more suitable cell and therefore proportionally more deaths. I then simulated the drifting movement of a dead whale along oceanographic surface current vectors representing the net movement of water masses over the course of a whole year (Mariano et al. 1995) (Fig. 3.5 A). The model allowed a certain percentage of carcasses to sink over time based on a pre-defined sigmoid sinking probability distribution (see below) and recorded the frequency with which the remaining drifting bodies would reach positions along the coastlines (see Fig. 3.1). I then thoroughly tested the sensitivity of the model to variations in sinking rates, simulation time steps, different start location selection procedures as well as the number of model runs to optimize settings.

Simulations for each of the 21 species of beaked whales were run one million times using two alternate starting point scenarios: (a) based on the predicted RES maps (PRED) and (b) the “standard” uniform distribution (STAND), represented in most cases by the distributional ranges published by Jefferson et al (1993) which served as the null model. Using the RES surfaces, the proportion of whales dying in a cell was determined by the product of the relative environmental suitability of the cell and the cell’s sea surface area. In contrast, for the uniform input distribution representing the null model, the number of whales dying in a cell was proportional only to the sea surface area of the cell. For each individual run drift rates and directions as well as start locations were selected using a stochastic approach. Based on the limited available information, I assumed a carcass half-life (sinking rate) of 10 weeks (i.e., inflection point of a logistic curve describing the probability of a whale to sink at a given time step) for the relatively large beaked whales.

3.2.4. Statistical analysis

For each species relative stranding frequencies generated based on both starting point distributions were compared with reported strandings using Kendall’s non-parametric rank correlation test (Zar 1996, JMP 2000). Only stranding records with high confidence in species identification and stranding locations were used. All known live stranding incidents were excluded to reduce the bias introduced by animals that may have actively swum to a stranding location rather than drifted there (Table 3.4). Correlation analysis is greatly influenced by large sample sizes and non-independence of spatially auto-correlated data (Zar 1996, Burrough & McDonnell 1998). Both are generally encountered in a geographic raster based data set and, combined with the lack of information about observed absences and effort, would have impacted the statistical outcomes substantially. To reduce these impacts, I grouped records based on biogeochemical provinces (PROV) for predicted and reported strandings, respectively (Longhurst 1995) (Fig. 3.5 A). To correct for the substantial size difference between provinces, stranding densities were computed using strandings per km² of water of all coastal cells of each province as a proxy for coastal length, which, having a fractal dimension, is largely indeterminate. The correlation between relative predicted and reported stranding densities in all provinces with at least one reported or predicted stranding was then tested.

Since information about stranding monitoring effort was unavailable on a global scale, the analysis suffered substantially from the impact of false negatives, i.e., the absence of reported strandings due to lack of monitoring effort rather than the true absence of a species in an area. Attempts to develop a suitable effort proxy using human population density etc., which would have helped to identify and exclude false negatives, were unsuccessful as I could detect no significant relationship between human population density and reporting frequencies. However, I investigated the effects of statistical outliers on the results using Mahalanobis and Jackknife distance analysis (JMP 2000).

Finally, I attempted to assess the sensitivity of the models to impacts of variation of input model parameters on the statistical outcome. Using regression analysis, I tested the relationship between certain model variables and the strength of the correlation between predicted and reported strandings of all species combined, but differentiating between PRED and STAND based models. Input parameters that were investigated included the total number of reported strandings, the total number of predicted strandings, the effective sample size (i.e. number of PROVs with predicted strandings) and the proportion of potential false negatives (i.e. PROVs with 0 reported stranding that could be due to lack of effort or the real absence of strandings) in each model.

3.3. RESULTS

The results indicated that the RES modelling approach can usefully be applied to data-deficient marine mammal species and that predictions of species distributions represent an improvement over the existing subjective outlines of maximum range extent.

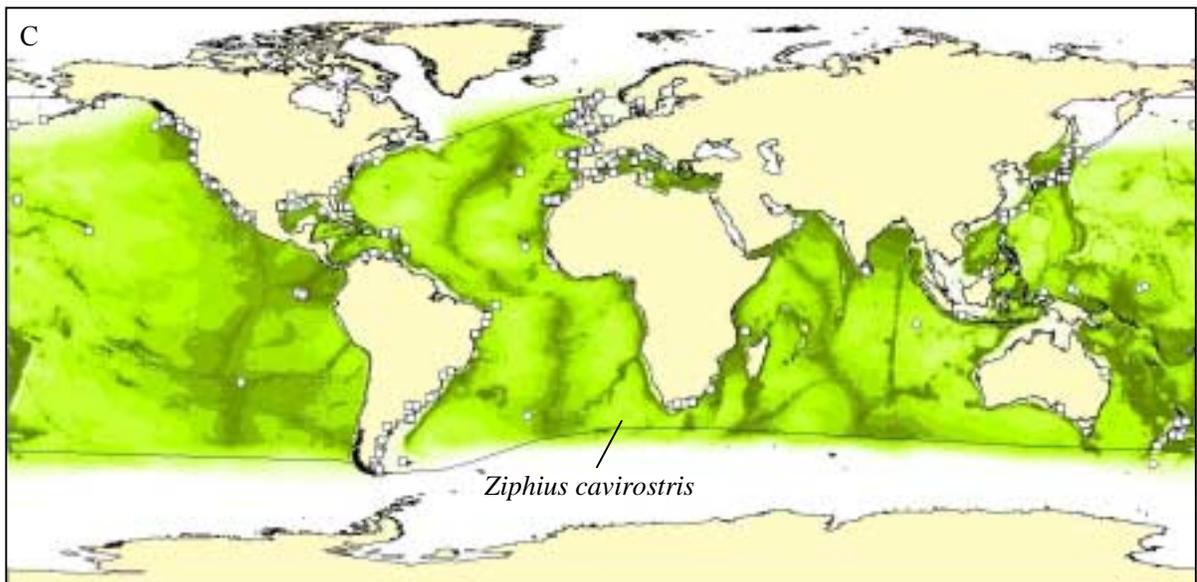
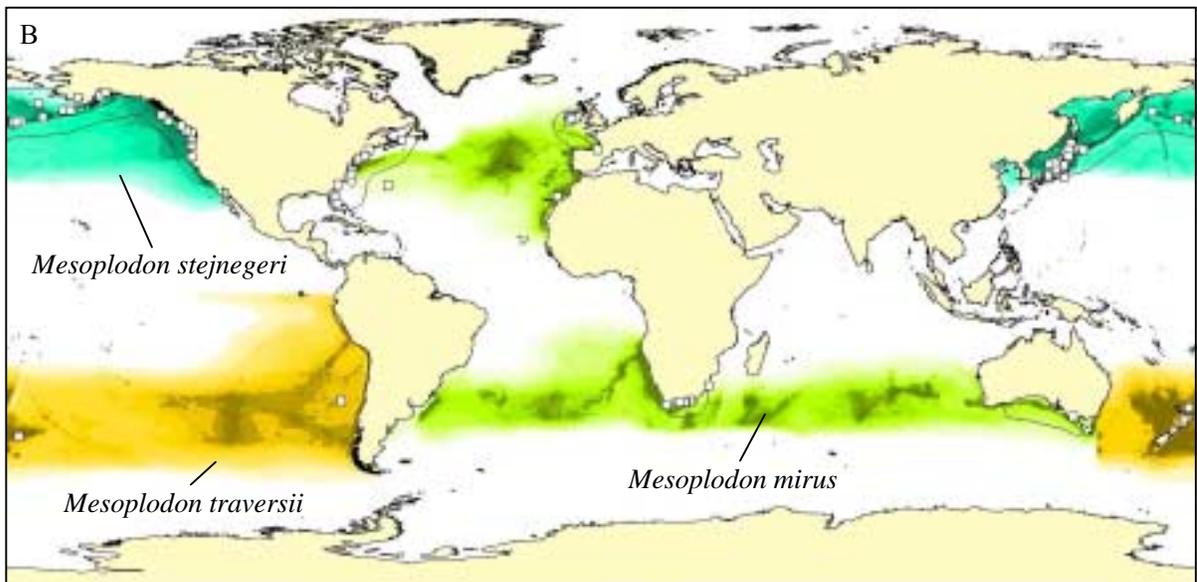
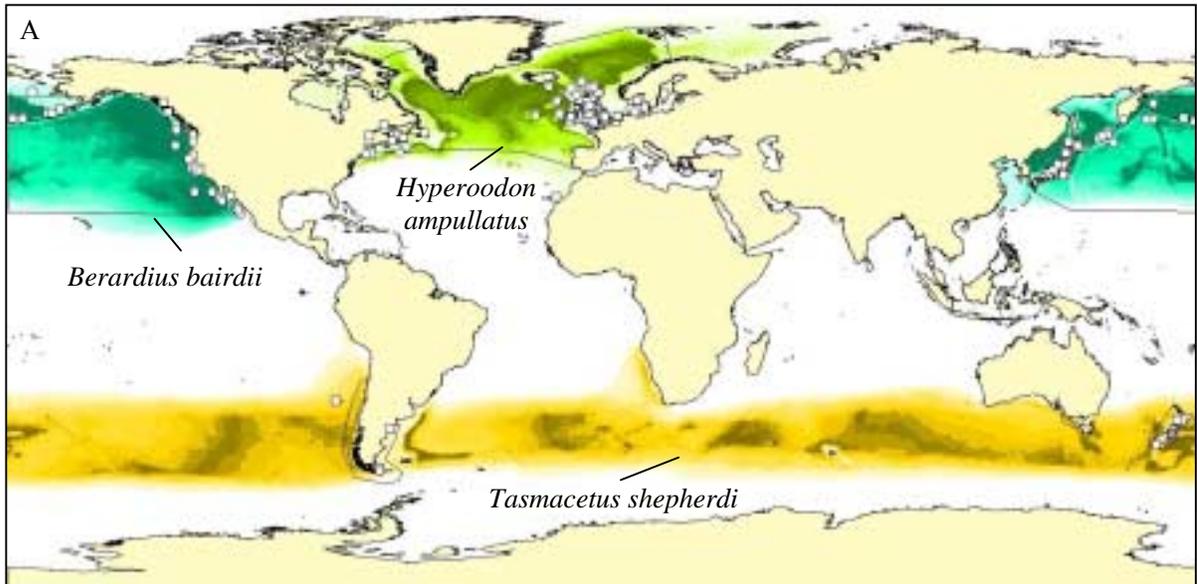
3.3.1. Prediction of relative environmental suitability

The maximum extent of the RES maps closely matched published outlines of distributional ranges in most cases for which such outlines exist. This lent some basic support for the modelling approach and indicated that the delineation of marine species' distributions may be quantitatively described using very few basic parameters. In addition, the raster based RES predictions provided information about the relative suitability of the environment for a species at high resolution, thus representing more specific hypotheses about likely heterogeneity in occurrence throughout a species' range.

Maps of the predicted environmental suitability for seven selected ziphiid examples are shown in Figs 3.4 A–C. The colour gradient in each map represents an index of the environmental suitability (ranging from light = *not suitable* to dark = *very suitable*) of each raster cell for a species given its habitat preferences. Wherever possible, I included existing published outlines of distributional ranges (Jefferson et al. 1993) as well as stranding and sighting records for visual comparisons. The examples shown were selected to illustrate the applicability of the model approach over a wide geographic and taxonomic range of species associated with varying numbers of existing stranding or sighting records (see Table 3.1).

Figure 3.4. A–C. (next page)

Examples of RES model outputs: Predicted relative environmental suitability (ranging from less suitable (light) to very suitable (dark)) based on habitat preference information for seven different ziphiid species (See Table 3.1 for common names). Known 'at-sea' (sightings, bycatch, whaling = ○) and stranding (□) locations and outlines of proposed maximum ranges (Jefferson et al, 1993) are included for comparison. RES maps for all species are provided in Appendix 3 or online at www.seararoundus.org/distribution/search.aspx.



The predicted relative environmental suitability surfaces, reported strandings and published distributional outlines for three of the larger ziphiid species are shown in Fig. 3.4 A. The northern bottlenose whale *Hyperoodon ampullatus* is a relatively well known and abundant species restricted to polar and cold temperate North Atlantic waters (Mead 1989b, Sigurjónsson & Víkingsson 1997, Bjørke 2001) while Baird's beaked whale *Berardius bairdii*, an also relatively abundant species, inhabits a similar niche in the North Pacific (Kasuya 1986, Miyashita 1986, Balcomb 1989). In contrast, Shepherd's beaked whale *Tasmacetus shepherdi* is a cold water southern hemisphere species with less than 10 published records (Mead 1989c).

Model outputs for three species of the genus *Mesoplodon* are shown in Fig. 3.4 B: Stejneger's beaked whale *Mesoplodon stejnegeri* is a North Pacific species known from numerous stranding records. Conversely, the spade-toothed beaked whale *Mesoplodon traversii* is a very poorly known species, recognized based on only three reported stranding records scattered throughout the South Pacific (van Helden et al. 2002). In addition, the RES based distribution of True's beaked whale, *Mesoplodon mirus*, is shown. Records of this species appear to be concentrated in the south-eastern United States, though a number of strandings have been reported along other coasts of the subtropical to tropical Atlantic and the southern Indian Ocean (Mead 1989a, MacLeod 2000). The predicted RES map of the most cosmopolitan beaked whale species, Cuvier's beaked whale *Ziphius cavirostris*, is presented in Fig. 3.4 C. This species is known from more than 300 stranding records and numerous sightings in cold temperate to tropical waters around the world (Heyning 1989, Heyning 2002). The predicted distributions for all other ziphiid species can be viewed in Appendix 3 (Section 8.2.49–69) or online at www.seaaroundus.org/distribution/search.aspx.

3.3.2. Stranding simulation

Table 3.4 summarizes and contrasts the results of statistical comparison of predicted versus reported stranding densities per biogeochemical province based on the two alternative input distributions for all 21 ziphiid species. Significant correlations with relatively high positive correlation coefficients were observed for almost 50% of all species when strandings were simulated based on the RES maps (Table 3.4), among them is Shepherd's beaked whale with only eight known stranding records. Another two models produced significant results, though only after outliers were excluded from the data set. In contrast, simulated stranding models for only two out of 21 species (9.5 %) produced significant correlations with observed stranding patterns if a uniform input distribution was used and exclusion of outliers could improve these results in only one case. Figs 3.5 B and C show examples of stranding simulation outputs based on the two input distributions that illustrate the significant differences in predicted stranding frequencies in coastal cells for three different *Mesoplodon* species.

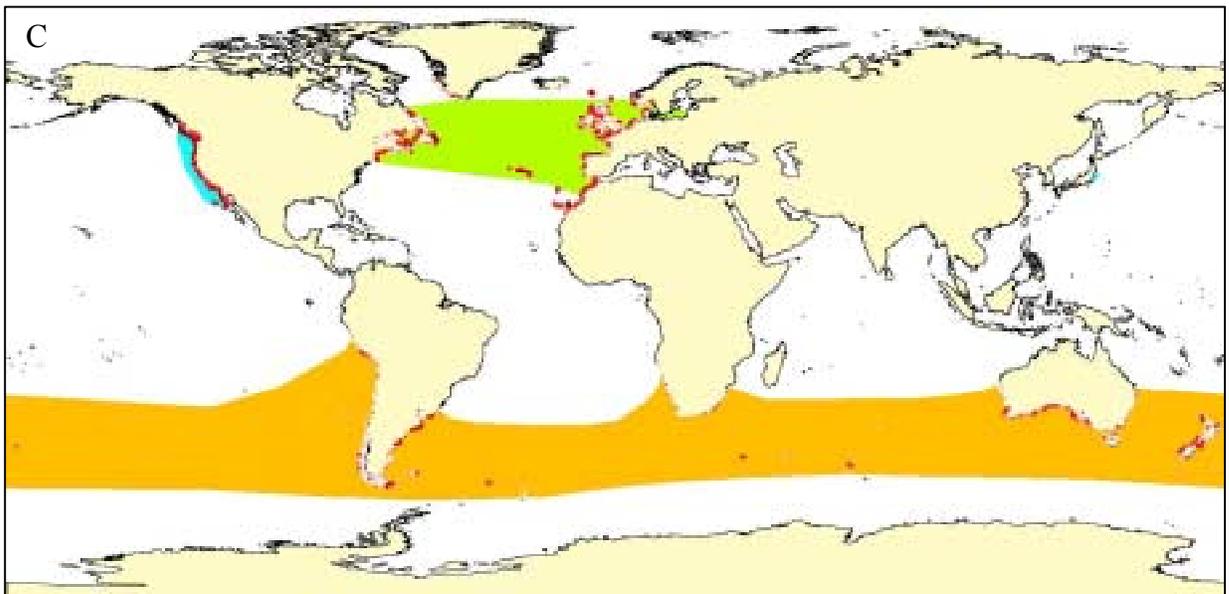
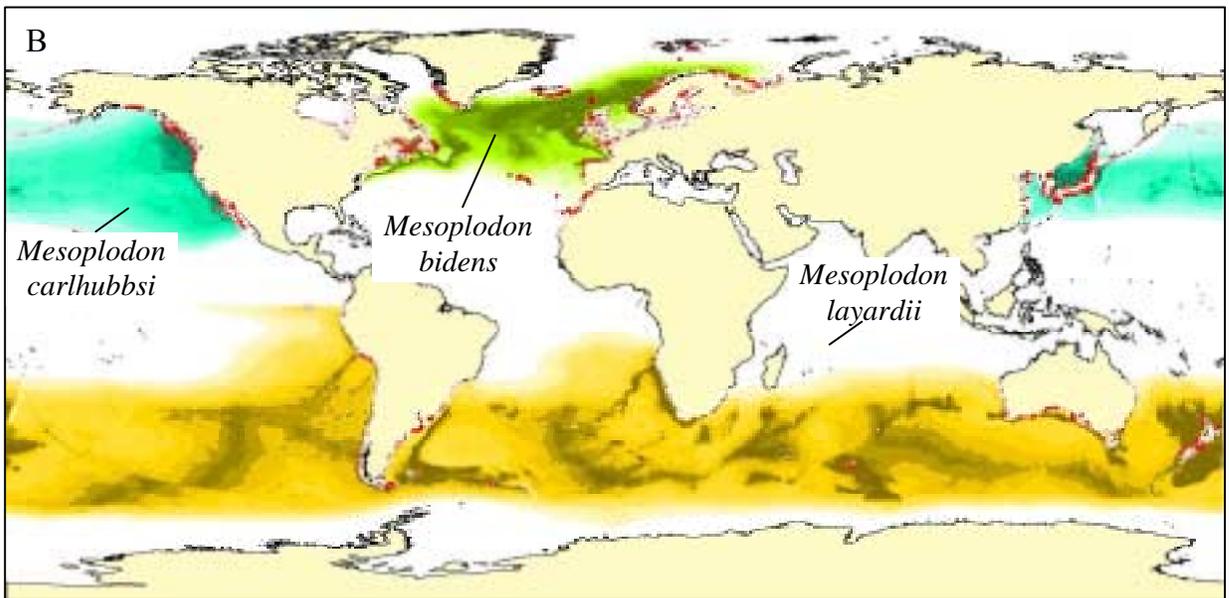
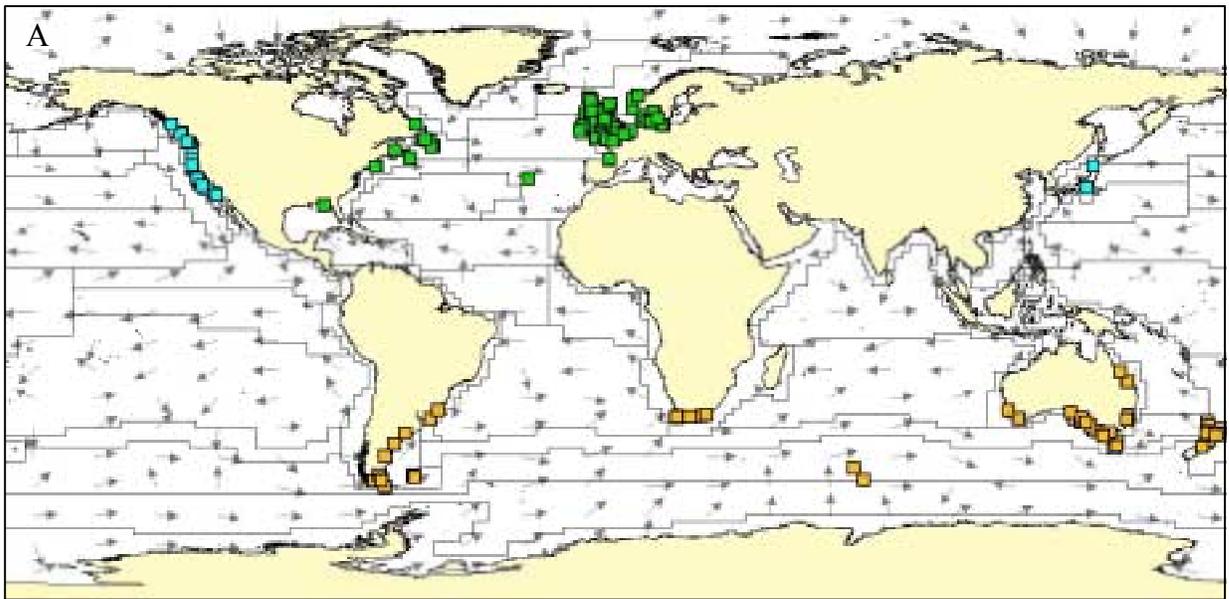
Table 3.4. Stranding simulation model: Results of statistical correlation analysis of relative predicted and reported stranding densities per Biogeochemical Province based on RES and uniform input distributions for all ziphiid species (* = significant correlations, ** = significant after exclusion of statistical outliers identified using Mahalanobis distance analysis). See Table 3.1 for common names.

Kendall's non-parametric rank correlation analysis
(coefficient tau & p-values) for predicted vs reported
strandings per Biogeochemical Province

Scientific name	No. of reported non-live strandings	RES input distribution (PRED)		uniform input distribution (STAND)	
		tau	p	tau	p
<i>Berardius arnuxii</i>	29	0.35	0.08**	0.39	0.04*
<i>Berardius bairdii</i>	35	0.47	0.05*	0.29	0.21
<i>Hyperoodon ampullatus</i>	152	0.08	0.76	-0.17	0.62
<i>Hyperoodon planifrons</i>	20	0.37	0.04*	0.34	0.09
<i>Indopacetus pacificus</i>	4	0.33	0.04*	0.31	0.07
<i>Mesoplodon traversii</i>	3	0.22	0.41	0.22	0.47
<i>Mesoplodon bidens</i>	128	0.66	0.01*	0.33	0.29
<i>Mesoplodon bowdoini</i>	32	0.53	0.00*	0.42	0.12
<i>Mesoplodon carlhubbsi</i>	30	0.53	0.02*	0.67	0.17
<i>Mesoplodon densirostris</i>	89	0.20	0.07**	0.13	0.26
<i>Mesoplodon europaeus</i>	91	0.26	0.15	-0.12	0.62
<i>Mesoplodon ginkgodens</i>	13	0.09	0.55	0.13	0.53
<i>Mesoplodon grayi</i>	36	0.37	0.04*	0.37	0.06**
<i>Mesoplodon hectori</i>	24	0.45	0.02*	0.49	0.01*
<i>Mesoplodon layardii</i>	73	0.42	0.01*	0.30	0.12
<i>Mesoplodon mirus</i>	40	0.20	0.15	0.34	0.08
<i>Mesoplodon peruvianus</i>	8	-0.06	0.82	-0.15	0.69
<i>Mesoplodon perrini</i>	5	0.58	0.14	N/A	N/A
<i>Mesoplodon stejnegeri</i>	105	0.11	0.70	-0.33	0.35
<i>Tasmacetus shepherdi</i>	8	0.49	0.02*	0.42	0.08
<i>Ziphius cavirostris</i>	295	0.10	0.34	0.17	0.09
No. of significant models			10		2

Figure 3.5. A–C. (next page)

Examples of inputs and outputs of stranding simulation (Refer to Table 3.1 for common names). (A) residual currents, delineation of Biogeochemical Provinces (Longhurst 1995) and reported strandings of species (squares corresponding in colour to RES distributions of species in B). (B) Predicted environmental suitability distribution (PRED) based on RES model and resulting predicted relative stranding frequencies per coastal cell (ranging from *low* (light red) to *high* (dark red)) using PRED as stranding simulation starting point distribution. (C) Standard published maximum range extent (Jefferson et al, 1993) with implicitly assumed uniform environmental suitability (STAND) and resulting predicted relative stranding frequencies per coastal cell using STAND as starting point distribution. Statistical analysis of predicted versus reported stranding densities by Biogeochemical Province for all three species showed a significant correlation when PRED was used as the input distribution, but the relationships were non-significant when using STAND as input.



3.4. DISCUSSION

3.4.1. Prediction of relative environmental suitability

RES modelling represents an innovative approach for mapping large-scale distributions of marine species using a new type of environmental envelope model. The principal strength of the RES approach lies in its greater objectivity compared to the more subjective sketched delineations of maximum range extents. Underlying assumptions and input parameters are clearly defined and results are quantitative and reproducible. For most species, RES predictions match published range extent outlines closely and encompass the majority of all sighting records. Even for species with very few sighting records (e.g., True's beaked whale or Shepherd's beaked whale), the predicted distributions seem more likely, – given the primarily oceanic life history of ziphiids – than the disjointed distributions implied by the narrowly drawn range extents encompassing existing stranding records (Jefferson et al. 1993).

In addition, the approach provides information about the potential occurrence of species throughout their distribution and it is noteworthy that a large number of 'at-sea' records coincide with areas predicted to be highly suitable for the species in question. Predicted patterns of heterogeneous species occurrence also match other types of available distributional information. This includes published maps of plotted catch concentrations of species targeted by whales, such as available for the northern bottlenose whale in the North Atlantic (Benjaminsen & Christensen 1979, Reeves et al. 1993) and Baird's beaked whale in the North Pacific (Nishiwaki & Oguro 1971, Balcomb 1989).

Another strength of the model lies in its flexibility that allows investigation of different scenarios and the easy visualization of relationships of multiple environmental factors that affect marine mammal species' distribution. RES predictions for Stejneger's beaked whale and Baird's beaked whale illustrate the effect of such multi-dimensional interactions. Based on available information, the two species seem to have very similar habitat preferences (Fig. 3.3 and Table 3.3). The combined effect of broader depth and temperature ranges of Baird's beaked whale, however, resulted in substantial differences in predicted environmental suitability for both species (Fig. 3.4 A and B).

Most importantly, however, RES modelling can help to assess the role that other factors may play in determining species distributions by showing how much (or how little) of the actual occurrence of a species is captured by the model. Obviously, a species' realized niche is influenced by far more factors than the three environmental parameters I considered in the model. Although a static model itself, the RES modelling approach allows some indirect assessment of the importance of some dynamic factors, such as intra- and inter-specific competition and other social interactions. For example, similarities in habitat preferences resulted in some overlap in the RES distributions for Stejneger's beaked whale (Fig. 3.4 B) and Hubb's beaked whale *Mesoplodon carlhubbsi* (Fig. 3.5 B), with highly suitable habitat predicted for both species along the central eastern and western coasts of the North Pacific. A number of

strandings records support the occurrence of both ziphiids along the western coast of Canada and the US. There is no evidence, however, for the occurrence of Hubb's beaked whale in the Sea of Japan, which contrasts sharply with a relatively large number of strandings of Stejneger's beaked whale in this area. A possible explanation for this may be niche partitioning due inter-specific competition, which resulted in exclusion of Hubb's beaked whale by Stejneger's beaked whale from this area.

Although RES predictions provide more spatial detail about relative differences in suitable habitat throughout a species' range and model resolution appears to be quite high, care should be taken to interpret model outputs on an appropriate scale. RES modelling does not intend to produce reliable predictions about the real probability of occurrence of a species at small geographic or temporal scales. It should therefore not be directly compared to other types of habitat prediction approaches that are based on point data sets such as (e.g., Moses & Finn 1997, Hedley et al. 1999, Gregr & Trites 2001, Hamazaki 2002). Rather than describing the likelihood for real encounters, RES predictions can usefully supplement other statistical models by generating multi-dimensional hypotheses about some important spatial aspects of a species' fundamental niche.

The current lack of consideration of seasonality in the RES model introduced some biases that affect the predictions. Relying on environmental data that has been averaged over large time spans, RES predictions represent the typical distribution of a species over the course of a whole year. Therefore, in areas exhibiting large inter-annual or seasonal fluctuations in environmental conditions, the actual distribution of a species may not be captured very well by the predictions (e.g., RES predictions for True's beaked whale along the east coast of the USA, Fig. 3.4). However, with accurate data on annual or seasonal variations in environmental conditions such as water temperature, these biases could easily be counteracted within the RES model. Predictions are also affected by seasonal changes in a species' habitat preferences that might not be captured by the broad categories. Such changes may be associated with annual migrations or other seasonal movements from feeding to breeding grounds (Kasuya & Miyashita 1997, MacLeod et al. 2004) where other parameters than those determining food availability may be of importance, such as predator avoidance (Corkeron & Connor 1999, Pitman et al. 2001). Again, these biases can be easily addressed within the RES model framework if seasonality was incorporated. Other biases affecting RES predictions are discussed in detail in Chapter 2.

3.4.2. Stranding simulation

Stranding data has been used previously to deduce mortality patterns and population demographics (Eguchi 2002, Silva & Sequeira 2003). However, to the knowledge, the stranding simulation presented here represents the first published attempt using such data to gain information about the origin of stranded animals by modelling the movement of drifting whale carcasses (although there are a few websites summarizing similar efforts such as <http://people.deas.harvard.edu/~robinson/Staccato/staccato.html>). While

transport and effects of ocean currents have been investigated and modelled extensively for smaller marine organisms, such as krill and fish larvae (e.g., Edvardsen et al. 2003, Hinrichsen et al. 2003), very little is currently known about the processes that play a role in the stranding of marine mammals.

By demonstrating the usefulness of stranding data for making inferences about species distribution, I hope to encourage research efforts similar to Ames et al. (2002) that explore the drifting or sinking behaviour of marine mammal carcasses at sea. Such investigations would allow the development of more sophisticated hydrodynamic models that could provide further insights about likely 'at-sea' species distributions.

The results of the statistical analysis of the validation approach are promising as they (a) indicate that RES model outputs describe marine species' distribution better than the standard outlines of maximum range extents, but (b) also provide some support for the simple simulation model I have developed. Predicted and reported stranding densities were significantly related for almost 50 % of all species, if strandings were modelled based on the RES predictions. This suggests that a large proportion of the variation observed in global stranding patterns and the underlying processes may be described by a few basic parameters. The relatively weak observed relationships between predicted and reported stranding densities is – in part – likely due to the lack of effort information that may be addressed in the future by incorporating an adequate proxy of monitoring effort. This would allow the identification of false absences and other effort-related phenomena (such as high concentrations of reported strandings in areas covered frequently by stranding networks), and thus likely strengthen observed weak correlations.

Some biases likely affected the results of the stranding simulation model. Biases will have been introduced by the basic assumption of the stranding simulation that surface ocean currents were the principal forcing agent for stranded ziphiids to reach their stranding locations, i.e., I exclusively modelled the drifting of dead whales, treating them effectively as passive oceanographic drifter buoys (Langarian drifters). A number of studies suggest that wind and surface currents play important roles in determining stranding locations in various areas of the world (Maugret 1979, Duguay & Wisdorff 1988, Geraci & Lounsbury 1993). Drifting 'behaviour' of carcasses, however, will tend to vary with a number of environmental parameters, including water temperature and depth (Moreno et al. 1993), as well as physiological factors, such as body composition and size of the animal and whether an animal is dead when it starts drifting. There is some indication that particularly offshore species, such as ziphiids, often strand alive (Best 1982). Thus some animals may have swum to a stranding location where they then actively beached themselves. I have attempted to minimize this bias by excluding all known live strandings from the 'reported' stranding data set (Table 3.4). It is noteworthy, though, that surface currents also appear to influence the movement patterns of live animals of some marine mammal species, as satellite tracking of northern fur seals and southern elephant seals (Loughlin et al. 1999, McConnell et al. 2002) and the investigation of herd strandings of live animals in New Zealand has shown (Brabyn &

MacLean 1992). Moreover, impaired navigation due to disease or injuries has been proposed as a major cause for single stranding events (Best 1982, Brabyn & MacLean 1992) and it is perceivable that a sick animal may have been at least partially carried along by prevailing currents. Although all these reasons reduce the bias of stranding locations introduced by actively swimming animals, the ‘reported’ data set will, nevertheless, include cases in which currents played a negligible role in determining the stranding location.

Very little is known about the length of time a dead whale is likely to float on the surface, before decomposition results in the final sinking of the carcass. Drift times will differ in different temperatures and conditions and are also likely to vary considerably between species. To date, drift behaviour of carcasses in the ocean has only been studied experimentally for two smaller species of marine mammals (harbour porpoises and sea otters) as well as for humans (Giertsen & Morild 1989, Moreno 1993, Ebbesmeyer & Haglund 1994, Ames et al. 2002). To my knowledge, no such studies have been conducted for larger odontocetes, which are likely to decompose less quickly due to their size and the thickness of their blubber layer. Consequently, these species may drift for much longer than I specified in the model. Trials with different settings of carcass half-life seemed to mainly affect absolute numbers of predicted strandings and maximum drift distances rather than the relative distribution patterns, indicating that sensitivity of the model to errors associated with the parameter may be relatively low in the context of this analysis.

The assumed carcass half-life of ten weeks combined with the vastness of the open ocean and relatively slow average drift speeds produced maximum drift distances for most species of less than 1000 km. Indirectly, this determined a comparatively narrow ocean strip adjacent to land in which stranded whales in the model may have originated. This obviously limited the area for which I can claim to have validated the RES model outputs using this stranding simulation.

Several studies report seasonal differences in stranding frequencies (Lopez et al. 1999, Ross 2003) that may be related to seasonal differences of current patterns that are especially pronounced in coastal waters (Mann & Lazier 1991). In addition to seasonality, coastal substructure and underwater topography has been shown to influence the location of marine mammal strandings (Best 1982, Brabyn & MacLean 1992, Stevick et al. 2002). Moreover, it seems likely that the drifting of long-submerged carcasses of beaked whales will be greatly affected by sub-surface currents, that have proven to be a crucial factor in southern ocean drift models of krill transport (Murphy et al. 1998). Given the scale and resolution of the model, however, the importance of all these factors is considered to be relatively small, although their future incorporation may nevertheless improve the model’s predictive capacity.

I conclude that the stranding simulation provided support that RES mapping represents an improvement in comparison to sketched subjective maximum range extents, even for data-poor species such as most beaked whales. RES modelling may therefore serve as a useful tool to investigate and re-evaluate current

assumptions and knowledge about the distributions of such species. The mapping of potentially important habitat areas will help focus research efforts in the context of conservation and management issues, such as risk assessment of impacts of underwater noise on ziphiids.

3.5. CHAPTER SUMMARY

The delineation of distributional ranges of poorly known marine species is often subjective and sometimes limited to rough outlines encompassing known records. The lack of information about where species may occur poses serious problems for conservation of these species. I developed a new, more objective approach to map the geographic ranges and relative environmental suitability of marine species based on existing knowledge about their habitat preferences. Here, I tested the validity of applying this generic environmental envelope model to data-deficient species, using beaked whales (Ziphiidae, Cetacea), which represent one of the least known families of mammals. I used available published information about species-specific habitat preferences with respect to depth, sea surface temperature and ice-edge association to assign species to broad-scale habitat categories. Using a raster-based GIS model, I related the quantified preferences to locally averaged environmental conditions. Predicted distributions closely matched published information about maximum range extents for most species, encompassing the majority of all known records. In addition, raster-based predictions provided information about the relative suitability of the environment and potential core habitat for a species throughout its range. To test the validity of the approach for data-deficient species, I developed a simulation model of ziphiid strandings using global data of residual ocean currents. Relative probabilities of strandings were generated based on two different input distributions: species-specific environmental suitability predictions and uniform distributions based on published information. Simulated strandings based on habitat suitability predictions produced significant correlations with observed strandings for five times as many species (10 of 21 ziphiid species) as those generated based on uniform distributions (2/21). This provided support for the quantitative approach to map species distributions as an improvement over existing simple outlines. The visualization of potentially important habitat based on this GIS approach will help to re-evaluate assumptions and knowledge about distributions of data-deficient marine species. This in turn will help focus research efforts in the context of management issues such as the risk assessment of underwater noise pollution on ziphiids.

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4. Modelling and mapping resource overlap between marine mammals and fisheries on a global scale ⁴

4.1. INTRODUCTION

Marine mammals are generally located near or at the top of marine food webs (Pauly et al. 1998a). It has been speculated that marine ecosystems may have been permanently altered by the long-lasting effects of the severe depletion of many of these and other top predator species through anthropogenic impacts (Parsons 1992, Caddy & Rodhouse 1998, Pauly et al. 1998b, Springer et al. 2003). On the other hand, as the crisis of global fisheries worsens (Pauly et al. 2002), claims have also been made in many international fora that marine mammals are impacting world fisheries by directly competing with humans for the world's limited fish resources. These claims have led to calls for culls of these predator species as a solution to increase net fisheries yields (Anonymous 2001a, b).

Studying the ecological role of marine mammals and the extent of interactions with fisheries has therefore been a major focus in marine mammal / fisheries science (e.g., Northridge 1984, Beddington et al. 1985, Northridge 1991, Bowen 1997, NAFO 1997, DeMaster et al. 2001). However, the direct investigation of the extent of actual competition between the fisheries and marine mammals has proven to be difficult – in part because of a seldom acknowledged underlying assumption that competition only occurs if the removal of either competitor results in a direct measurable increase of food available to the other (Cooke 2002). The development of sufficiently detailed models needed to demonstrate this unequivocally, however, is greatly hampered by the complexity of trophic interactions in marine food webs and the difficulties to obtain reliable data about players and linkages in these systems (Harwood & McLaren 2002, Plagányi & Butterworth 2002). Currently existing ecosystem models (e.g., Ecopath with Ecosim, Christensen & Walters (2000), Pauly et al. (2000); MULTSPEC, Bogstad et al. (1997); or MSVPA Livingston & Jurado-Molina (2000)), though useful to generate hypotheses about possible impacts of fisheries on marine ecosystems, are generally considered inadequate to provide reliable answers, sufficient as a basis for management advice, in the context of competition between marine mammals and fisheries (IWC 2003). As a consequence, most efforts to date have focused on the simpler assessment of resource overlap, i.e. the extent to which marine mammal species and fisheries may be exploiting the same food resources.

⁴ Chapter has been submitted as manuscript. Kaschner, R. Watson, A.W. Trites, V. Christensen and D. Pauly. Modelling and mapping resource overlap between marine mammals and fisheries on a global scale. This chapter was also presented as Document SC/56/E31 at the Environmental Concerns Sub-Committee of the Scientific Committee of the International Whaling Commission (2004).

To quantify the degree of resource overlap, estimates of marine mammal food intake are required. Existing food consumption models differ in three main aspects: geographic scale, number of species included and model complexity, i.e. number of parameters taken into account. To date, the majority of studies have focused on small numbers of species in limited geographic areas (e.g., Harwood & Croxall 1988, Bax 1991, Butterworth & Thompson 1995, Punt & Butterworth 1995, Bjørge et al. 2002, Furness 2002). These small-scale models are generally relatively complex in structure, but – with a few exceptions (Shelton et al. 1997, Potelov et al. 2000, Bjørge et al. 2002) – rarely consider spatial and temporal patterns in marine mammal food intake. Moreover, in the context of potential competition between marine mammals and fisheries, such models often only represent a limited geographical snapshot of these interactions – given the large distributions of many marine mammal species. The evaluation of potential competition based on such snapshots, however, may result in a dangerously distorted perception of the overall extent of the problem.

The few models that have attempted to investigate competition and/or resource overlap at larger geographic scales and for more species tend to be overly simplistic (Tamura & Ohsumi 1999, Young 1999) and they – with the exception of Trites et al. (1997) – largely ignore important spatial aspects. The simple comparison of the total food consumed by marine mammals, estimated based on such models with amounts taken by fisheries without further considerations of ‘who-is-feeding-on-what-where’ is of limited value in terms of assessing potential impacts that either group may have on the other.

However, the data needed for the development of spatially-explicit models, i.e., information about marine mammal species occurrence and the geographic origin of fisheries catches, are currently unavailable at larger scales. Surveys investigating marine mammal species occurrence are generally restricted to small geographic areas (e.g., Gregr & Trites 2001, Baumgartner et al. 2003, Griffin & Griffin 2003) and information about large-scale distributions are often limited to sketched outlines of maximum range extents (e.g., Jefferson et al. 1993). Similarly, the spatial origin of fisheries catches can generally only be traced back to the fairly large statistical areas that they were reported in (e.g., BFA 2003). However, even though exact location point data sets are lacking, there are large amounts of non-quantitative information about marine mammal species occurrences (such as general habitat preferences) and fisheries operations that may represent an under-exploited resource in the context of modelling large-scale marine mammal-fisheries interactions.

Relying primarily on this type of information, this study provides the first assessment of spatially-explicit resource overlap between marine mammals and fisheries on a global scale. The objective was to investigate the extent to which fisheries and marine mammals exploit the same food types in the same geographic areas during the 1990s by expanding on existing simple food consumption models using spatial modelling techniques. To achieve this, I derive spatially-explicit estimates of food intake by marine mammal species groups and disaggregated fisheries catches using new rule-based approaches

within a GIS modelling framework (Watson et al. 2004 & Chapter 2). Combining spatial predictions with information about diet and catch composition then allowed the mapping of hotspots of resource overlap that may indicate potential conflict between marine mammals and fisheries. I discuss the predicted large-scale patterns with respect to potential management and research implications for the investigation of competition between marine mammal and fisheries.

4.2. METHODS

4.2.1. Marine mammal species

The model encompassed 115 species of marine mammals that live predominantly in the marine environment (Appendix 4), but did not include sirenians, sea otters and the polar bear or any of the exclusively freshwater cetacean or pinniped species. I largely followed Rice (1998) taxonomically, but recognised three separate species of right whales as supported by most recent findings (Bannister et al. 2001, Rosenbaum et al. 2000). In addition, I incorporated a recently described additional species, Perrin's beaked whale (*Mesoplodon perrini*; Dalebout et al. 2002).

4.2.2. Basic food consumption model

A relatively simple generic model, developed by Trites et al. (1997), was used to generate estimates of feeding requirements, specified by food type, of all marine mammal species:

$$Q_i = 365 * \sum_s N_{i,s} W_{i,s} R_{i,s} \dots\dots\dots 1)$$

where the annual food consumption Q of species i was assumed to be 365 times the daily food consumption. Daily food consumption is calculated based on the number of individuals N of the sex s of a species i , the mean individual body mass W of sex s belonging to species i , and a weight-specific daily ration R consumed by each individual of species i and sex s .

The main advantage of this model is that it can be applied to the numerous data-poor species of marine mammals. Unknown parameter values can be inferred through empirical relationships (e.g., those of Innes et al. (1986), or Trites & Pauly (1998)), wherein required parameters are estimated based on other, often more readily available data. Below is a brief description of the approach taken for each of the main parameters in Eq.1.

4.2.2.1. Abundance estimates and sex ratios

To obtain an estimate of the worldwide abundance of marine mammal species during the 1990s, I extracted available regional abundance estimates and information about associated uncertainties from more than 1,000 published primary (e.g., Branch & Butterworth 2001, Whitehead 2002, Bester et al.

2003, Mullin & Fulling 2003, Small et al. 2003, Stevick et al. 2003) and secondary sources (e.g., Reijnders et al. 1993, Ridgway & Harrison 1999, Perrin et al. 2002). Estimates were compiled into a database, along with information about the time period and geographical area covered by the estimate, the method used to obtain it and any other relevant information. I then assigned estimates to specific standardized areas and time periods, and ranked them based on the reliability of the surveying technique and the estimate itself. For each species, the most recent abundance estimates were assigned to the 1990s time period, even though for some species and/or regions, the only available estimates pre-date 1990. If multiple surveys were conducted during the 1990s (e.g., abundance estimates compiled for different species in Waring et al. (2002)), I either used weighted multi-year averages (if provided in the source) or selected a mid-1990s estimate. Global mean abundance estimates for each species were then derived through summing the most reliable mean regional estimates available. These are presented in Appendix 4, together with an assigned level of confidence that reflects the associated uncertainties. Mean estimates were used in subsequent analyses. However, to further convey the extent of uncertainty, I estimated the proportion of the total distributional area covered by reliable surveys within the 1990s (Appendix 4). In addition, I generated extreme minimum and maximum estimates of global abundance for each species. Minimum estimates were obtained by summing all reliable conservative regional estimates, although I recognise that this lower range estimate is unrealistic (i.e., based on the central limit theorem (Zar 1996), it is highly unlikely that all mean estimates were biased in the same direction). Maximum estimates are biased upwards in analogous fashion, as they represent the sum of the upper ranges provided for regional estimates, which were then further adjusted upwards in proportion to the area yet unsurveyed within the species distributional range.

I assumed sex ratios were balanced for most species, except for those for which available published information explicitly indicated otherwise (e.g., Wickens & York 1997) or if unequal sex ratios seemed highly likely based on information about closely related species with similar life history traits.

4.2.2.2. Mean body mass

I used the sex-specific mean body mass estimates for each species generated by Trites & Pauly (1998) who estimated female and male body weights averaged across all age classes for 106 species based on the strong relationship between more readily available maximum length information and species-specific growth rates, survival and longevity. The functional relationship between body mass and maximum length can be expressed as:

$$W_{i,s} = a_{i,s} * L_{max_{i,s}}^{b_{i,s}} \dots\dots\dots 2)$$

where W is the mean body mass of an individual of the species i and the sex s , and L_{max} is the corresponding maximum length reported for any individual belonging to this species. Variables a_{is} and b_{is} are sex-specific regression coefficients varying for different high-order taxonomic groups (established by

regressing maximum length against mean body mass in 30 marine mammal species with known growth curves and life tables. Further details and species-specific body mass estimates for individual marine mammal species are contained in Trites & Pauly 1998).

The higher number of species considered in the model is largely due to the slightly different taxonomic classification system used here which assigned species status to several groups formerly considered sub-species (Rice 1998, Bannister et al. 2001). I assumed the same mean body mass for each of these recently recognised sister species (e.g., Antarctic minke whale and dwarf minke whale).

4.2.2.3. *Feeding rates, daily rations*

I calculated daily food rations consumed by each species based on different models of weight-specific energy requirements (the ‘feeding rate’ of Sergeant 1969). These were expressed by the general relationship of $R = A * W^B$, where R is the daily food intake, W is body mass and A and B are estimated based on different data sources and physiological assumptions. I used four models that have been applied in similar studies estimating food intake of various marine mammal species groups and that have been reviewed in detail by Leaper & Lavigne (2002). Models are briefly summarized in the following (Method 1 – 4):

Method 1:

Innes et al. (1987) developed an empirical model to estimate food consumption of cetaceans that was later modified by Trites et al. (1997) to account for the difference between consumption for growth and for maintenance and then applied to all marine mammal species. Food intake of specific species per day was calculated using:

$$R_{i,s} = 0.1 * W_{i,s}^{0.8} \dots\dots\dots 3)$$

where R is the daily food intake of an individual of sex s belonging to species i and W is the mean body weight of that individual, in kilograms.

Method 2:

Armstrong & Siegfried (1991), studying food consumption of minke whales in the Antarctic, suggested a modification of the Innes et al. (1986) equation for baleen whales to account for larger body sizes and seasonal variations in food intake. This approach was later used to estimate food consumption of whales around Iceland (Sigurjónsson & Víkingsson 1997) and represents one of the methods used by Tamura (2003) to estimate global food intake of cetaceans. The modified feeding rate is described by:

$$R_{i,s} = 0.42 * W_{i,s}^{0.67} \dots\dots\dots 4)$$

Method 3:

Tamura (2003) also estimated worldwide food consumption of cetaceans using an approach proposed by Klumov (1963), where food intake per day was calculated using:

$$R_{i,s} = 0.035 * W_{i,s} \dots\dots\dots 5)$$

Method 4:

While reviewing the different approaches applied to the estimation of food consumption, Leaper & Lavigne (2002) also provided a modified version of a field metabolic rate suggested by Boyd (2002a) for pinnipeds described by:

$$R_{i,s} = 0.482 * W_{i,s}^{0.524} \dots\dots\dots 6)$$

4.2.2.4. Diet composition

I specified consumption of individual marine mammal species by food types using a standardized diet composition which expresses diets as proportions of eight broad prey type categories based on the analysis of close to 200 published qualitative and quantitative studies of species-specific feeding habits (Pauly et al. 1998a) (Table 4.1). I again assumed that species included in the model, but not covered by Pauly et al. (1998a) due to differences in the taxonomic approach, had the same diet composition as closely related sister species. I also added an additional food type, called ‘non-marine mammal food’. This food type category contained all fisheries catches (see below) of prey types unlikely to ever be taken by marine mammals, such as large sharks, and was consequently set to zero for all marine mammal species. Food type categories and criteria used to allocate taxa to different categories are briefly described in Table 4.1. Total consumption by food type was estimated by substituting $R_{i,s}$ in the basic food consumption equation with:

$$R_{i,s} = \sum_{k=1}^9 pDC_{i,k} * R_{i,s} \dots\dots\dots 7)$$

where the daily ration R of an individual of the sex s and species i represents the sum of the proportions pDC of all food types k in the diet of species i .

Table 4.1. Definition of food type categories defined by Pauly et al (1998) and taxa included in each category based on habitat preferences and body length using information available from FishBase (Froese & Pauly 2000).

Food group	Taxa included	ISSCAAP ^a
Benthic invertebrates	all crustaceans (except krill), squirts, bivalves, gastropods, but also octopus	42-45, 47, 52-56, 58, 74-77
Large zooplankton	krill	46
Small squid	mantlelength < 50 cm (e.g., Gonatidae)	part of 57
Large squid	mantlelength > 50 cm, (e.g., Onychoteuthida)	part of 57
Small pelagics	FishBase attributes: pelagic habitat & common length < 60 cm	part of 35
Meso-pelagics	FishBase attributes: bathypelagic habitat & common length < 150 cm	Not covered
Miscellaneous fishes	FishBase attributes: ((demersal, benthic, benthopelagic, bathydemersal, reef-associated habitat) & common length <150 cm) or (pelagic habitat & common length > 60 cm & < 150 cm)	21-25, 32-34, 36-39
Higher vertebrates	all higher vertebrates, such as birds, turtles and mammals	Not covered
Non-marine mammal	includes all species not taken by marine mammals; Fishbase attributes: (all habitats & common length > 150 cm) or (reef-associated & Max Length > 200 cm)	Not covered

a) From FAO's International Standard Statistical Classification of Aquatic Animals and Plants

4.2.3. Marine mammal distribution

To incorporate spatial differences in species occurrence and food consumption, I predicted global distributions of all 115 species of marine mammals using a large-scale Relative Environmental Suitability (RES) model (Chapter 2). This rule-based, environmental envelope modelling approach relied on published qualitative and quantitative information about species-specific habitat preferences with respect to three basic environmental parameters (depth, sea surface temperature, and association with ice-edges) to assign species to broad-scale niche categories. Species-specific hypotheses about maximum range extents and relative suitability of the environment within this range were then generated by relating quantified habitat preferences to locally averaged environmental conditions in a global grid system of 0.5 degree latitude by 0.5 longitude cell dimensions. Annual average distribution of all marine mammal species generated using this model can be viewed in Appendix 3 or online at www.seaaroundus.org/distribution/search.aspx. Although RES predictions more often describe a species' fundamental niche rather than its realized one (i.e., potential vs. utilized habitat), extensive validation of the model suggested that the RES predictions already capture significant amounts of the variation in

occurrence for many species (Chapter 2 & 3). For the purpose of this study, I therefore assumed that the RES value assigned to each cell is directly proportional to the probability of occurrence of a marine mammal species in that cell, i.e., a relative density calculated based on a global abundance estimate (see below).

4.2.4. Fisheries distribution

Annual fisheries landings from FAO and other sources from the 1950s onward were taxonomically disaggregated and re-assigned in the same global grid system using a rule-based approach and ancillary data about distributions of fished taxa and fishing access of reporting countries (Watson et al. 2004). Here, I used averages generated for the 1990s to make fisheries catches comparable to marine mammal food consumption estimates. Fisheries catches were re-expressed as proportions of the same food types as used to express marine mammal diets by assigning each individual target species / taxa to the appropriate categories based on life history, size and habitat preferences of the target species or taxa.

4.2.5. Spatially explicit food consumption/catches and resource overlap index

By linking species-specific estimates of annual global food consumption to corresponding predictions of species distribution, I obtained spatially-explicit estimates of annual food consumption rates for each species, expressed as food intake per km² per year for each cell in the global grid. I assumed that food consumption of a species in any area was directly proportional to the predicted environmental suitability of that area, as the current version of RES model did not account for seasonal differences in species occurrences associated with migrations. Furthermore, I ignored all spatial effects of feeding patterns.

For the assessment of resource overlap between marine mammals and fisheries, I grouped marine mammal species into four major taxonomic groups, based on similarities in life history and feeding characteristics: (1) mysticetes; (2) pinnipeds; (3) large odontocetes (all ziphiid species and the sperm whale), and (4) small odontocetes (all other marine odontocetes). Food intake specified by food types was then summed across all species belonging to the same group within each cell. The thus obtained group diet composition in each cell therefore reflected the differences in marine mammal species assemblages in different areas as well as the different abundances and dietary preferences of all species present.

The assessment of overlap between marine mammal food consumption and fisheries catches per cell was performed using a modified version of an ecological niche overlap index, derived from or related to the ‘competition coefficients’ of the Lotka-Volterra equations by Morisita (1959) and Horn (1966). This index originally only considered the qualitative overlap of resource utilization of two players exploiting the same resources (i.e., the similarity of marine mammal diet and fisheries catch composition), but ignored the absolute amounts of the resource that is being used or consumed. I therefore further modified this index by introducing a weighting factor to provide a measure of the importance of each cell for either

fisheries or marine mammals based on the overall quantity of catch or food taken by either consumer in this cell, leading to:

$$\alpha_{j,l} = \left(\frac{2 \sum_k p_{l,k} p_{j,k}}{\sum_k p_{l,k}^2 + p_{j,k}^2} \right) * (p_{Q_l} * p_{C_j}) \dots \dots \dots 8$$

where α_{jl} describes the quantitative overlap between a fishery j and a marine mammal group l in each cell, and the first term expresses the qualitative similarity in diet/catch composition between the marine mammal group l and fisheries j sharing the resource or food type k as the ratio of ‘niche proximity’ to ‘niche breadth’ (MacArthur & Levins 1967), with p_{lk} and p_{jk} representing the proportions of the nine resources in the diet or catch. This term is multiplied by the product of the proportion of global food consumption of the mammal group Q and the total fisheries’ catches C taken within this cell. The continuous resource overlap values thus generated were subsequently converted into a categorical index ranging from low to high.

4.3. RESULTS

Although I estimated that food intake of all marine mammal species combined was several times as high as global fisheries catches in the 1990s, the model predicted low overlap in resource exploitation between all marine mammal groups and fisheries if spatial and dietary aspects were taken into account.

4.3.1. Global estimates of total annual food consumption of marine mammals and fisheries’ catches

Estimated mean annual food consumption of individual marine mammal species groups during the last decade was similar in order of magnitude as global fisheries catches using all four feeding rate models, with baleen whales, though comparatively low in numbers, taking the bulk of the food due to their large size (Table 4.2).

Table 4.2. Global food consumption estimates for four major marine mammal groups (in million tonnes per year) during an average year of the 1990s generated using four different feeding rate models. Global mean fisheries catches for the same time period amounted to 81 million tonnes.

Taxonomic group	Abundance	Food consumption			
		Feeding rate method			
		1	2	3	4
Mysticetes	1,250,000	82	98	202	28
Pinnipeds	36,000,000	62	135	60	76
Large odontocetes	1,000,000	40	50	95	35
Small odontocetes	16,000,000	30	63	31	15
Total	54,250,000	214	348	388	154

Estimates for baleen whales and pinnipeds based on Method 1 were almost as high or slightly higher than globally reported fisheries catches (although it should be noted that total fisheries catches are likely underestimated, Pauly et al. 2002) (Fig. 4.1). Using this feeding rate model, estimated food intake of larger toothed whales and small odontocetes was predicted to amount to less than half of global commercial catches. In comparison to the other feeding rate models, Method 1 produced intermediate estimates of food intake for the baleen whales and large toothed whales. These two species groups combined likely consume the majority of all food taken by marine mammals. Method 1 estimates were therefore used in subsequent analysis, even though food intake of small odontocetes and pinnipeds, estimated using this method, were in the lower range of estimates (Table 4.2 & Fig. 4.1). Method 3 produced the highest estimates for groups consisting mostly of species with large mean body mass, such as the baleen and larger toothed whales (Table 4.2). In contrast, food intake of the smaller sized species groups (i.e., pinnipeds and small cetaceans) was estimated to be highest based on Method 2 (Table 4.2). The observed range of estimates produced by the different models varied between species groups. While maximum estimates for dolphins were only twice as high as minimum values, for baleen whales, minimum and maximum estimates of food intake varied by an order of magnitude (Table 4.2 & Fig. 4.1).

Note that error bars in Fig. 4.1 represent the maximum and minimum value produced for each species group by any of the 4 daily ration models, but do not reflect the uncertainties associated with any of the other model parameters (i.e., abundances, sex ratios, mean body mass and diet composition). In terms of food types targeted also by fisheries (shown in light grey in Fig. 4.1 and mainly consisting of small pelagics, benthic invertebrates and ‘miscellaneous fishes’), all species groups were predicted to consume less than half the amounts taken by fisheries when food intake was estimated based on Method 1. Using other feeding rate models, top estimates of marine mammal consumption of food types targeted also by fisheries were – at the most – approximately as high as total fisheries catches.

More than 90% of all fisheries catches fell into 3 food type categories (shown in hues of red and yellow in Fig. 4.2 that illustrates the proportional food intake and fisheries catches by the 9 food types). Main fisheries food types consisted of ‘benthic invertebrates’, ‘small pelagics’ and ‘miscellaneous fishes’ with small pelagics representing the single most important prey type. In contrast, these food types made up less than a third of the diets of any marine mammal group, whose diets were dominated by either the ‘large zooplankton’ food type (baleen whales and pinnipeds), or ‘large squids’ (large toothed whales). Diets of small odontocetes (dolphins) appeared to be most varied with ‘miscellaneous fishes’, ‘large squids’ and ‘small squids’ contributing in equal parts, closely followed in relative importance by ‘meso-pelagic fishes’.

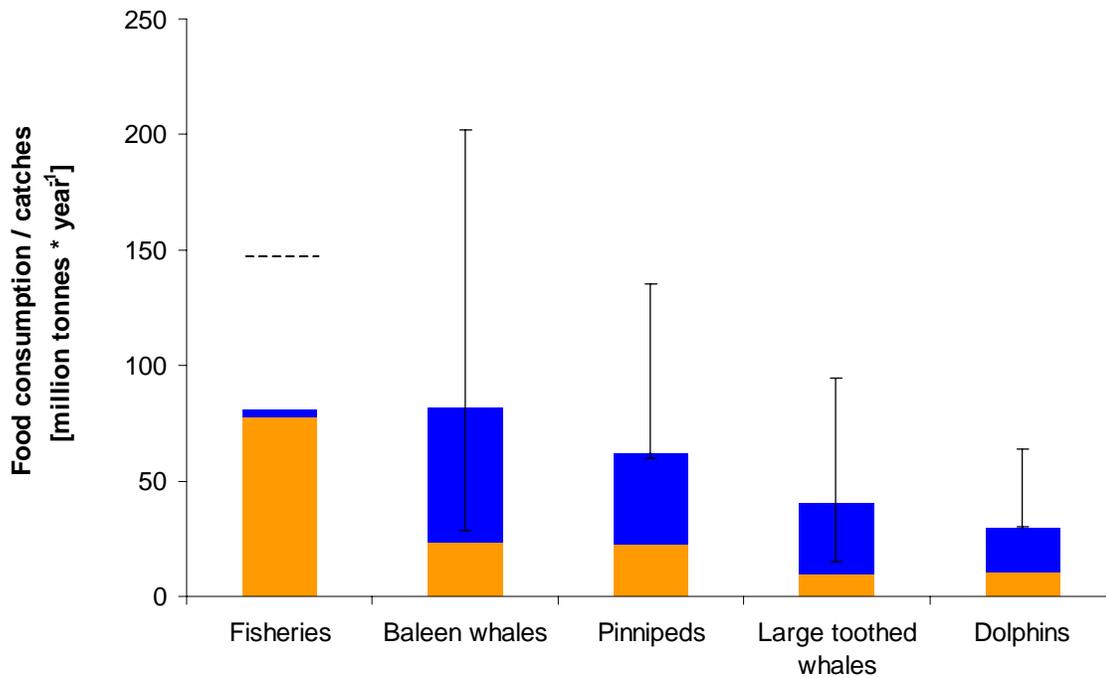


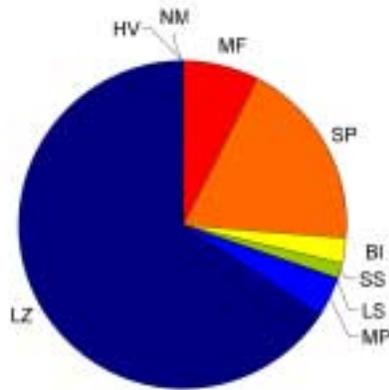
Figure 4.1.

Estimated annual global catch and food consumption of fisheries and major marine mammal groups during the 1990s (based on feeding rate Method 1). Error bars of marine mammal food consumption indicate minimum and maximum estimates based on different feeding rates (Leaper & Lavigne 2002). Total fisheries catches are probably closer to 150 million tonnes per year (dashed line) if illegal, unreported or unregulated catches are taken into account (Pauly et al. 2002). Marine mammal food intake consisting of prey types that are also targeted predominantly by fisheries is presented in grey (mainly small pelagic fishes, miscellaneous fishes and benthic invertebrates). Although mean global food consumption of all marine mammals combined is estimated to be several times higher than total fisheries catches, the majority of food types consumed by the various marine mammal groups are not targeted by fisheries.

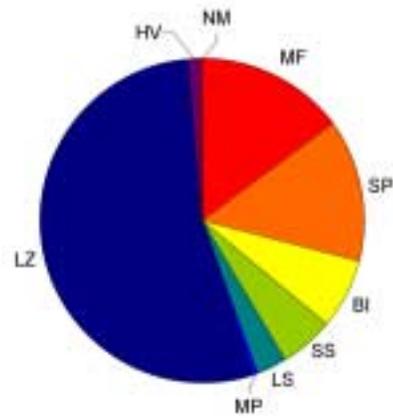
Figure 4.2. (next page)

Estimated mean annual global catch and food consumption by nine major food types during an average year in the 1990s expressed as proportions of total amounts taken. The percentage of different food types in marine mammal consumption were computed based on diet composition standardised across species (Pauly et al. 1998a). Corresponding percentages of different food types in fisheries catches were obtained by assigning individual target species/taxa to the appropriate food type category based on life history, size and habitat preferences of the target species/taxa. Food types mainly consumed by marine mammals are presented in hues of blue and green and food types that are major fisheries target groups are presented in yellows/reds. Food types primarily targeted by fisheries only represents a small proportion of the diet of any marine mammal group.

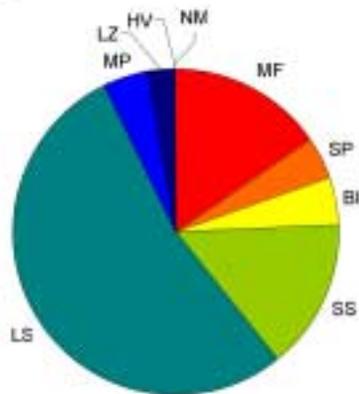
Baleen whales



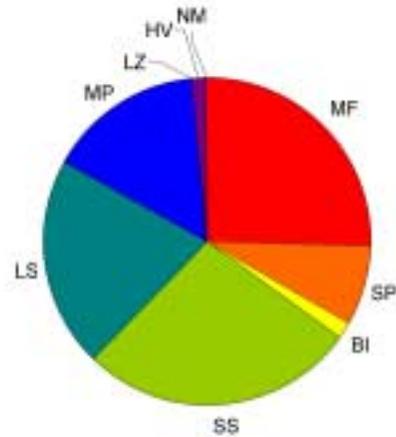
Pinnipeds



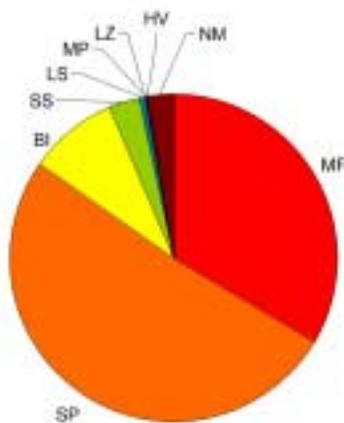
Large toothed whales



Dolphins



Fisheries



Food Types

- Non-marine mammal food (NM)
- Misc. fishes (MF)
- Small pelagic fishes (SP)
- Benthic invertebrates (BI)
- Small squids (SS)
- Large squids (LS)
- Mesopelagic fishes (MP)
- Large zooplankton (LZ)
- Higher vertebrates (HV)

4.3.2. Spatially-explicit annual food consumption of marine mammals and fisheries' catches

Spatial disaggregation of fisheries catches in the 1990s shows that the vast majority of reported catches appeared to be taken on the continental shelves of Europe, North America, Southeast Asia and the west coast of South America (Fig. 4.3). Fisheries were concentrated in relatively small areas and fishing rates can be extremely high, amounting to more than 1,000 tonnes per km² per year in many of the dark red areas shown in Fig. 4.3. Highest catches occurred in areas where continental shelves are wide, such as the Bering, East China or North Seas, or in productive upwelling systems, such as those that can be found along the west coasts of South America and South Africa. However, despite the many distant water fleets and the development of deep-sea fisheries operating far offshore, major fishing grounds generally lay in close proximity to areas with high coastal human populations in the northern hemisphere (i.e., off the coasts of major industrial fishing nations). In contrast, comparatively little catch was taken off the coasts of many densely populated developing countries, such as East Africa or the east coast of the Indian subcontinent, although catch rates were also relatively high along the coasts of Northwest Africa and the west coast of the Indian subcontinent.

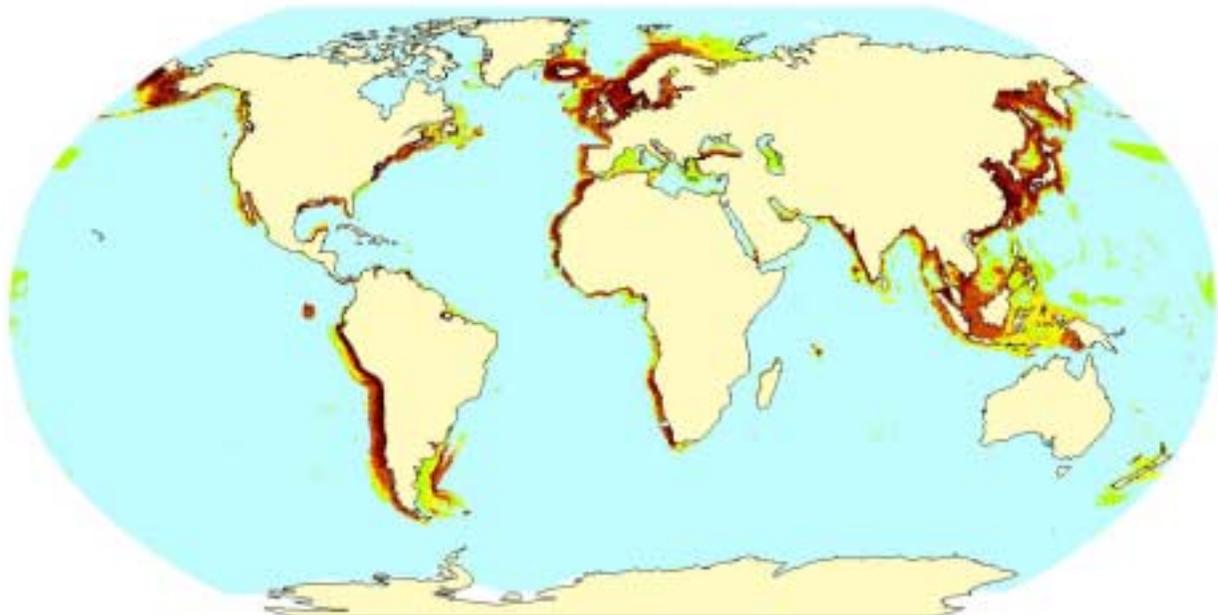


Figure 4.3.

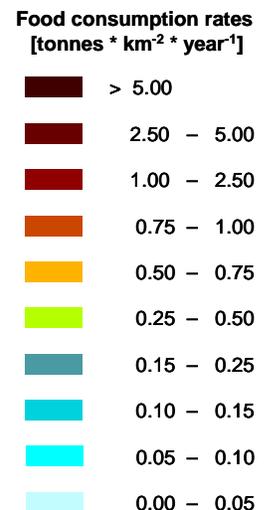
Map of predicted spatially-explicit global fisheries catch rates during an average year in the 1990s, generated through spatial disaggregation of reported annual catches (based on data from Watson et al. (2004) with catches averaged over the last decade). Non-regular colour-coded scale, described in the legend, is the same as in Fig. 4.4, except for the lowest category, which combines the three lowest marine mammal categories. Highest concentrations of fisheries catches are taken from northern hemisphere shelf areas and from the upwelling systems around western South America and Africa. Note open ended scale of legend and that top fisheries catch rates (dark red) in some areas can amount >1,000 tonnes per km² per year – more than 100 times the top marine mammal food consumption rates predicted anywhere in the world.

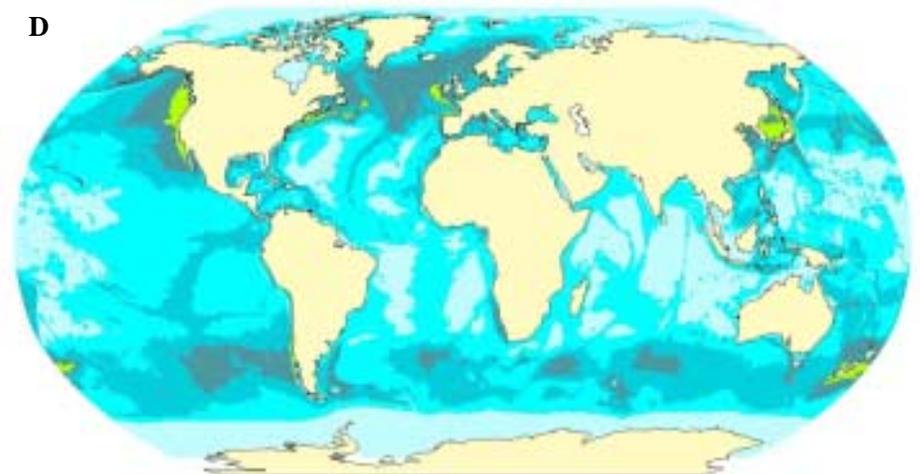
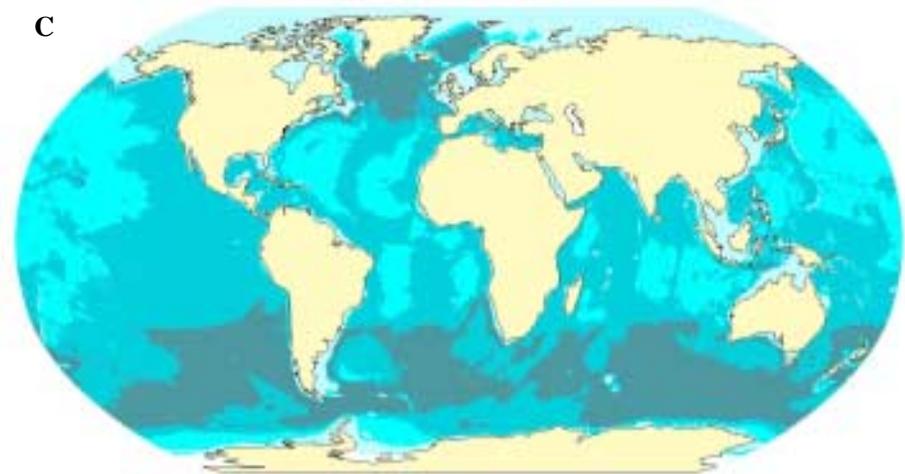
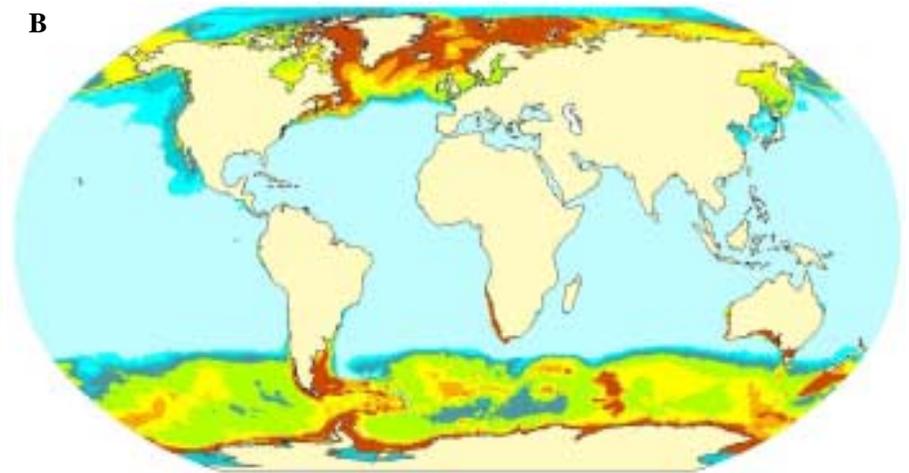
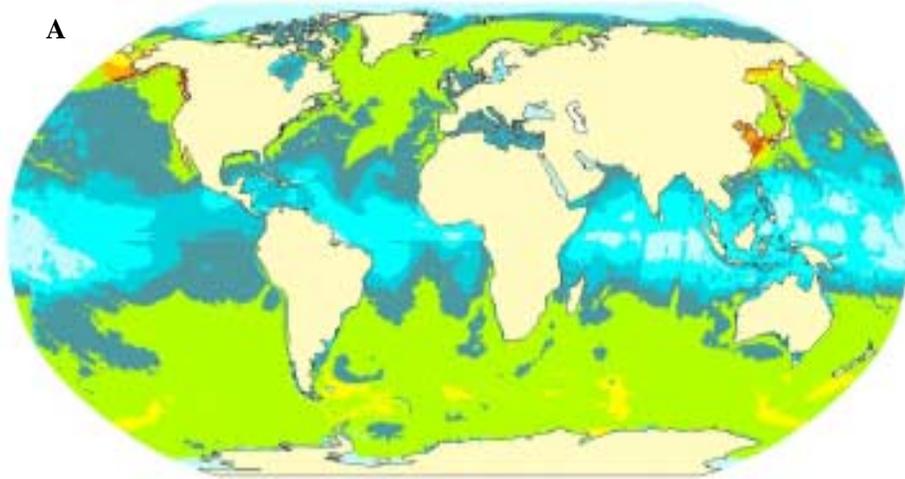
Fisheries catch rates [tonnes * km ² * year ⁻¹]	
Dark red	> 5.00
Red	2.50 – 5.00
Dark orange	1.00 – 2.50
Orange	0.75 – 1.00
Yellow	0.50 – 0.75
Light green	0.25 – 0.50
Light blue	0.001 – 0.25
Very light blue	0.000 – 0.001

I predicted most of the food that marine mammals consume to be taken further offshore and/or in polar waters (Fig. 4.4). Due to the sheer size of the distributional ranges of many of the baleen and larger toothed whale species, consumption densities (annual food intake per km²) for these groups were comparatively low in most regions and fairly homogenous across large areas (Fig. 4.4 A & C). Food consumption densities of the smaller odontocetes were even lower and appeared to be concentrated in temperate waters of both hemispheres (Fig. 4.4 D). Pinniped food intake, in contrast, tended to be more closely associated with coasts and shelf areas, with feeding taking place mostly in the polar waters of both hemispheres, but appeared to be particularly high in the North Atlantic. For this species group, the restriction to smaller areas in combination with high abundances of most species resulted in much higher, locally concentrated feeding densities (Fig. 4.4 B). However, predicted maximum food consumption densities did not exceed 10 tonnes per km² per year for any species group anywhere in the world. Note that predictions of high overlap in some areas, such as the north-western Pacific for the baleen whales, are misleading as these are based on overestimates of food consumption in these regions. These overestimates resulted from a specific feature of the modelling approach that currently does not account for the effects of population structure and varying degrees of depletion of different populations of the same species. As a consequence of using a single global abundance estimate, regional differences in stock size are ignored and areas of highly depleted populations, such as the western population of gray whales, are ‘subsidized’ by higher abundances of other stocks (e.g., the eastern population of gray whales) in other areas (see Section 4.4. for more details).

Figure 4.4. A–D. (next page)

Maps of predicted spatially-explicit global food consumption rates of marine mammal groups during an average year in the 1990s. Spatially-explicit estimates of food consumption rates for baleen whales (A), pinnipeds (B), larger toothed whales (C) and dolphins (D) are shown. Non-regular colour-coded scale, described in the legend, is the same as in Fig. 4.3, except for three added low-density categories needed to make patterns visible for all species groups. Food consumption is more homogenously distributed than fisheries catches (Compare Fig. 4.3). Areas of highest concentrations vary for different species group, but are generally more concentrated in the southern hemisphere, and located in regions further offshore or in higher latitudes seldom visited by fisheries. Note open-ended scale of legend and that maximum food consumed (dark red) by any species group does not exceed 10 tonnes per km² per year anywhere in the world’s oceans – 100 times less than top fisheries extraction rates. Also note that some areas of apparent high consumption, such as the north-western Pacific for the baleen whales, represent overestimates of food intake rates that are related to the lack of consideration of population structure and varying degrees of depletion of different populations of the same species in the current version of this model.





4.3.3. Comparison of global annual food consumption of marine mammals and fisheries' catches by latitudinal range

The amount of food consumed by each marine mammal group per 10 degrees latitude and total fisheries catches from corresponding regions were directly compared (Fig. 4.5 A–D). Fisheries catches were much higher in the northern hemisphere, with the majority of all catches stemming from areas between 20 and 60 degrees North and < 4 % taken south of 50 degrees South. In contrast, food intake of all marine mammal groups was predicted to be higher in the southern hemisphere where more than 65 % of all food of marine mammals was taken, the majority of which was consumed south of 30 to 50 degrees South. Latitudinal food consumption patterns of both the larger toothed whales and smaller odontocetes exhibited a unimodal distribution skewed towards the higher southern latitudes. Consequently, spatial overlap between these groups and fisheries in terms of absolute amounts taken by either player was predicted to be highest in equatorial areas. In contrast, the shape of latitudinal food intake distribution of baleen whale and pinniped was bimodal, showing a stronger peak in the southern hemisphere in both cases. Spatial overlap in terms of total amounts taken by fisheries and baleen whales appeared to be highest in the lower latitudinal ranges of the northern hemisphere, but also occurred in the lower latitudes of the southern hemisphere. Bimodality in food consumption patterns was most strongly pronounced in pinnipeds, resulting in the concentration of highest overlap – in terms of absolute amounts taken – in the mid to high latitudes of the northern hemisphere.

Food consumption / fisheries catches
[million tonnes * year⁻¹]

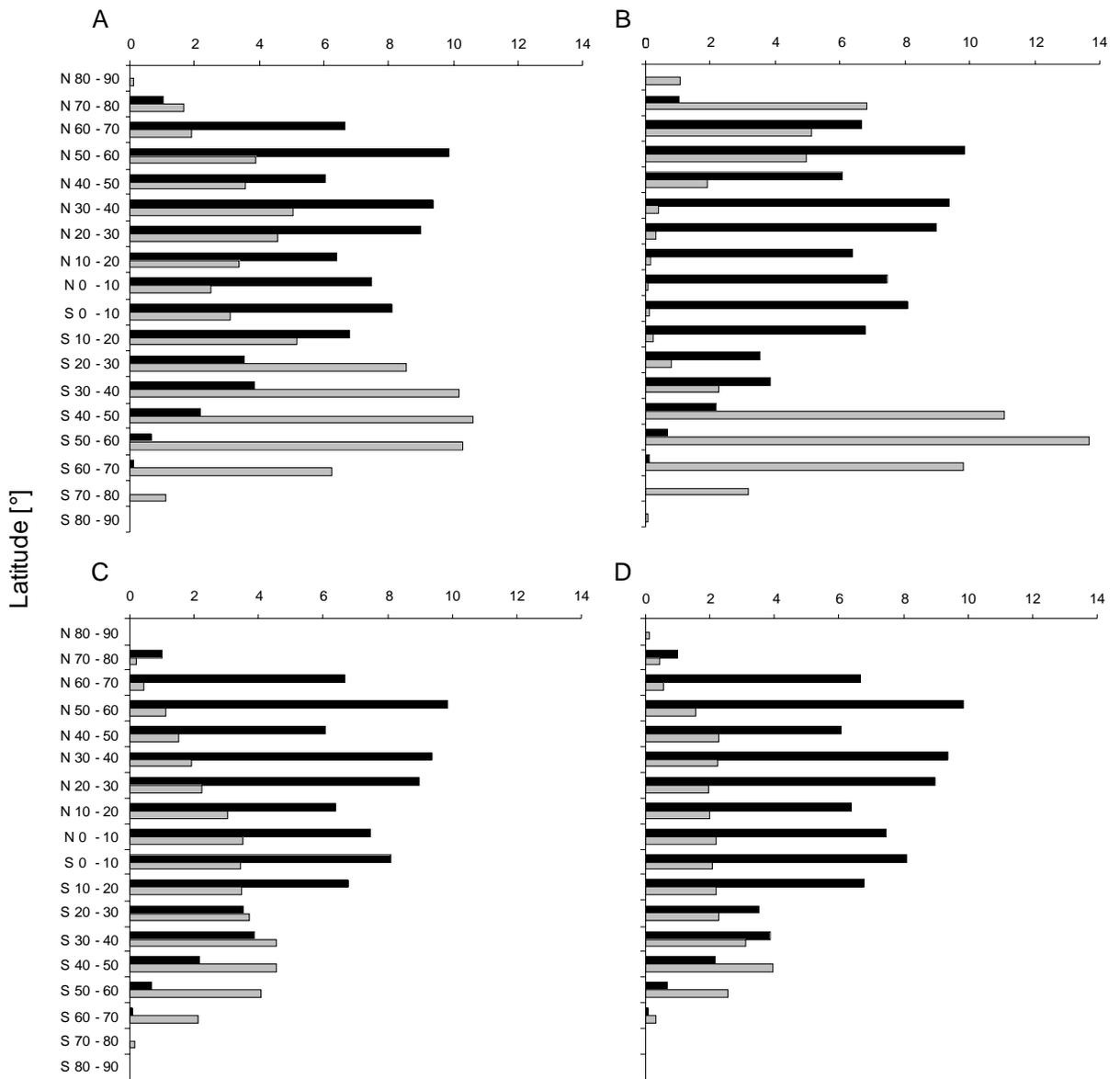


Figure 4.5. A–D.

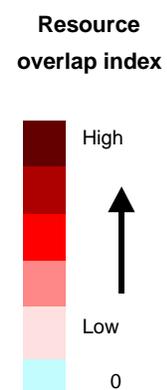
Estimated food consumption / catches of major marine mammal groups (grey bars) and fisheries (black bars) per 10 degree latitudinal range. Comparison of total food intake and catches taken in different latitudinal ranges are shown for baleen whales (A), pinnipeds (B), large toothed whales (C) and dolphins (D). Overall, more than 65 % of all food consumed by marine mammals is taken in the southern hemisphere, mostly south of 30 degrees latitude South, where < 4 % of all fisheries catches are taken.

4.3.4. Spatially-explicit resource overlap between marine mammals and fisheries

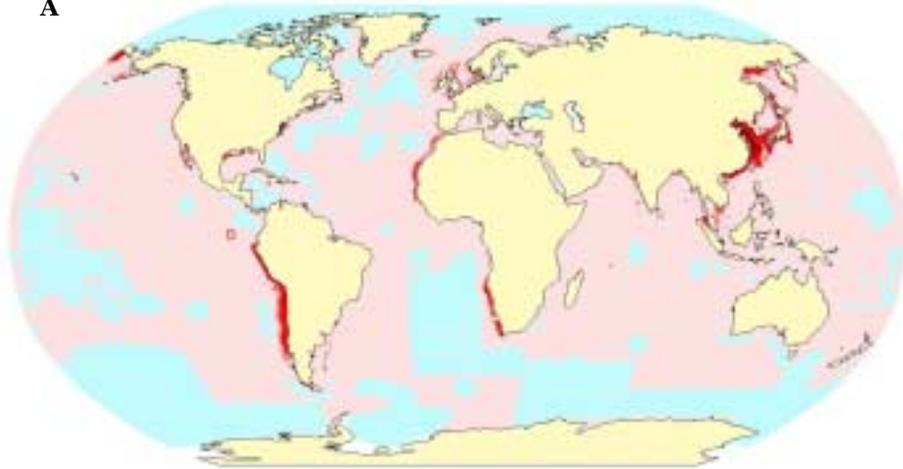
Overall, the model predicted low overlap in resource exploitation between all marine mammal groups and fisheries in the 1990s in most areas of the world (Fig. 4.6 A–D). High overlap appeared to be restricted to small geographical regions and was mostly concentrated in temperate continental shelf areas of the northern hemisphere and the highly productive upwelling systems in the southern hemisphere. I predicted highest overlap to occur between pinnipeds and fisheries, with particularly high concentrations in the North Atlantic, Bering Sea and Sea of Okhotsk (Fig. 4.6 B). In contrast, fisheries overlap with baleen whales appeared to be comparatively low in the North Atlantic, but was relatively high in the major upwelling systems of the southern hemisphere (Fig. 4.6 A). The model also predicted some hotspots in the western North Pacific. However, these are largely due to the previously discussed biases associated with food consumption estimates in these areas. Predicted overlap levels between smaller odontocetes and fisheries were mostly only intermediate, partially due to the comparatively low total food intake of these species. Though overlap with fisheries for this mammal group also appeared to be more concentrated in the northern hemisphere, hotspots were more ubiquitously distributed throughout the shelf areas of all oceans. Lowest overall overlap was predicted to occur between fisheries and the larger, deep-diving toothed whales with their mainly offshore distributions and diets primarily consisting of large squid species and meso-pelagic fish, which are not currently exploited by fisheries (Fig. 4.6 C).

Figure 4.6. A–D. (next page)

Maps of estimated spatially-explicit resource overlap between baleen whales and fisheries (A), pinnipeds and fisheries (B), large toothed whales and fisheries (C) and dolphins and fisheries (D). Maps were produced by computing a modified niche overlap index for each 0.5 degree latitude/longitude cell in the global grid. Predicted overlap between any marine mammal group and fisheries is quite low from a global perspective with only a few potential and isolated ‘hotspots’ concentrated in shelf areas. Comparison with mapped fisheries catch rates suggests that areas of potential high conflict are largely driven by high concentrations of fisheries catches taken from relatively small areas. Note that predictions of high overlap in some areas, such as the north-western Pacific for the baleen whales, are misleading as these are based on overestimates of food consumption (see text for more details).



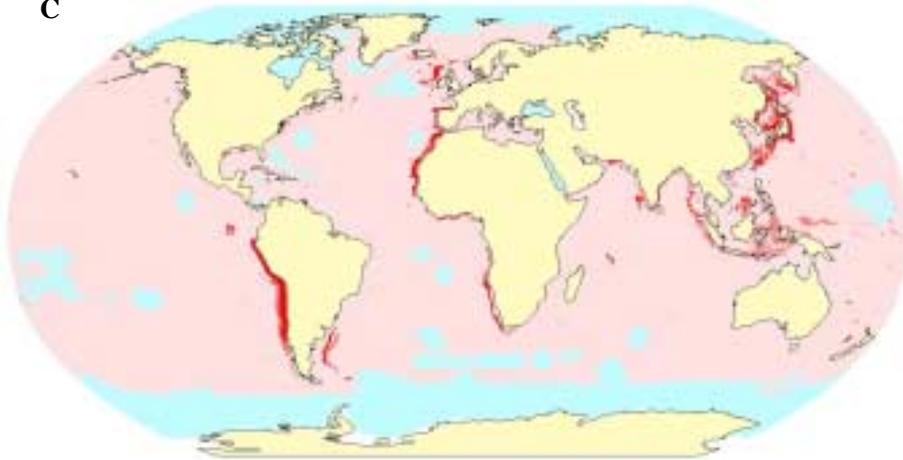
A



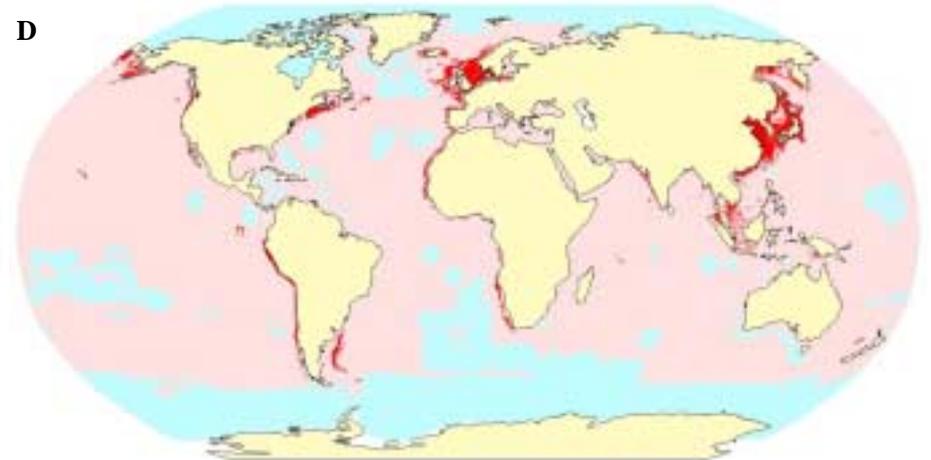
B



C



D



I calculated the proportion of food consumption that stems from areas of predicted high overlap. In the 1990s, < 1 % of all food taken by any marine mammal group was, on average, consumed in areas of predicted high spatial and/or dietary overlap with fisheries catches (Fig. 4.7 A–D). Similarly the majority of all fisheries catches (i.e., > 85 %) stemmed from areas of low overlap.

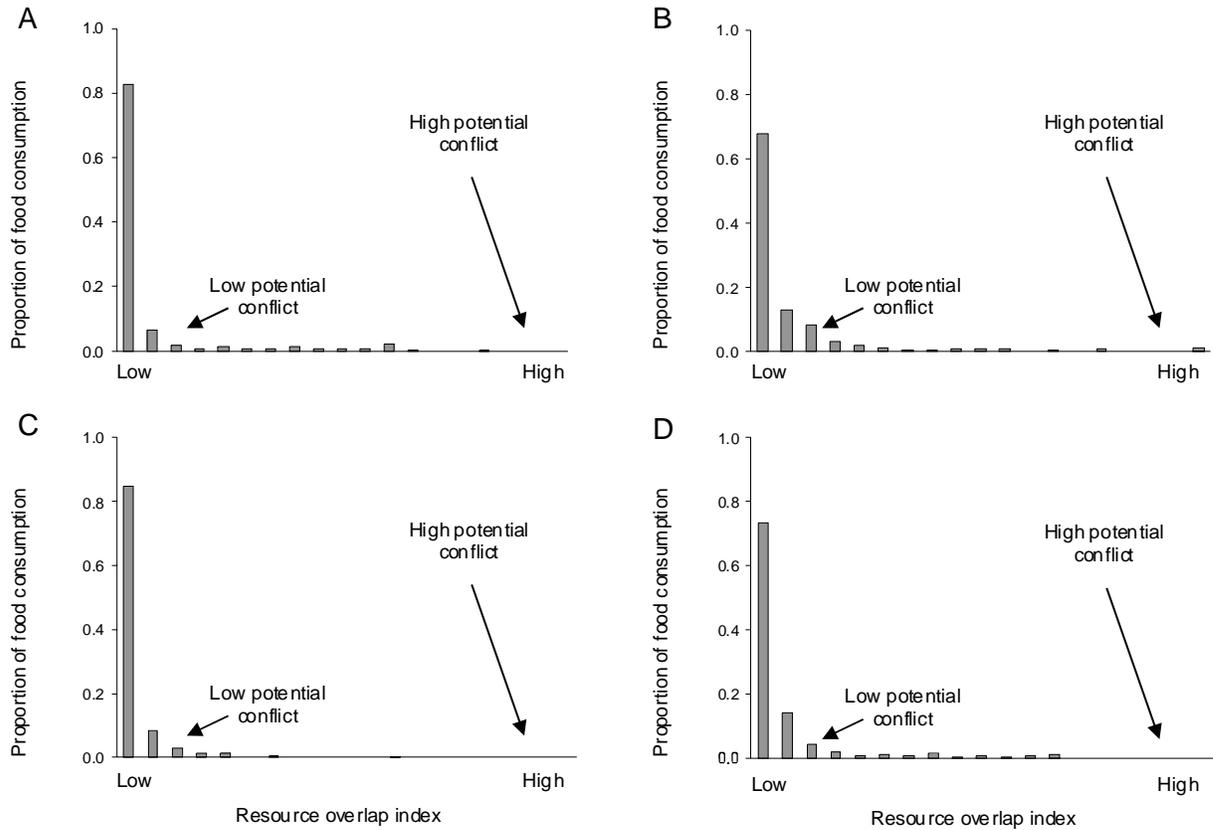


Figure 4.7. A–D.

Proportion of mean annual global catch / food consumption taken by baleen whales (A), pinnipeds (B), large toothed whales (C), and dolphins (D) in the 1990s in areas of predicted high or low resource overlap, respectively. Note that in all cases > 99 % of all marine mammal food consumption stems from areas of very low overlap.

4.4. DISCUSSION

4.4.1. Spatially-explicit food consumption and resource overlap

Few studies have attempted to incorporate spatial aspects into marine mammal food consumption and fisheries interaction models and most of these have focussed on smaller geographic scales (Shelton et al. 1997, Bjørge et al. 2002, García-Tiscar et al. 2003). The study represents the first quantitative, spatially-explicit investigation of marine mammal food consumption patterns on a global scale. Extensive validation of the RES distribution model, underlying the spatially-explicit food consumption estimates, indicated that this environmental envelope model may already capture actual patterns of species occurrence surprisingly well across a wide range of species and different spatial and temporal scales (Chapter 2 & Chapter 3), providing support for the approach taken here. The worldwide consumption by major marine mammal groups I estimated is similar to previously published global estimates (Trites et al. 1997, Young 2000, Tamura 2003). However, the mapped hypotheses about heterogeneous food consumption densities allow spatial patterns and regional differences in food consumption to be assessed at much higher resolutions than previously possible.

Investigation of marine mammal food consumption is, in many cases, closely linked to the issue of potential competition between marine mammal and fisheries (Hammill & Stenson 2000, Furness 2002, Tamura 2003). This type of marine mammal-fisheries interaction has been an issue of much debate in recent years and there is a general perception that competition may be a global problem – or may at least become one in the near future (DeMaster et al. 2001, Plagányi & Butterworth 2002). Related suggestions that the current crisis of world fisheries may be solved by reducing marine mammal populations have been fuelled by the numerous studies investigating trophic competitive interactions on smaller geographic scales (Harwood & Croxall 1988, Bax 1991, Butterworth & Thompson 1995, Punt & Butterworth 1995, Bjørge et al. 2002, Furness 2002). Despite the fact that there is some indication that humans, on a single species level, are the much greater marine predators across most scales (Fowler & Perez 1999), on smaller scales aggregated food intake of commercially targeted prey species by marine mammal species groups is often estimated to be several times higher than fisheries catches (Sigurjónsson & Víkingsson 1997, Schweder et al. 2000, Boyd 2002b). Implicitly extrapolating these findings to larger areas, some of these studies leave the impression that the amounts consumed by marine mammals make large-scale competition with fisheries likely and suggest that this should indeed be made one of the major concerns of fisheries management (reviewed in Kaschner & Pauly 2004).

The generated maps of resource overlap presented here add new perspectives to the issue of potential competition. The predictions indicate that the current perception of the extent of this problem may be severely biased because of a skewed distribution of research efforts that focused primarily on small areas where both fisheries and marine mammals coincide in high densities or ignored important spatial aspects

on larger scales. The findings suggest that – from a global perspective – only a negligible amount of food taken by marine mammals likely stems from areas where human fisheries operate. Likewise, only a relatively small proportion of fisheries catches are taken in areas of predicted high resource overlap.

Given the complexity of trophic interactions and food web dynamics (e.g. Trites 2002), I need to emphasize that high overlap in resource exploitation between marine mammals and fisheries by itself is not a direct indication for the extent of real competition that may occur between the two players. Recent reviews of existing models developed to study competitive interactions (e.g., UNEP 1999, Harwood & McLaren 2002, IWC 2003) stress the necessity of using sophisticated models that incorporate temporal dynamic changes in biomass on all trophic levels and consider the effects of different functional responses of predator prey interactions (Cooke 2002, Mackinson et al. 2003) and beneficial predation (Parsons 1992, Punt & Butterworth 1995, Yodzis 2000, 2001). However, extensive data requirements and the difficulties involved to adequately describe uncertainties will likely preclude the development of such models to investigate the problem of competition between marine mammals and fisheries on a global scale in the foreseeable future (e.g., UNEP 1999, Harwood & McLaren 2002, IWC 2003). In the meantime, the assessment of spatially-explicit resource overlap on larger geographic scales, using simpler models and more readily available types of data, as demonstrated here, can provide some useful insights about the likely extent of the problem.

Based on the small size of predicted ‘hotspots’ of potential conflict, in combination with highly concentrated fishing operations and the mobility of many marine mammal species, I suggest that it is unlikely for direct competition to pose a severe threat to marine mammal species with large foraging ranges. In contrast, the findings support a previously proposed hypothesis that the most common type of harmful competitive interaction will be one in which fisheries adversely impact marine mammal species with restricted distributional ranges (DeMaster et al. 2001), indicating that local depletions of food resources through intensive fisheries may pose serious threats to species such as the vaquita in the Gulf of California, or South Africa’s Heaviside’s dolphins and also to localised populations of other species.

Quantitative validation of the resource overlap analysis will be difficult to achieve. However, even though resource overlap does not automatically imply competition and *vice versa*, it is reassuring that the ‘hotspots’ of potential conflict highlighted by the approach coincide with many areas that have been the focal points of much previous debate about marine mammal-fisheries interactions, particularly in the case of pinnipeds. This indicates that the model captures at least some important aspects of the processes that drive these interactions. Prominent hotspots in Fig. 4.5 include the Bering Sea where the potential negative impacts of the US groundfish fisheries on the endangered western population of Steller sea lions have been a great concern (Fritz et al. 1995, Loughlin & York 2000) and the east coast of North America where the largest annual marine mammal cull worldwide is – in part – being justified based on the perception that the growing harp seal population impedes the recovery of the northwest Atlantic cod

stocks (see review in Yodzis 2001). In addition, the model identified areas of potential conflict in the Benguela system off southwest Africa with the potential impacts of the increasing population of South African fur seals on the hake stocks has been a issue of much debate (Wickens et al. 1992, Punt & Butterworth 1995) or in the waters surrounding Japan where the perception of marine mammals as competitors appears to be particularly prevalent (Anonymous 2001b, a). Looking at my maps, the skewed perception of this issue by nations in close vicinity to these hotspots of interaction becomes an understandable, if somewhat myopic viewpoint when extrapolated to the global scale.

4.4.2. Biases and limitations

4.4.2.1. Basic food consumption model

All input parameters of the basic food consumption model are affected by a number of conceptual and/or methodological biases.

Abundances

Estimating abundance of any marine mammal species, but particularly for cetaceans, is challenging due to the vast distributional ranges of most species and the fact that animals spend the majority of their time underwater. Reliable and comprehensive abundance estimates are still lacking for most species as estimation techniques that account for submerged animals missed during surveys have only been developed fairly recently (Buckland et al. 1993). Moreover, dedicated surveys are labour- and cost-intensive, generally conducted at irregular intervals and covering only a small proportion of a species' total range. Lack of standardisation of surveying techniques and coverages, and seasonal and inter-annual variation in species occurrence patterns, hampers direct comparison and summation of available regional areas. For all of these reasons, the global estimates used here should be regarded with caution. Nevertheless, I arrived at abundance estimates that are largely comparable to those previously used in similar studies assessing food consumption of major marine mammal groups on very large scales (Trites et al. 1997, Young 2000, Tamura 2003), with the notable exception of the global estimate for sperm whale population, which was a substantially downward adjusted estimate based on Whitehead (2002). Given the large body weight of this species, this much lower abundance estimate by itself accounts for most of the observed differences between these results and previously estimated large-scale marine mammal food consumption (Trites et al. 1997, Young 2000, Tamura 2003).

Feeding rates

As apparent from the range of results presented in Table 4.2 and Fig. 4.1, the selection of feeding rates used in any food consumption model strongly affects estimates of total consumption. Feeding rates have been estimated based on a variety of different methods ranging from direct measurements of food intake or maximum stomach contents (Innes et al. 1987) to bioenergetic models (Lockyer 1981b, a, Winship et al.

2002). All models are based on certain assumptions about physiological parameters and the feeding requirements of a specific individual (e.g., Klumov 1963, Innes et al. 1986) or standard metabolic rates of species (Sigurjónsson & Víkingsson 1997). Models are thus associated with high uncertainties, particularly for baleen whales owing, e.g., to the difficulties associated with studying metabolic rates of large animals and the non-linear relationship between body mass and consumption (Leaper & Lavigne 2002).

For the large filter-feeding baleen whales, there is little support for the exponent B in the general feeding rate equation being close to 1 (Leaper & Lavigne 2002, IWC 2003) as assumed by Method 3. This method generated the highest estimate of global food consumption for this species group and the large toothed whales. Similarly, the second highest estimate for baleen whales, based on the Method 2 feeding rate proposed by Armstrong & Siegfried (1991), is probably upwards biased for whales. This was indicated by a comparison of food consumption estimates expressed in percent body weight with findings of Tamura et al. (1997), which were based on an investigation of minke whale krill consumption in the Antarctic. Method 2 generated the highest estimates for pinnipeds, however, this method may be unsuitable for this species group since the underlying feeding rate was primarily derived for baleen whales. In contrast, Method 4, based on pinniped data (Boyd 2002a, Leaper & Lavigne 2002) is likely more appropriate for smaller animals, but probably underestimated food consumption of the larger species. Method 1 produced intermediate estimates for both baleen whales and pinnipeds, which represent the two species groups likely taking the bulk of total food consumed by all marine mammals. I consequently considered Method 1 to be the best choice for a generic model even though estimates of food intake for large and small odontocetes are closer to the lower end of the range for both species groups.

In terms of estimating annual food consumption, the model is also biased because of seasonal differences in food intake not considered here. The annual life cycle of many marine mammal species includes extensive fasting periods, often coinciding with reproductive activities (Brown & Lockyer 1984) and/or moulting in pinnipeds (Laws 1984). The time spent by baleen whales in Antarctic feeding grounds, for instance, has been estimated to be only 120 days (Lockyer 1981b), although there is currently some debate about how much individual species may consume during the migration between feeding and breeding grounds or at the breeding grounds themselves (Best et al. 1995, Best & Schell 1996). Some of the methods used to estimate daily rations implicitly account for the seasonal differences in food intake through the adjustment of the feeding rate exponent, but mostly the effects of such feeding patterns are mostly ignored in these simple models. As a consequence, I therefore likely overestimated total marine mammal consumption. Unfortunately, evaluating the impact of the lack of seasonal feeding patterns on total estimates is difficult as direct comparisons with other studies that have considered such seasonal

variation (Kenney et al. 1997, Shelton et al. 1997, Sigurjónsson & Vikingsson 1997, Boyd 2002b) is hampered by the differences in modelling approaches and parameterization.

Diet composition

Like all other parameters in the basic food consumption model, the determination of marine mammal diet composition is affected by various uncertainties. Problems arise due to the difficulties associated with obtaining diet information from sufficient sample sizes in the wild (Barros & Clarke 2002). Diet composition estimates based on stomach content or scat analyses tend to be biased with respect to cephalopods, as their hard parts are less readily digested than those of other prey groups and accumulate in the stomach (Zeppelin et al. 2004). Such biases may, however, be addressed by applying correction factors that compensate for differential effects of digestion on different prey types (Tollit et al. 1997, Tollit et al. 2003). More serious biases are introduced by the predominance of stranded animals in the overall sample. Such animals may not be representative of the rest of the population, as they are often sick and/or their stomach contents over-represent the coastal components of their diet (Barros & Clarke 2002). Overall, stomach and scat samples only represent brief snapshots of what often is a highly variable, geographically and inter- and intra-annually changing diet spectrum of a given species (Haug et al. 1995, Nilssen 1995, Tamura 2001). More recently developed molecular methods, including stable isotope (Best & Schell 1996, Hooker et al. 2001, Das et al. 2003) and fatty acid (Iverson 1993, Hooker et al. 2001, Lea et al. 2002, Grahl-Nielsen et al. 2003) analyses allow the investigation of diets over longer time periods, but results are often difficult to interpret and come with their own set of uncertainties (Smith et al. 1997).

The standardized diet composition used here may be fairly robust to these sources of biases, as the food type categories were very broad. Consequently, most prey switching – common among many of the marine mammal species that are opportunistic predators (e.g., Ohizumi et al. 2000; Stenson et al. 1997) – is unlikely to involve radical changes in prey categories (i.e., most targeted prey types would likely still fall into the same food type category; Haug et al. 2001, Lindstrøm & Haug 2001, Tamura 2001). With respect to my predictions, however, the use of a standardized diet composition means that the similarity in food types exploited by fisheries and marine mammals shown in Fig. 4.2 is likely to be even lower than suggested here, especially if other aspects, such as differences in prey size targeted by fisheries and marine mammals (Zeppelin et al. 2004), are also taken into consideration.

4.4.2.2. Spatially-explicit food consumption model

There are a number of discrepancies between the RES predictions for species distributions that underlie the food consumption maps in Fig. 4.4 and the currently documented occurrence of a species. This is not surprisingly given the broad approach I took.

By their nature, RES predictions are often closer to likely historical distributions of species than their currently utilized range extent (Chapter 2). In combination with a current feature of the modelling approach, which relies on global abundance estimates to generate local densities and which therefore does not account for the effects of population structure and varying degrees of depletion of different populations of the same species, food consumption rates are overestimated in some areas. In the North Pacific, for example, the eastern subpopulation of 18,000-20,000 grey whales that feed and breed along the Pacific coast of North America (Angliss & Lodge 2002, Perryman et al. 2002, Wade 2002) effectively ‘subsidizes’ the highly depleted western subpopulation. This latter subpopulation historically occurred all along the coasts of Russia, Japan and probably as far down as the East China Sea, but is now on the brink of extinction – reduced to barely a hundred animals concentrated in the Sea of Okhotsk (Weller et al. 2002a, Weller et al. 2002b). As a result, the predicted high food consumption by baleen whales in the coastal north-western Pacific is largely driven by the high abundance of the eastern gray whale population. Since the RES model predicted this area to be as suitable for grey whales as the north-eastern Pacific, a large proportion of the total (i.e., combined eastern and western stock) grey whale abundance and biomass was falsely allocated to this area.

Similarly, the predictions likely overestimate food intake in the lower latitudes by not considering seasonal differences in species occurrence and associated feeding patterns. Many marine mammal species undertake extensive annual or semi-annual migrations that cover large distances between areas used primarily for foraging and reproductive purposes (Stern 2002, Stevick et al. 2002). In its current version, the RES model predictions describe average annual distributions of species, which in many cases represent a sub-optimal compromise between sometimes substantially different feeding and breeding distributions. By simply linking global abundance estimates to these predictions, I ignored large differences in food intake in feeding versus breeding grounds. Food consumption is likely much more concentrated in polar areas than I predicted, given that the majority of the food taken by marine mammals is being consumed by baleen whales and pinnipeds. Many of the species belonging to these groups feed to a large extent in the productive areas around the edge of the sea ice in the polar summer (Laws 1984, Ribic et al. 1991, Murase et al. 2002), but migrate to subantarctic (pinnipeds) or even tropical breeding grounds (baleen whales).

4.4.2.3. Spatially-explicit resource overlap and sensitivity analysis

A multitude of different conceptual approaches have been developed to investigate different aspects of ecological niche overlap between species and communities (Hanski 1978, Hurlbert 1978, Chase & Leibold 2003). The index developed by Horn (1966) and Morisita (1959) that formed the basis for the resource overlap index (Eq. 8) has been deemed as inappropriate to measure ecological niche overlap by some (e.g., Hurlbert 1978). Hurlbert (1978)’s main criticism concerns an implicit assumption of this approach that the overlap index is partially determined by the niche width outside the overlap zone (i.e.

the extent of utilization of non-shared resources by either player and that the overall availability of the resource used is not taken into account). However, in the context of investigating marine mammal-fisheries interactions, I regarded the extent to which either relied on resources **not** consumed/targeted by the others as an important factor. The abundance or availability of resources would be an important consideration that will partially determine the extent of actual competition between two players (i.e., if the resource is limited and available amounts cannot sustain existing demands of all present consumers). Given the index used here, the model would, for instance, predict low overlap in areas where both marine mammals and fisheries take relatively small amounts, however, if the abundance of the targeted food type is very low, competition may still conceivably be high in areas of predicted low resource overlap. Efforts are underway to develop models to generate large-scale biomass estimates of fish (Christensen et al. 2003) that could be incorporated into the analysis in the future. However, for the most part, global estimates for most prey types are currently unavailable, making the consideration of prey abundance in overlap equations difficult.

The analysis of resource overlap was affected by the biases of all input parameters as discussed above. However, the nature of the model and the type of data used make it difficult to attach a quantitative estimate of uncertainty to the generated predictions. Nevertheless, conducting a basic sensitivity analysis by running the model with global marine mammal food consumption estimates varying by an order of magnitude had little to no effect on the spatial extent of areas of predicted high resource overlap. This indicates that areas of high overlap are largely driven by the extremely high catch rates of the much more concentrated fisheries.

4.4.3. Future work & management implications

Global predictions of marine mammal food consumption will be improved by incorporating seasonality into future versions of the RES model and by considering species-specific stock structure and/or estimation of global abundances using approaches similar to that developed by Whitehead (2002). Cross-validation of predicted food consumption rates with available regional estimates of food intake of subsets of marine mammal species in different parts of the world may also provide some quantitative support for the validity of the approach taken here. Substituting the currently used definition of resource overlap with alternative conceptual models of ecological niche overlap may allow this issue to be examined from different angles in the future. In general, investigating spatially-explicit resource overlap between marine mammals and fisheries on higher taxonomic levels will be a helpful and cost-effective starting point for exploring potential impacts of fisheries on specific species or species groups and *vice versa* – particularly for the many data-poor marine mammals that occur in less studied regions of the world. The identification of potential hotspots of marine mammal-fisheries interactions, as highlighted by the model, can

furthermore help to determine research priorities and select appropriate scales for the development of management approaches that deal with these.

4.5. CONCLUSIONS

I estimated global food consumption of the four major groups of marine mammals and found them to be similar in magnitude as reported catches of world fisheries. However, the majority of food consumed by any species group was estimated to consist of food types not regularly targeted by fisheries. Moreover, the new spatially-explicit approach taken here shows that marine mammals likely feed to a large extent in areas that are little exploited by fisheries. Consequently, I predicted direct overlap in food resource exploitation between marine mammals and fisheries to be very low throughout most of the world. Predicted hotspots that indicate potential for conflict are restricted to small geographic regions where the issue of competition between marine mammals and fisheries warrants further investigation. It is noteworthy that these hotspots appear to be largely driven by extreme concentrations of fishing operations in relatively small areas. Overall, the demonstrated limited overlap between marine mammals and fisheries, in terms of both dietary preferences and spatial co-occurrence, indicates that food competition between marine mammals and fisheries is likely low from a global perspective, even considering all associated uncertainties and the complexity of trophic interactions. Consequently, there is little basis to blame marine mammals for the crisis world fisheries are facing today and no support for the notion that global fisheries catches could be measurably increased by reducing marine mammal populations (Kaschner & Pauly 2004). Conversely, even though the model does not allow an assessment of actual competition between marine mammals and fisheries, the results from this study provide some support for the previously proposed scenario that the most common type of competitive interactions between the two players will be one where fisheries have an adverse impact on marine mammals, especially on those with small restricted distributional ranges.

The analysis, in conjunction with others that have focused on fisheries-related issues at the same global scale (Watson & Pauly 2001, Pauly et al. 2002, Myers & Worm 2003, Pauly et al. 2003, Worm et al. 2003, Watson et al. 2004), demonstrates the value of using relatively simple rule-based modelling approaches relying on alternative data types to investigate large-scale ecological patterns and global anthropogenic impacts on marine ecosystems.

4.6. CHAPTER SUMMARY

The impact of fisheries on marine mammals and other megafaunal components of marine ecosystems is a major concern. Fisheries – in addition to causing bycatch mortalities – may affect marine mammals through direct or indirect competition for food. I assessed the potential direct impact of fisheries on mammal populations on a global scale by quantifying the spatial overlap in resource exploitation between

both groups using modelling and mapping tools. Within a GIS framework, I developed a generic model to predict the relative probability of occurrence of 115 marine mammal species by relating information about species-specific habitat preferences to average environmental conditions in a global grid with 0.5 degree latitude by 0.5 degree longitude cell dimensions. For each species annual food consumption estimates (specified by food types) were generated from syntheses of population abundances, sex-specific mean weights, standardized diet compositions, and weight-specific feeding rates, compiled through screening of more than 1,000 publications. By linking species-specific probabilities of occurrences with estimated consumption, I obtained spatially-explicit food consumption estimates (expressed as food intake per km² per year). Superimposing geographically disaggregated fisheries catches (generated by a similar model) allowed the calculation of overlap between catches and consumption with respect to both food types consumed/taken and the areas where food or catches were taken. The model indicates that, in the 1990s, average consumption of all marine mammal species combined was several times higher than total fisheries catches during the same time period. However, effective spatial overlap and exploitation of the same food types was relatively low, indicating that actual competition between fisheries and marine mammals may be much lower than previously proposed. I predict the highest overlap in the temperate to subpolar shelf regions of both hemispheres, though overlap is more pronounced in the North. Overall, < 15 % of all fisheries catches and < 1% of all estimated marine mammal food consumption stem from areas of high predicted overlap. Nevertheless, overlap between marine mammals and fisheries may be an issue on smaller scales (especially for species with small feeding distributions) that requires more detailed local investigations. The mapping of geographical 'hotspots' of marine mammal-fisheries interactions will help to identify potential areas of highest conflict, which may aid in focusing small-scale research efforts and the development of management approaches on appropriate scales.

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5. Conclusions

5.1. CONCLUDING SUMMARY

In this thesis I investigated the degree of overlap in food resource exploitation between marine mammals and fisheries on a global scale using new spatial modelling and mapping techniques. The exploitation of the same food resources in the same areas by marine mammals and fisheries does not necessarily imply competition. Nevertheless, the assessment of resource overlap can provide some insight into the extent of potential competitive interactions, which themselves are more difficult to study due to the complexity of food web dynamics in marine ecosystems and the lack of available data. I chose to study resource overlap on a global scale because of the large, often close to cosmopolitan distributions of many marine mammal species. Investigations that focus on geographic scales representing only a part of a species total range may therefore result in a distorted view of marine mammal-fisheries interactions.

The extent to which marine mammal foraging geographically overlaps with fishing operations plays an important role in determining resource overlap and to some extent food competition. Consequently, information about marine mammal species occurrence and the spatial origin of fisheries catches are crucial pre-requisites when studying this issue. Since such information was unavailable at a global scale, I developed a new, more objective approach to map global geographic ranges and relative environmental suitability (RES) of 115 marine mammal species using not only quantitative data, but also alternative, non-quantitative and more readily available information about species' habitat preferences such as expert knowledge (Chapter 2).

RES maps closely matched published distributions for most species and raster-based predictions provided additional information about the heterogeneous patterns of suitable habitat. I was able to successfully validate RES predictions for a number of species across a wide taxonomic and geographic range (Chapter 2). I therefore propose that this simple model may already be able to capture a substantial amount of the observed heterogeneity in marine mammal species occurrences. Based on results from the stranding simulation used to validate RES predictions for data-deficient species such as beaked whales, I furthermore conclude that the model represents an improvement over simple outlines of maximum ranges, even for poorly known species (Chapter 3).

The extensive validation indicated that the RES predictions capture patterns of species occurrence sufficiently enough to be used as the basis for large-scale investigations of marine mammal-fisheries interactions. I therefore used the model to assess the importance of spatial considerations for the investigation of overlap between marine mammals and fisheries in terms of food resource exploitation.

Based on species-specific RES predictions of suitable habitat and additional corresponding information about abundances, body mass, feeding rates and diet compositions for each species, I generated spatially-explicit estimates of global food consumption rates of marine mammals. Using matching fisheries data generated by a similar model developed by Watson et al. (2004), I could then investigate the degree of overlap in food resource exploitation between marine mammals and fisheries during an average year of the 1990s. The resource overlap analysis indicated that – although aggregated marine mammal consumption is several times higher than the amount taken by fisheries – marine mammals primarily feed on food types rarely targeted by fisheries. Even more importantly though, all major taxonomic species groups (investigated in Chapter 4), appear to predominantly feed in areas that are currently little exploited by fisheries. Consequently, I predicted direct overlap in food resource exploitation between marine mammals and fisheries to be very low throughout most of the world during the 1990s.

Although resource overlap can not be directly equated to food competition, I conclude that the limited overlap in terms of both dietary preferences and spatial co-occurrence of marine mammals and fisheries suggests that competition between the two is likely to be also low from a global perspective, even after taking all associated uncertainties and the complexity of trophic interactions into account. Hotspots of high resource overlap that are indicative of potential competition are restricted to small geographic regions and appear to be largely driven by extreme concentrations of fishing operations in relatively small areas. Predicted large-scale patterns of resource overlap matched known hotspots of perceived conflict, which provided support that the model presented here has captured some of the important underlying processes that drive these interactions. In these hotspots potential and perceived competitive interactions between marine mammals and fisheries therefore warrant further investigation using more sophisticated dynamic ecosystem modelling tools.

My findings contrast with a widespread but likely distorted perception of the severity of competitive interactions between marine mammals and fisheries. This common perception, sometimes voiced in conjunction with calls for marine mammal culls, is probably largely due to the focus on smaller geographic scale of most previous studies (Hammill et al. 1995, Sigurjónsson & Víkingsson 1997, Lindstrøm et al. 2002) or the lack of consideration of spatial aspects in other large-scale models (Young 1999, Tamura 2003). Based on my results, I propose that there is little basis to blame marine mammals for the crisis world fisheries are facing today, and find no support for the notion that global fisheries catches could be measurably increased by reducing marine mammal populations (Kaschner & Pauly 2004). Conversely, I have found some support for the previously proposed scenario that the most common type of competitive interactions between the two players will be one where fisheries have an adverse impact on marine mammals, especially on those with small restricted distributional ranges (DeMaster et al. 2001).

5.2. LIMITATIONS AND FUTURE IMPROVEMENTS

I view the RES model primarily as a tool to visualize the extent of our knowledge and provide an objective basis for further discussion (see also below). Given the broad taxonomic and geographic scope of the thesis, the depth of my knowledge and understanding of each of the 115 marine mammal species included in the model is certainly exceeded by that of experts who have focussed their efforts on individual species or groups of species in smaller geographic regions. Consequently, the RES predictions for all species would greatly benefit from critical evaluation by such local experts. By making predicted distributions for all species available online (www.seaaroundus.org/distribution/search.aspx) I hope to invite feedback from other scientists that will allow me to improve RES predictions for individual species. Furthermore, I hope to engage in discussions about the generic differences and similarities of factors and processes determining species occurrence that may allow me to continue to improve the RES model structure itself.

A crucial factor in this context is seasonality, which should be incorporated into the RES model in the near future. This will especially improve predicted distributions for the many marine mammal species that undergo large annual migrations. If the model was used with seasonally or monthly averaged environmental data, it would likely better capture breeding and feeding ground distributions as well as intermediate migratory occurrences of these species. In addition, seasonally differentiated habitat preference settings may be required in some cases if the species is known to inhabit different environmental niches during different seasons. For further investigation of spatially-explicit food intake and resource overlap, the consideration of seasonally varying feeding patterns would be equally important to capture the seasonally varying food consumption of many species.

Better environmental data sets and the use of sea-ice concentration instead of 50% ice coverage data, would improve predictions of suitable environment, particularly for pack-ice and fast-ice species or species that occur in close vicinity to the ice edge. Furthermore, it will be worthwhile to investigate which other environmental and/or biological factors could be fruitfully added to the RES model that would improve its predictive capacities. In some cases, however, effectively utilized habitat is unlikely to be determined by such factors alone and the introduction of further geographic constraints that exclude species from areas of known local extinctions or depletions would be beneficial.

Further evaluation of the RES approach would be useful and may be achieved by testing predictions for other marine mammal species than those already tested. For validation purposes, sightings test data sets should ideally include direct measurements of effort that would be more appropriate than the proportional encounter rates used in Chapter 1. Although direct field tests of RES predictions would be desirable for validation, such tests may be impractical given the logistical and financial effort involved on the scale of the predictions. Applying the stranding simulation model to richer strandings data sets that also contain some effort information would help to evaluate the performance of the simulation model. Such data sets

may be available for more common species like the harbour porpoise from geographic regions with long histories of active stranding networks such as the United Kingdom or the United States. Finally, the stranding simulation model itself would greatly benefit if more reliable information about sinking rates and floating times of whale carcasses became available.

To improve spatially-explicit estimates of marine mammal food consumption the incorporation of population structure into the model would be a crucial next step to address the problematic overestimation of food consumption in certain areas of the world discussed in Chapter 4. This could be achieved by using a similar approach to that developed by Whitehead (2002) in order to obtain a more realistic estimate of global population size of sperm whales. Whitehead (2002) converted existing regional abundance estimates into local densities based on the known extent of the survey areas. He then scaled up densities using several different approaches, which allowed predictions of sperm whale densities in unsurveyed areas based on the habitat preferences and association with primary production identified within surveyed areas. The predictions generated by the RES model easily lent themselves for similar analyses, which would provide some more objective ballpark estimates of global abundance for many marine mammal species. Moreover, this type of analysis would account for stock structure by using abundance estimates assigned to the exact survey areas, thereby improving predictions of local abundance and food consumption.

Finally, the original marine mammal diet compositions analysis conducted by Pauly et al. (1998) should be using the large amount of diet information already collected and compiled in the global marine mammal database during the course of my thesis.

5.3. FUTURE APPLICATIONS

In the future, RES modelling may serve as a useful tool to address basic ecological questions as well as management and conservation issues on larger geographic scales.

In an ecological context, the RES model can produce an objective visualization of existing non-quantitative knowledge about species distributions that allows the re-evaluation of current assumptions and highlights existing data gaps. Moreover and most importantly, the extent to which RES generated hypotheses describe observed patterns in species occurrence also allows more specific questions to be asked about the role that other factors play in determining distributions. In my experience, RES maps and the observed discrepancies between predictions and known distributions are always thought-provoking and can greatly stimulate discussions about underlying ecological processes and conceptual frameworks. Insights into the ecological role of marine mammals may be gained through the analyses of basin-scale patterns in distribution and food intake of aggregated species groups. Such group predictions are easy to generate due to the standardized generic approach across all species and the grid-based nature of RES predictions.

Since the approach I took relies on more readily available types of data, such as general descriptions and expert knowledge, RES modelling may be particularly useful in situations where the paucity of data precludes the application of other more data-intensive habitat modelling approaches. This is not limited to the predicting the distributions of data-deficient species such as beaked whales as demonstrated in Chapter 3, although RES predictions for species like Peale's dolphin, pygmy right whales and other less well-known species may represent useful starting points to focus research efforts and address data gaps. In addition, however, RES modelling could also be usefully applied to generate hypotheses about historical distributions of heavily depleted species (e.g., gray whales in the North Atlantic; Mitchell & Mead 1977), potential offshore calving grounds of endangered baleen whale species (yet unknown for species such as the North Pacific right whale; Gaskin 1991) or changes in species distributions due to environmental regime shifts. Although some of these questions may also be addressed using other types of habitat suitability models, the RES approach may be more suitable in many cases since it allows the incorporation of non-quantitative, 'fuzzy logic'-type information (archaeological findings, expert knowledge and anecdotal records etc.).

Alternatively, RES modelling can usefully complement other habitat suitability models by, for instance, comparing RES predictions with outputs of point-data based statistical models. As discussed in Chapter 2 such comparisons may help to identify discrepancies that may be symptomatic of underlying sampling biases and related issues but can also highlight the problems of misapplications of such models using non-effort corrected data.

In a management context, RES predictions represent cost-efficient starting points to focus future research and survey efforts. This is especially practical when dealing with one of the many data-poor marine mammal species in the lesser-studied regions of the world. The application of habitat prediction models to design marine reserves that would minimize anthropogenic impacts on endangered marine mammal species has already been demonstrated on relatively small scales (Mullin et al. 1994, Moses & Finn 1997, Hooker et al. 1999). By generating global spatially explicit indices of biodiversity and species richness, or by visualizing potential geographic hotspots of high conflict with fisheries or other human operations, RES modelling may be equally useful when attempting to delineate efficient marine protected areas or critical habitat on larger temporal and geographic scales. Specifically, RES modelling could be used to conduct a spatially-explicit analysis of marine mammal bycatch or – in combination with sound propagation models – to investigate the potential effects of noise pollution on vulnerable species.

5.5. FINAL CONCLUSIONS AND RECOMMENDATIONS

I have demonstrated here that the visualization or mapping of non-quantitative, expert-knowledge-type information using rule-based approaches can reveal that we probably actually know a lot more than we think we know. Evaluation of predictions generated by the environmental envelope RES model indicated

that it can already describe heterogeneous patterns of species occurrence remarkably well using just a few basic environmental parameters. This suggests that – at larger geographic and temporal scales – the underlying processes determining species distributions may be quite simple and fundamentally similar across a large taxonomic range of species inhabiting different ecological niches. As illustrated by the investigation of global resource overlap between marine mammals and fisheries, using rule-based modelling approaches that allow the structured synthesis of large amounts of information can stimulate discussion and add valuable perspective to more detailed small-scale studies. Based on the results of the resource overlap analysis, I conclude that competition between marine mammals and fisheries is unlikely to be a problem of global concern and recommend that future research and management efforts should concentrate on local scales using more sophisticated ecosystem models.

Rule-based approaches obviously oversimplify the complexity of ecosystems, which should – ideally – be investigated using sophisticated models that sufficiently capture the dynamic interactions of marine food webs. The paucity of data and our limited understanding of trophic and other ecosystem interactions, however, currently precludes the development and application of adequate and sufficiently detailed models in many cases, especially on larger geographic scales.

Until such models become available, I conclude that we may be able to investigate large-scale ecological patterns and some pressing conservation issues related to global anthropogenic impacts on marine ecosystems by applying relatively simple rule-based models (such as the RES model) that exploit the wealth of alternative available information and can help us to visualize the extent of our knowledge.

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6. Appendix 1: Species List

Appendix 1. Names, taxonomy and ranges of 115 marine mammal species covered by RES model.

Common name	Scientific name	Suborder	Distribution
Bowhead whale	<i>Balaena mysticetus</i>	Mysticeti	Circumpolar N hemisphere
North Pacific right whale	<i>Eubalaena japonicus</i>	Mysticeti	N Pacific
Southern right whale	<i>Eubalaena australis</i>	Mysticeti	S hemisphere
North Atlantic right whale	<i>Eubalaena glacialis</i>	Mysticeti	N Atlantic
Sei whale	<i>Balaenoptera borealis</i>	Mysticeti	Circumglobal
Blue whale	<i>Balaenoptera musculus</i>	Mysticeti	Circumglobal
Eden/Bryde's whale	<i>Balaenoptera edeni</i>	Mysticeti	Indo-Pacific
Bryde's whale	<i>Balaenoptera brydei</i>	Mysticeti	Circumglobal
Fin whale	<i>Balaenoptera physalus</i>	Mysticeti	Circumglobal
Antarctic minke whale	<i>Balaenoptera bonaerensis</i>	Mysticeti	S hemisphere
Dwarf minke whale	<i>Balaenoptera acutorostrata</i>	Mysticeti	Circumglobal
Humpback whale	<i>Megaptera novaeangliae</i>	Mysticeti	Circumglobal
Gray whale	<i>Eschrichtius robustus</i>	Mysticeti	N Pacific
Pygmy right whale	<i>Caperea marginata</i>	Mysticeti	S hemisphere
Heaviside's dolphin	<i>Cephalorhynchus heavisidii</i>	Odontoceti	SW African waters
Hector's dolphin	<i>Cephalorhynchus hectori</i>	Odontoceti	New Zealand waters
Commerson's dolphin	<i>Cephalorhynchus commersonii</i>	Odontoceti	SE S American waters & Kerguelen
Black dolphin	<i>Cephalorhynchus eutropia</i>	Odontoceti	SW S American waters
Long-beaked common dolphin	<i>Delphinus capensis</i>	Odontoceti	Circumglobal (exc. N Indian O.)
Arabian common dolphin	<i>Delphinus tropicalis</i>	Odontoceti	N Indian O. & S China Sea
Short-beaked common dolphin	<i>Delphinus delphis</i>	Odontoceti	Circumglobal (exc. S Atlantic & Indian O.)
Pygmy killer whale	<i>Feresa attenuata</i>	Odontoceti	Circumglobal

Appendix 1 (cont.).

Common name	Scientific name	Suborder	Distribution
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	Odontoceti	Circumglobal
Long-finned pilot whale	<i>Globicephala melas</i>	Odontoceti	Circumglobal
Risso's dolphin	<i>Grampus griseus</i>	Odontoceti	Circumglobal
Fraser's dolphin	<i>Lagenodelphis hosei</i>	Odontoceti	Circumglobal
White-beaked dolphin	<i>Lagenorhynchus albirostris</i>	Odontoceti	N Atlantic
Hourglass dolphin	<i>Lagenorhynchus cruciger</i>	Odontoceti	S hemisphere
Dusky dolphin	<i>Lagenorhynchus obscurus</i>	Odontoceti	S hemisphere
Atlantic white-sided dolphin	<i>Lagenorhynchus acutus</i>	Odontoceti	N Atlantic
Pacific white-sided dolphin	<i>Lagenorhynchus obliquidens</i>	Odontoceti	N Pacific
Peale's dolphin	<i>Lagenorhynchus australis</i>	Odontoceti	S American waters
Northern right whale dolphin	<i>Lissodelphis borealis</i>	Odontoceti	N Pacific
Southern right whale dolphin	<i>Lissodelphis peronii</i>	Odontoceti	S hemisphere
Irrawaddy dolphin	<i>Orcaella brevirostris</i>	Odontoceti	Indo-Pacific
Killer whale	<i>Orcinus orca</i>	Odontoceti	Circumglobal
Melon-headed whale	<i>Peponocephala electra</i>	Odontoceti	Circumglobal
False killer whale	<i>Pseudorca crassidens</i>	Odontoceti	Circumglobal
Tucuxi	<i>Sotalia fluviatilis</i>	Odontoceti	NE S American waters
Indian hump-backed dolphin	<i>Sousa plumbea</i>	Odontoceti	W Indian O.
Atlantic hump-backed dolphin	<i>Sousa teuszii</i>	Odontoceti	NW African waters
Pacific hump-backed dolphin	<i>Sousa chinensis</i>	Odontoceti	Indo-Pacific
Pantropical spotted dolphin	<i>Stenella attenuata</i>	Odontoceti	Circumglobal
Atlantic spotted dolphin	<i>Stenella frontalis</i>	Odontoceti	Atlantic
Striped dolphin	<i>Stenella coeruleoalba</i>	Odontoceti	Circumglobal

Appendix 1 (cont.).

Common name	Scientific name	Suborder	Distribution
Clymene dolphin	<i>Stenella clymene</i>	Odontoceti	Atlantic
Spinner dolphin	<i>Stenella longirostris</i>	Odontoceti	Circumglobal
Rough-toothed dolphin	<i>Steno bredanensis</i>	Odontoceti	Circumglobal
Indian Ocean bottlenose dolphin	<i>Tursiops aduncus</i>	Odontoceti	Indo-Pacific
Bottlenose dolphin	<i>Tursiops truncatus</i>	Odontoceti	Circumglobal
Pygmy sperm whale	<i>Kogia breviceps</i>	Odontoceti	Circumglobal
Dwarf sperm whale	<i>Kogia simus</i>	Odontoceti	Circumglobal
Beluga or white whale	<i>Delphinapterus leucas</i>	Odontoceti	Circumpolar N hemisphere
Narwhal	<i>Monodon monoceros</i>	Odontoceti	Circumpolar N hemisphere
Finless porpoise	<i>Neophocoena phocaenoides</i>	Odontoceti	Indo-Pacific
Burmeister's porpoise	<i>Phocoena spinipinnis</i>	Odontoceti	S American waters
Harbour porpoise	<i>Phocoena phocoena</i>	Odontoceti	N hemisphere
Vaquita	<i>Phocoena sinus</i>	Odontoceti	Gulf of California, NE Pacific
Spectacled porpoise	<i>Phocoena dioptrica</i>	Odontoceti	S hemisphere
Dall's porpoise	<i>Phocoenoides dalli</i>	Odontoceti	N Pacific
Sperm whale	<i>Physeter macrocephalus</i>	Odontoceti	Circumglobal
Franciscana	<i>Pontoporia blainvillei</i>	Odontoceti	E S American waters
Arnoux's beaked whale	<i>Berardius arnuxii</i>	Odontoceti	S hemisphere
Baird's beaked whale	<i>Berardius bairdii</i>	Odontoceti	N Pacific
Northern bottlenose whale	<i>Hyperoodon ampullatus</i>	Odontoceti	N Atlantic
Southern bottlenose whale	<i>Hyperoodon planifrons</i>	Odontoceti	S hemisphere
Longman's beaked whale	<i>Indopacetus pacificus</i>	Odontoceti	Indo-Pacific

Appendix 1 (cont.).

Common name	Scientific name	Suborder	Distribution
Gray's beaked whale	<i>Mesoplodon grayi</i>	Odontoceti	S hemisphere
True's beaked whale	<i>Mesoplodon mirus</i>	Odontoceti	Atlantic & Indian O.
Andrews' beaked whale	<i>Mesoplodon bowdoini</i>	Odontoceti	S hemisphere
Gervais' beaked whale	<i>Mesoplodon europaeus</i>	Odontoceti	Atlantic
Ginkgo-toothed beaked whale	<i>Mesoplodon ginkgodens</i>	Odontoceti	Indo-Pacific
Stejneger's beaked whale	<i>Mesoplodon stejnegeri</i>	Odontoceti	N Pacific
Hector's beaked whale	<i>Mesoplodon hectori</i>	Odontoceti	S hemisphere
Spade-toothed beaked whale	<i>Mesoplodon traversii</i>	Odontoceti	S Pacific
Pygmy beaked whale	<i>Mesoplodon peruvianus</i>	Odontoceti	E Pacific
Sowerby's beaked whale	<i>Mesoplodon bidens</i>	Odontoceti	N Atlantic
Strap-toothed whale	<i>Mesoplodon layardii</i>	Odontoceti	S hemisphere
Perrin's beaked whale	<i>Mesoplodon perrini</i>	Odontoceti	NE Pacific
Hubb's beaked whale	<i>Mesoplodon carlhubbsi</i>	Odontoceti	N Pacific
Blainville's beaked whale	<i>Mesoplodon densirostris</i>	Odontoceti	Circumglobal
Tasman or Shepherd's beaked whale	<i>Tasmacetus shepherdi</i>	Odontoceti	S hemisphere
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	Odontoceti	Circumglobal
Walrus	<i>Odobenus rosmarus</i>	Pinnipedia	Circumpolar N hemisphere
Guadalupe fur seal	<i>Arctocephalus townsendi</i>	Pinnipedia	NE Pacific
South American fur seal	<i>Arctocephalus australis</i>	Pinnipedia	S American waters
Galapagos fur seal	<i>Arctocephalus galapagoensis</i>	Pinnipedia	Galapagos Is., E Pacific
South African & Australian fur seal	<i>Arctocephalus pusillus</i>	Pinnipedia	S African & S Australian waters
Subantarctic fur seal	<i>Arctocephalus tropicalis</i>	Pinnipedia	Circumpolar S hemisphere (exc. SE Pacific)
Antarctic fur seal	<i>Arctocephalus gazella</i>	Pinnipedia	Circumpolar S hemisphere (exc. SE Pacific)

Appendix 1 (cont.).

Common name	Scientific name	Suborder	Distribution
Juan Fernandez fur seal	<i>Arctocephalus philippii</i>	Pinnipedia	Juan Fernandez Islands, SE Pacific
New Zealand fur seal	<i>Arctocephalus forsteri</i>	Pinnipedia	New Zealand & S Australian waters
Northern fur seal	<i>Callorhinus ursinus</i>	Pinnipedia	N Pacific
Steller's sea lion	<i>Eumetopias jubatus</i>	Pinnipedia	N Pacific
Australian sea lion	<i>Neophoca cinerea</i>	Pinnipedia	SE Indian O., S & SW Australia
South (American) sea lion	<i>Otaria flavescens</i>	Pinnipedia	S American waters
Hooker's or New Zealand sea lion	<i>Phocarctos hookeri</i>	Pinnipedia	New Zealand waters, SW Pacific
Galapagos sea lion	<i>Zalophus wollebaeki</i>	Pinnipedia	Galapagos Islands, E Pacific
California sea lion	<i>Zalophus californianus</i>	Pinnipedia	NE Pacific
Hooded seal	<i>Cystophora cristata</i>	Pinnipedia	N Atlantic
Bearded seal	<i>Erignathus barbatus</i>	Pinnipedia	Circumpolar N hemisphere
Gray seal	<i>Halichoerus grypus</i>	Pinnipedia	N Atlantic
Ribbon seal	<i>Histriophoca fasciata</i>	Pinnipedia	N Pacific
Leopard seal	<i>Hydrurga leptonyx</i>	Pinnipedia	Circumpolar S hemisphere
Weddell seal	<i>Leptonychotes weddellii</i>	Pinnipedia	Circumpolar S hemisphere
Crabeater seal	<i>Lobodon carcinophagus</i>	Pinnipedia	Circumpolar S hemisphere
Southern elephant seal	<i>Mirounga leonina</i>	Pinnipedia	Circumpolar S hemisphere
Northern elephant seal	<i>Mirounga angustirostris</i>	Pinnipedia	NE Pacific
Hawaiian monk seal	<i>Monachus schauinslandi</i>	Pinnipedia	Hawaiian waters, NE Pacific
Mediterranean monk seal	<i>Monachus monachus</i>	Pinnipedia	Mediterranean & NE Atlantic
Ross seal	<i>Ommatophoca rossii</i>	Pinnipedia	Circumpolar S hemisphere
Harp seal	<i>Pagophilus groenlandica</i>	Pinnipedia	N Atlantic & Russian Arctic

Appendix 1 (cont.).

Common name	Scientific name	Suborder	Distribution
Largha or spotted seal	<i>Phoca largha</i>	Pinnipedia	N Pacific
Harbour seal	<i>Phoca vitulina</i>	Pinnipedia	N hemisphere
Ringed seal	<i>Pusa hispida</i>	Pinnipedia	Circumpolar N hemisphere

7. Appendix 2: Habitat Preferences

Appendix 2. Habitat preferences in terms of depth, mean annual sea surface temperature and distance to the edge of sea ice for 115 marine mammal species. Superscripts denote the particular habitat preference type about which the reference provided information: ¹ = depth preferences, ² = temperature preferences, ³ = distance to edge of sea ice. For species marked by *, distance from land was used as an additional constraining factor, limiting species to waters < 500 km (*) or < 1000 km (**) from land.

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
Bowhead whale	mainly coast.-cont. shelf to end of cont. slope	polar only	mainly around edge of pack-ice	N hemisphere - (Baltic)	Jefferson et al, 1993 ² ; Klinowska, 1991 ² , Krutzikowsky & Mate, 2000 ³ ; Mate et al, 2000 ^{1,3} ; Moore & DeMaster, 1997 ^{1,3} ; Moore, 2000 ¹ ; Treacy, 2000 ³
North Pacific right whale	mainly coast.-cont. slope to v. deep wat.	subpolar-subtropical	reg. but not pref. in areas of max. ice extent	N Pacific - (Lat < 10°N)	Angliss & Lodge, 2002 ³ ; Jefferson et al, 1993 ² ; Kenney, 2002 ^{1,2,3} ; Moore et al, 2000a ^{1,2} ; Scarff, 1983 ^{1,3} ; Tynan et al, 2001 ²
Southern right whale	mainly coast.-cont. slope to v. deep wat.	polar-subtropical	reg. but not pref. around edge of the pack-ice	S hemisphere	Hamner et al, 1988 ^{1,2,3} ; IWC, 2001 ³ ; Kenney, 2002 ¹ ; Moore et al, 1999 ¹ ; Ohsumi & Kasamatsu, 1983 ² ; Payne, 1983 ¹ ; Tormosov et al, 1998 ³
North Atlantic right whale	mainly coast.-cont. shelf to deep wat.	subpolar-tropical	no assoc. with ice edge, but season. close to areas of max. ice extent	N Atlantic - (Med., Black S., Hudson's Bay & Strait, Baltic)	Baumgartner et al, 2003 ¹ ; Evans, 1980 ¹ ; Gaskin, 1991 ² ; Jefferson et al, 1993 ³ ; Kenney, 2002 ² ; Knowlton et al, 1992 ¹ ; Mitchell et al, 1983 ² ; Woodley & Gaskin, 1996 ¹
Sei whale	mainly cont. slope-abyss. plains to v. deep wat.	subpolar-tropical	no assoc. with ice edge, but season. close to areas of max. ice extent	World - (Black S., Med., Red S.)	Best & Lockyer, 2002 ¹ ; COSEWIC, 2003 ^{1,2} ; Horwood, 1987 ^{2,3} ; Kawamura, 1974 ² ; MacLeod et al, 2003 ¹ ; Ohsumi, 1977 ² ; Rice, 1998 ³ ; Sigurjonsson, 1995 ¹
Blue whale	mainly low. cont. slope-abyss. plains to v. deep wat.	polar-full tropical	mainly around edge of pack-ice, but also elsewhere	World - (Black S., Med., Red S.)	Heide-Joergensen, 2001 ¹ ; Hooker et al, 1999 ² ; Kasamatsu et al, 1996 ³ ; Kasamatsu et al, 2000 ^{1,2,3} ; Mate et al, 1999 ¹ ; Murase et al, 2000 ¹ ; Perry et al, 1999 ² ; Tynan, 1998 ³ ; Yochem & Leatherwood, 1985 ³ ; Zerbini et al, 1997 ²
Eden/Bryde's whale	mainly coast.-cont. shelf to deep wat.	subtropical-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Black S., Med., Red S., Persian Gulf, N Atlantic, SW Atlantic)	Best et al, 1984 ¹ ; Cummings, 1985 ² ; Jefferson et al, 1993 ³ ; Kato, 2002 ¹ ; Klinowska, 1991 ² ; Nemoto, 1959 ² ; Ohsumi, 1977 ² ; Rice, 1998 ³ ; Tersy, 1992 ¹

Appendix 2 (cont.).

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
Bryde's whale	mainly cont. slope-abyss. plains to v. deep wat.	subtropical-tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Black S., Med.)	Best et al, 1984 ¹ ; Cummings, 1985 ² ; Jefferson et al, 1993 ³ ; Jefferson & Schiro, 1997 ¹ ; Kawamura & Satake, 1976 ² ; Kawamura, 1982 ¹ ; Miyashita et al, 1996 ² ; Rice, 1998 ^{2,3} ; Shimada & Pastene, 1995 ¹
Fin whale	mainly cont. slope-abyss. plains to v. deep wat.	polar-tropical	predom. in areas of max. ice extent, but also elsewhere	World - (Black S., Red S., Persian Gulf)	Aguilar, 2002 ² ; Kasamatsu et al, 2000 ^{1,2} ; MacLeod et al, 2003 ¹ ; Moore et al, 2000b ¹ ; Notarbartolo-di-Sciara et al., 2003 ¹ ; Rice, 1998 ^{2,3} ; Zerbini et al, 1997 ²
Antarctic minke whale	mainly cont. slope to v. deep wat.	polar-tropical	mainly around edge of pack-ice, but also elsewhere	S hemisphere	Kasamatsu et al, 2000 ¹ ; Murase et al, 2002 ^{1,3} ; Perrin & Brownell, 2002 ^{1,3} ; Ribic et al, 1991 ² ; Rice, 1998 ^{2,3}
Dwarf minke whale	mainly coast.-cont. slope to v. deep wat.	polar-tropical	predom. in areas of max. ice extent, but also elsewhere	World - (Baltic, Black S., Hudson's Bay & Strait, Red S., Persian Gulf)	Hamazaki, 2002 ¹ ; IWC, 2001 ¹ ; Jefferson et al, 1993 ³ ; Klinowska, 1991 ³ ; Moore et al, 2002 ¹ ; Rice, 1998 ^{2,3} ; Sigurjonsson, 1995 ¹
Humpback whale	mainly coast.-cont. slope to v. deep wat.	polar-tropical	reg. but not pref. in areas of max. ice extent	World - (Med., Black S., Baltic, Hudson's Bay & Strait, Red S.)	Benson et al, 2001 ² ; Clapham, 2002 ² ; Gregr & Trites, 2001 ¹ ; Hamazaki, 2002 ^{1,2} ; Kasamatsu et al, 2000 ³ ; Moore et al, 2000b ¹ ; Nicol et al, 2000 ^{1,3} ; Rice, 1998 ³ ; Winn & Reichley, 1985 ² ; YoNAH, 2001 ³
Gray whale	mainly estuar. to beyond shelf break	subpolar-subtropical	reg. but not pref. around edge of the pack-ice	N Pacific	Deecke, 2003 ^{1,2} ; Gardner & Chavez-Rosales, 2000 ² ; Jones & Swartz, 2002 ^{1,2,3} ; Moore & DeMaster, 1997 ^{1,3} ; Moore, 2000 ³ ; Rugh et al, 1999 ³ ; Weller et al, 2002 ^{1,2}
Pygmy right whale	mainly coast.-cont. slope to v. deep wat.	subpolar-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	S hemisphere	Jefferson et al, 1993 ^{1,2} ; Kemper, 2002 ^{1,2} ; Matsuoka et al, 1996 ² ; Rice, 1998 ³
Heaviside's dolphin	mainly estuar. to end of cont. shelf	cold temperate-warm temperate	no assoc. with ice edge, nowhere near ice at any time of the year	S hemisphere - (Lon: > 50°E & > 20°W)	Best & Abernethy, 1994 ^{1,2} ; Dawson, 2002 ¹ ; Jansen van Vuuren et al, 2002 ^{1,2} ; Jefferson et al, 1993 ¹ ; Rice, 1998 ³
Hector's dolphin	mainly estuar. to end of cont. shelf	cold temperate-warm temperate	no assoc. with ice edge, nowhere near ice at any time of the year	S hemisphere - (Lon: > 180°E & < 150°E)	Dawson, 2002 ¹ ; Jefferson et al, 1993 ¹ ; Slooten & Dawson, 1994 ² ; Rice, 1998 ³
Commerson's dolphin	mainly estuar. to beyond shelf break	subpolar-cold temperate	no assoc. with ice edge, but season. close to areas of max. ice extent	S hemisphere - (Lon: > 120°E & > 72°W)	Dawson, 2002 ¹ ; Goodall, 1994b ^{1,2} ; Goodall et al, 1988a ³ ; Jefferson et al, 1993 ¹ ; Rice, 1998 ³

Appendix 2 (cont.).

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
Black dolphin	mainly estuar. to end of cont. shelf	subpolar-warm temperate	no assoc. with ice edge, but season. close to areas of max. ice extent	S hemisphere - (Lon: < 70°W & < 180°E)	Aguayo, 1975 ² ; Dawson, 2002 ¹ , Goodall, 1994a ^{1,2} ; Goodall et al, 1988b ^{1,2} ; Jefferson et al, 1993 ¹ ; Rice, 1998 ³
Long-beaked common dolphin	mainly coast.-cont. shelf to deep wat.	subtropical only	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Med., Black S.)	Findlay et al, 1992 ¹ ; Perrin, 2002b ^{1,2} ; Rice, 1998 ^{1,2,3}
Arabian common dolphin	mainly coast.-up. cont. shelf to up. cont. slope	full tropical only	no assoc. with ice edge, nowhere near ice at any time of the year	N hemisphere - (Med., Black S.; Lon > 180°E & < 30°E)	Balance & Pitman, 1998 ¹ ; Perrin, 2002b ² ; Rice, 1998 ³
Short-beaked common dolphin	mainly cont. slope to deep wat.	cold temperate-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Indian Ocean, S Atlantic)	Evans, 1994 ¹ ; Griffin, 1997 ¹ ; Hooker et al, 1999 ¹ ; Perrin, 2002b ² ; Selzer & Payne, 1988 ² ; Rice, 1998 ^{1,2,3}
Pygmy killer whale	mainly cont. slope to v. deep wat.	full tropical only	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Med., Black S., Red S.)	Donahue & Perryman, 2002 ² ; Findlay et al, 1992 ¹ ; Jefferson et al, 1993 ^{1,2} ; Miyazaki & Wada, 1978 ² ; Rice, 1998 ³ ; Ross & Leatherwood, 1994 ²
Short-finned pilot whale	mainly cont. slope to v. deep wat.	subtropical-tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Med., Black S.)	Davis et al, 1998 ^{1,2} ; Jefferson et al, 1993 ¹ ; Mullin et al, 1994b ¹ ; Payne & Heinemann, 1993 ^{1,2} ; Rice, 1998 ³ ; Smith et al, 1986 ² ; Wade & Guerrodette, 1993 ²
Long-finned pilot whale	mainly cont. slope to v. deep wat.	polar-warm temperate	no assoc. with ice edge, but season. close to areas of max. ice extent	World - (Hudson's Bay, N Pacific)	Bernard & Reilly, 1999 ¹ ; Findlay et al, 1992 ² ; Hamazaki, 2002 ¹ ; Hooker et al, 1999 ² ; Jefferson et al, 1993 ² ; Kasamatsu & Joyce, 1995 ^{2,3} ; Mullin et al, 1994b ¹ ; Payne & Heinemann, 1993 ¹ ; Rice, 1998 ³
Risso's dolphin	mainly up. cont. slope to deep wat.	cold temperate-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Baltic)	Baird, 2002 ¹ ; Davis et al, 1998 ¹ ; Jefferson et al, 1993 ² ; Rice, 1998 ³ ; Ross, 1984 ¹
Fraser's dolphin	mainly low. cont. slope-abys. plains to v. deep wat.	subtropical-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Med., Black S., Red S.)	Dolar, 2002 ^{1,2} ; Jefferson et al, 1993 ² ; Jefferson & Leatherwood, 1994 ^{1,2} ; Jefferson & Schiro, 2000 ¹ ; Perrin et al, 1994a ^{1,2} ; Rice, 1998 ³
White-beaked dolphin	mainly coast.-cont. shelf to deep wat.	polar-cold temperate	no assoc. with ice edge, but season. close to areas of max. ice extent	N Atlantic - (Baltic, Hudson's Bay & Strait)	Kinze, 2002 ^{1,2} ; Northridge et al, 1997 ^{1,3} ; Reeves et al, 1999b ^{1,2} ; Rice, 1998 ^{1,2}
Hourglass dolphin	mainly low. cont. slope-abys. plains to v. deep wat.	polar-warm temperate	mainly in areas of max. ice extent, but also elsewhere	S hemisphere	Gaskin, 1972 ² ; Goodall, 2002a ^{1,2} ; Goodall, 1997 ^{1,2,3} ; Jefferson et al, 1993 ^{1,3} ; Kasamatsu et al, 1988 ² ; Kasamatsu & Joyce, 1995 ³

Appendix 2 (cont.).

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
Dusky dolphin	coast.-cont. slope to deep wat.	cold temperate-warm temperate	no assoc. with ice edge, but season. close to areas of max. ice extent	S hemisphere	Brownell & Cipriano, 1999 ¹ ; Cipriano, 1992 ² ; Goodall et al, 1997 ^{1,3} ; Kasamatsu et al, 1990 ² ; van Waerebeek & Würsig, 2002 ^{1,2} ; Würsig & Würsig, 1980 ² ; Würsig et al, 1997 ¹
Atlantic white-sided dolphin	mainly low. cont. slope to v. deep wat.	subpolar-warm temperate	reg. but not pref. in areas of max. ice extent	N Atlantic - (Hudson's Bay & Strait)	Cipriano, 2002 ¹ ; Hamazaki, 2002 ² ; Hooker et al, 1999 ¹ ; Leopold & Couperus, 1995 ² ; Northridge et al, 1997 ³ ; Reeves et al, 1999a ¹ ; Selzer & Payne, 1988 ^{1,2} ; Sergeant et al, 1980 ²
Pacific white-sided dolphin	mainly cont. slope to v. deep wat.	cold temperate-subtropical	no assoc. with ice edge, but season. close to areas of max. ice extent	N Pacific	Barlow, 1995 ¹ ; Brownell et al, 1999b ² ; Buckland et al, 1993 ¹ ; Dahlheim & Towell, 1986 ² ; Forney & Barlow, 1998 ¹ ; Green et al, 1992 ¹ ; Heise, 1997 ³ ; Rice, 1998 ³ ; Smith et al, 1986 ² ; van Waerebeek & Würsig, 2002 ²
Peale's dolphin	mainly estuar. to beyond shelf break	subpolar-warm temperate	no assoc. with ice edge, but season. close to areas of max. ice extent	S hemisphere - (Lon: <20°W & >140°W)	Brownell et al, 1999a ¹ ; Crespo et al, 1997 ¹ ; Goodall et al, 1997 ^{1,2,3} ; Goodall, 2002b ¹ ; Lescrauwaet, 1997 ² ; Oporto, 1984 ^{2,3}
Northern right whale dolphin	mainly low. cont. slope-abys. plains to v. deep wat.	subpolar-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	N Pacific - (Lat: < 10°N)	Bjørge et al, 1991 ^{1,2} ; Forney & Barlow, 1998 ¹ ; Jefferson & Newcomer, 1993 ¹ ; Jefferson et al, 1993 ¹ ; Jefferson et al, 1994 ³ ; Rice, 1998 ³ ; Smith et al, 1986 ²
Southern right whale dolphin	mainly cont. slope to v. deep wat.	polar-subtropical	no assoc. with ice edge, but season. close to areas of max. ice extent	S hemisphere	Cruickshank & Brown, 1981 ² ; Findlay et al, 1992 ¹ ; Gaskin, 1968a ² ; Jefferson et al, 1993 ¹ ; Kasamatsu et al, 1988 ² ; Lipsky, 2002 ³ ; Newcomer et al, 1996 ¹ ; Rose & Payne, 1991 ^{1,2} ; Rice, 1998 ³
Irrawaddy dolphin	mainly estuar. to end of cont. shelf	full-on tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Lon: > 156°E & < 80°E)	Arnold, 2002 ^{1,2} ; Freeland & Bayliss, 1989 ¹ ; Mörzner Bruyns, 1971 ² ; Parra et al, 2002 ^{1,2} ; Rice, 1998 ³ ; Stacey, 1996 ^{1,2}
Killer whale	mainly cont. slope-abys. plains to v. deep wat.	polar-tropical	mainly around edge of pack-ice, but also elsewhere	World - (Hudson's Bay & Strait, Black S., Red S., Persian Gulf)	Ford, 2002 ³ ; IWC-BWIS, 2001 ^{1,2,3} ; Jefferson et al, 1993 ² ; Jefferson & Schiro, 1997 ¹ ; Kasamatsu et al, 2000 ^{2,3} ; Pitman et al, 2001 ¹ ; Thiele & Gill, 1999 ³

Appendix 2 (cont.).

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
Melon-headed whale	mainly cont. slope to v. deep wat.	full tropical only	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Med., Black S.)	de Boer, 2000 ² ; Gunnier, 2000 ¹ ; Jefferson et al, 1993 ^{1,2} ; Jefferson & Schiro, 1997 ¹ ; Perryman et al, 1994 ^{1,2} ; Rice, 1998 ³
False killer whale	mainly low. cont. slope to v. deep wat.	warm temperate-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Black S., Red S, Persian Gulf)	de Boer, 2002 ² ; Findlay et al, 1992 ¹ ; Jefferson et al, 1993 ¹ ; Miyazaki & Wada, 1978 ² ; Rice, 1998 ³ ; Shallenberger, 1981 ¹ ; Stacey et al, 1994 ² ; Wade & Gerrodette, 1993 ^{1,2}
Tucuxi	mainly estuar. to end of cont. shelf	full tropical only	no assoc. with ice edge, nowhere near ice at any time of the year	W Atlantic - (Lat: > 13°N & Lon: < 20°W & > 70°W)	Borobia et al, 1991 ² ; da Silva & Best, 1996 ¹ ; Flores, 2002 ¹ ; Jefferson et al, 1993 ² ; Rice, 1998 ³
Indian hump-backed dolphin	mainly estuar. to end of cont. shelf	subtropical-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Med., Black S.; Lon > 90°E & < 14°E)	Findlay et al, 1992 ¹ ; Jefferson et al, 1993 ² ; Jefferson & Karczmarski, 2001 ¹ ; Karczmarski et al, 2000 ¹ ; Rice, 1998 ³ ; Ross, 2002 ^{1,2}
Atlantic hump-backed dolphin	mainly estuar. to end of cont. shelf	subtropical-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	E Atlantic - (Lat: > 27°N & Lon: > 13°E & > 20°W)	Jefferson et al, 1993 ^{1,2} ; Rice, 1998 ³ ; Ross et al, 1994 ² ; Ross, 2002 ¹
Pacific hump-backed dolphin	mainly estuar. to end of cont. shelf	full tropical only	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Lon: > 180°E & < 90°E)	Corkeron et al, 1997 ¹ ; Dolar et al, 1997 ¹ ; Jefferson et al, 1993 ² ; Jefferson & Karczmarski, 2001 ^{1,2} ; Rice, 1998 ³ ; Ross, 2002 ^{1,2}
Pantropical spotted dolphin	mainly low. cont. slope to v. deep wat.	full tropical only	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Med., Black S.)	Baumgartner et al, 2000 ² ; Baumgartner et al, 2001 ¹ ; Fiedler & Reilly, 1994 ² ; Hamazaki, 2002 ^{1,2} ; Miyazaki et al, 1974 ² ; Mullin et al, 1994b ¹ ; Perrin & Hohn, 1994 ¹ ; Rice, 1998 ³
Atlantic spotted dolphin	mainly coast-up. cont. slope to deep wat.	subtropical-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	Atlantic - (Lon: > 18°E & > 70°W)	Davis et al, 1998 ^{1,2} ; Hamazaki et al, 2002 ² ; Herzing, 1990 ¹ ; Mullin et al, 1994b ¹ ; Perrin, 2002a ¹ ; Rice, 1998 ³
Striped dolphin	mainly cont. slope to v. deep wat.	cold temperate-tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Black S.)	Baird et al, 1993 ¹ ; Bloch et al, 1996 ² ; Davis et al, 1998 ¹ ; Focada et al, 1990 ² ; Gannier & Gannier, 1998 ¹ ; Hooker et al, 1999 ² ; Jefferson & Schiro, 1997 ¹ ; Rice, 1998 ³
Clymene dolphin	mainly cont. slope-abys. plains to v. deep wat.	full tropical only	no assoc. with ice edge, nowhere near ice at any time of the year	Atlantic - (Lon: > 15°E & > 70°W)	Davis et al, 1998 ^{1,2} ; Mullin et al, 1994a ^{1,2} ; Perrin et al, 1981 ¹ ; Rice, 1998 ³

Appendix 2 (cont.).

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
Spinner dolphin	mainly cont. slope to v. deep wat.	full tropical only	no assoc. with ice edge, nowhere near ice at any time of the year	World	Davis et al, 1998 ^{1,2} ; de Boer, 2000 ² ; Dollar et al, 2003 ¹ ; Jefferson et al, 1997 ¹ ; Mullin et al, 1994b ¹ ; Miyazaki & Wada, 1978 ² ; Perrin, 2002c ² ; Rice, 1998 ³
Rough-toothed dolphin	mainly cont. slope to v. deep wat.	subtropical-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Black S. S, Red S.)	Davis et al, 1998 ^{1,2} ; Gannier, 2000 ¹ ; Jefferson et al, 1993 ² ; Jefferson & Schiro, 1997 ¹ ; Rice, 1998 ³
Indian Ocean bottlenose dolphin	mainly estuar. to end of cont. shelf	full tropical only	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Med., Black S.; Lon: >180°E & <15°E)	Findlay et al, 1992 ¹ ; Hale et al, 2000 ¹ ; Rice, 1998 ³ ; Ross et al, 1987 ¹ ; Wells & Scott, 2002 ²
Bottlenose dolphin	mainly coast.-up. cont. slope to deep wat.	cold temperate-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World	Baumgartner et al, 1999 ² ; Canadas et al, 2002 ¹ ; Findlay et al, 1992 ¹ ; Hastie et al, 2003 ¹ ; Hooker et al, 1999 ² ; Jefferson et al, 1993 ² ; Rice, 1998 ³ ; Wells et al, 1999 ¹ ; Wells & Scott, 1999 ²
Pygmy sperm whale	mainly cont. slope to v. deep wat.	warm temperate-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Med., Black S., Red S.)	Baumgartner et al, 2001 ¹ ; Davis et al, 1998 ¹ ; Jefferson et al, 1993 ² ; McAlpine, 2002 ³ ; Mullin et al, 1994b ¹ ; Rice, 1998 ^{1,3}
Dwarf sperm whale	mainly up. cont. slope to deep wat.	warm temperate-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Med., Black S., Red S.)	Baumgartner et al, 2001 ¹ ; Davis et al, 1998 ¹ ; Jefferson et al, 1993 ² ; McAlpine, 2002 ^{1,2} ; Mullin et al, 1994b ¹ ; Rice, 1998 ³
Beluga or white whale	coast.-cont. slope to deep wat.	polar-subpolar	mainly restricted to fast & deep pack-ice	N hemisphere - (Baltic)	Harwood et al, 1996 ³ ; Moore et al, 1993 ¹ ; Moore & DeMaster, 1997 ^{1,3} ; Moore et al, 2000a ^{1,3} ; O'Corry-Crowe, 2002 ² ; Rice, 1998 ^{1,2} ; Suydam et al, 2001 ³ ; Watts et al, 1991 ²
Narwhal	mainly up. cont. slope to deep wat.	polar only	mainly restricted to fast & deep pack-ice	N hemisphere	Dietz & Heide-Jørgensen, 1995 ¹ ; Heide-Jørgensen, 2002 ^{1,3} ; Heide-Jørgensen et al, 2003 ¹ ; Jefferson et al, 1993 ² ; Martin et al, 1994 ¹ ; Rice, 1998 ³
Finless porpoise	mainly estuar. to end of cont. shelf	warm temperate-full tropical	no assoc. with ice edge, but season. close to areas of max. ice extent	World - (Med., Black S.; Lat: > 8° S & Lon: > 180°E & < 48°E)	Amano, 2002 ^{1,2} ; Jefferson et al, 1993 ^{1,2} ; Kasuya, 1999 ² ; Rice, 1998 ³ ; Yoshida et al, 2001 ¹
Burmeister's porpoise	mainly coast.-cont. shelf to end of cont. slope	cold temperate-subtropical	no assoc. with ice edge, but season. close to areas of max. ice extent	S hemisphere - (Lon: < 40°W & > 125°W)	Brownell & Praderi, 1983 ² ; Brownell & Clapham, 1999 ¹ ; Jefferson et al, 1993 ^{1,2} ; Goodall et al, 1995 ¹ ; Reyes, 2002 ¹ ; Rice, 1998 ³

Appendix 2 (cont.).

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
Harbour porpoise	mainly estuar. to beyond shelf break	subpolar-warm temperate	reg. but not pref. in areas of max. ice extent	N hemisphere - (Hudson's Bay & Strait)	Bjørge & Øien, 1995 ³ ; Dahlheim et al, 2000 ¹ ; Gaskin et al, 1993 ² ; Palka, 1995 ^{1,2} ; Raym-Suryan & Harvey et al, 2001 ^{1,2} ; Raym-Suryan & Harvey, 1998 ² ; Read & Westgate, 1997 ^{1,2}
Vaquita	mainly estuar. to end of cont. shelf	narrow subtropical only	no assoc. with ice edge, nowhere near ice at any time of the year	NE Pacific	Jefferson et al, 1993 ^{1,3} ; Rojas-Bracho & Jaramillo-Legoretta, 2002 ^{1,2} ; Silber, 1990 ¹ ; Silber et al, 1994 ²
Spectacled porpoise	mainly coast.-cont. slope to v. deep wat.	polar-cold temperate	no assoc. with ice edge, but season. close to areas of max. ice extent	S hemisphere - (Lat: > 65°S)	Goodall, 1978 ¹ ; Goodall & Schiavini, 1995 ² ; Goodall, 2002c ^{1,2,3} ; Jefferson et al, 1993 ¹
Dall's porpoise	mainly coast.-cont. slope to v. deep wat.	subpolar-warm temperate	no assoc. with ice edge, but season. close to areas of max. ice extent	N Pacific	Jefferson, 1988 ^{1,2} ; Jefferson, 2002 ¹ ; Jones et al, 1987 ² ; Miyashita & Kasuya, 1988 ² ; Moore et al, 2002 ¹ ; Rice, 1998 ³ ; Smith et al, 1986 ¹
Sperm whale	mainly low. cont. slope-abyss. plains to v. deep wat.	polar-full tropical	reg. but not pref. in areas of max. ice extent	World - (Red S., Black S.)	Davis et al, 1998 ² ; Gordon et al, 2000 ¹ ; Griffin, 1999 ¹ ; Jaquet & Gendron, 2002 ^{1,2} ; Kasuya & Miyashita, 1988 ² ; Rice, 1998 ³ ; Whitehead, 2002 ³
Franciscana	mainly estuar. to end of cont. shelf	warm temperate-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	Atlantic - (Lat: > 0°N & Lon: < 20°W & > 70°W)	Crespo, 2002 ^{1,2} ; Jefferson et al, 1993 ¹ ; Rice, 1998 ³ ; Secchi et al, 2001 ¹
Arnoux's beaked whale	mainly low. cont. slope to v. deep wat.	polar-subtropical	predom. in areas of max. ice extent, but also elsewhere	S hemisphere	Balcomb, 1989 ^{1,2,3} ; D'Amico et al, 2003 ^{1,2,3} ; Jefferson et al, 1993 ^{1,2} ; Hobson & Martin, 1996 ³ ; Ponganis & Kooyman, 1995 ¹
Baird's beaked whale	mainly low. cont. slope-abyss. plains to v. deep wat.	polar-subtropical	no assoc. with ice edge, but season. close to areas of max. ice extent	N Pacific - (Lat: < 10°)	D'Amico et al, 2003 ^{1,2,3} ; Fedoseev, 1984 ³ ; Jefferson et al, 1993 ¹ ; Kasuya et al, 1997 ¹ ; Kasuya, 2002 ^{1,2,3} ; Reeves & Mitchell, 1993 ^{1,2,3}
Northern bottlenose whale	mainly low. cont. slope to v. deep wat.	polar-warm temperate	predom. in areas of max. ice extent, but also elsewhere	N Atlantic - (Black S.)	Benjaminsen, 1972 ¹ ; Benjaminsen & Christensen, 1979 ^{1,2,3} ; D'Amico et al, 2003 ^{1,2,3} ; Hooker et al, 1999 ¹ ; Jefferson et al, 1993 ² ; Reeves et al, 1993 ^{1,3}
Southern bottlenose whale	mainly low. cont. slope-abyss. plains to v. deep wat.	polar-subtropical	mainly around edge of pack-ice, but also elsewhere	S hemisphere	D'Amico et al, 2003 ^{1,2,3} ; Jefferson et al, 1993 ¹ ; Gowans, 2002 ¹ ; Kasamatsu & Joyce, 1995 ¹ ; Mead, 1989b ^{1,3} ; Rice, 1998 ³

Appendix 2 (cont.).

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
Longman's beaked whale	rest. to abyss. to v. deep wat.	subtropical-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Atlantic, Med., Black S.)	D'Amico et al, 2003 ^{1,2,3} ; Mead, 1989a ^{1,2,3} ; Pitman, 2002a ²
Gray's beaked whale	mainly cont. slope to v. deep wat.	subpolar-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	S hemisphere	D'Amico et al, 2003 ^{1,2,3} ; Gaskin, 1971 ² ; Mead, 1989a ^{1,2,3} ; Pitman, 2002b ¹ ; Rice, 1998 ²
True's beaked whale	mainly cont. slope to v. deep wat.	warm temperate-tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Med., Black S., Red S., Persian Gulf; Lon: > 150°E & > 70°W)	D'Amico et al, 2003 ^{1,2,3} ; Houston, 1990d ^{1,2,3} ; MacLeod, 2000 ² ; Mead, 1989a ^{1,2} ; Pitman, 2002 ^{1,2} ; Waring et al, 2001 ¹
Andrews' beaked whale	mainly cont. slope to v. deep wat.	cold temperate-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	S hemisphere	Baker, 2001 ² ; Gaskin, 1968b ² ; Gaskin, 1971 ² ; Mead, 1989a ^{1,3} ; Pitman, 2002b ¹
Gervais' beaked whale	mainly cont. slope to v. deep wat.	subtropical-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	Atlantic - (Lon: > 30°E)	D'Amico et al, 2003 ^{1,2,3} ; Davis et al, 1998 ¹ ; Mead, 1989a ^{2,3} ; MacLeod, 2000 ² ; Pitman, 2002b ^{1,2} ; Rosario-Delestro et al, 1999 ² ; Waring et al, 2001 ¹
Ginkgo-toothed beaked whale	mainly cont. slope to v. deep wat.	subtropical-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Atlantic, Med., Black S.)	Mead, 1989a ^{1,2,3} ; Miyakazi et al, 1987 ² ; Pitman, 2002b ¹
Stejneger's beaked whale	mainly cont. slope to v. deep wat.	subpolar-warm temperate	no assoc. with ice edge, but season. close to areas of max. ice extent	N Pacific	D'Amico et al, 2003 ^{1,2,3} ; Houston, 1990c ² ; Loughlin et al, 1982 ¹ ; Loughlin & Perez, 1985 ^{2,3} ; Mead, 1989a ¹ ; Miyazaki et al, 1987 ² ; Pitman, 2002b ¹ ; Rice, 1998 ^{1,2}
Hector's beaked whale	mainly cont. slope to v. deep wat.	cold temperate-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	S hemisphere	D'Amico et al, 2003 ^{1,2,3} ; Mead, 1989a ^{1,2,3} ; Pitman, 2002b ¹ ; Rice, 1998 ²
Spade-toothed beaked whale	mainly cont. slope to v. deep wat.	cold temperate-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	S hemisphere - (Lon: > 70°W & < 30°E)	van Helden et al, 2002 ^{2,3} ; depth preference inferred from other species
Pygmy beaked whale	mainly cont. slope to v. deep wat.	subtropical-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	Pacific	D'Amico et al, 2003 ^{1,2,3} ; Jefferson et al, 1993 ³ ; Mead, 1989a ¹ ; Pitman, 2002b ¹
Sowerby's beaked whale	mainly cont. slope to v. deep wat.	subpolar-warm temperate	no assoc. with ice edge, but season. close to areas of max. ice extent	N Atlantic - (Med., Black S., Hudson's Bay & Strait, Baltic)	Carlström et al, 1997 ¹ ; D'Amico et al, 2003 ^{1,2,3} ; Houston, 1990 ¹ ; Hooker & Baird, 1999 ^{1,2} ; MacLeod, 2000 ^{2,3} ; Waring et al, 2001 ¹
Strap-toothed whale	mainly cont. slope to v. deep wat.	polar-subtropical	no assoc. with ice edge, but season. close to areas of max. ice extent	S hemisphere	D'Amico et al, 2003 ^{1,2,3} ; Guiler et al, 1987 ² ; Mead, 1989a ^{1,2,3} ; Pitman, 2002b ¹
Perrin's beaked whale	mainly cont. slope to v. deep wat.	warm temperate-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	NE Pacific - (Lat: < 10°N)	Dalebout et al, 2002 ¹ ; D'Amico et al, 2003 ^{1,2,3} ; Mead, 1998 ² ; Miyazaki et al, 1987 ² ; Pitman, 2002b ¹ ; Rice, 1998 ³

Appendix 2 (cont.).

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
Hubb's beaked whale	mainly cont. slope to v. deep wat.	cold temperate-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	N Pacific - (Lat: < 10°N)	Houston, 1990b ^{2,3} ; MacLeod, pers comm ¹ ; Mead, 1989a ^{1,2}
Blainville's beaked whale	mainly cont. slope to v. deep wat.	warm temperate-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Med., Black S. S., Red S., Persian Gulf)	D'Amico et al 2003 ^{1,2,3} ; Houston, 1990a ^{1,2,3} ; Moore, 1966 ¹ ; Pitman, 2002b ² ; Ritter & Brederlau, 1999 ¹ ; Rosario-Delestro et al, 1999 ² ; Shallenberger, 1981 ¹
Tasman or Shepherd's beaked whale	mainly low. cont. slope to v. deep wat.	subpolar-warm temperate	no assoc. with ice edge, nowhere near ice at any time of the year	S hemisphere	D'Amico et al, 2003 ^{1,2,3} ; Gaskin, 1971 ² Jefferson et al, 1993 ^{1,2} ; Mead, 1989c ² ; Mead, 2002 ^{1,2} ; Rice, 1998 ³
Cuvier's beaked whale	mainly low. cont. slope to v. deep wat.	cold temperate-full tropical	no assoc. with ice edge, nowhere near ice at any time of the year	World - (Black S., Red S., Persian Gulf)	D'Amico et al, 2003 ^{1,2,3} ; Dolar et al, 1997 ¹ ; Gannier, 2000 ¹ ; Heyning, 2002 ² ; Rice, 1998 ^{2,3} ; Waring et al, 2001 ¹
Walrus	mainly estuar. to beyond shelf break	polar only	mainly around edge of pack-ice	N hemisphere	Born et al, 2003 ¹ ; Estes & Gilbert, 1978 ³ ; Jay et al, 2001 ¹ ; Jefferson et al, 1993 ¹ ; Kastelein, 2002 ^{1,3} ; Rice, 1998 ^{2,3}
Guadalupe fur seal*	mainly low. cont. slope to v. deep wat.	warm temperate-tropical	no assoc. with ice edge, nowhere near ice at any time of the year	NE Pacific - (Lat: < 10°N & Lon: > 150°W)	Belcher & Lee, 2002 ² ; Lander et al, 2000 ¹ ; Reijnders et al, 1993 ² ; Rice, 1998 ³
South American fur seal*	mainly coast.-cont. shelf to end of cont. slope	subpolar-warm temperate	no assoc. with ice edge, but season. close to areas of max. ice extent	S hemisphere - (Lon: < 20°W & > 100°W)	Bonner, 1981 ² ; Daneri et al, 1997 ³ ; Jefferson et al, 1993 ¹ ; Rice, 1998 ³
Galapagos fur seal*	mainly coast.-up. cont. shelf to up. cont. slope	narrow subtropical only	no assoc. with ice edge, nowhere near ice at any time of the year	E Pacific - (Lat: > 10°N & Lon: < 70°W & > 140°W)	Reijnders et al, 1993 ^{1,2} ; Rice, 1998 ³
South African & Australian fur seal*	mainly coast.-up. cont. shelf to up. cont. slope	warm temperate-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	S hemisphere - (Lon: > 160°E & > 20°W)	Arnould & Hindell, 2001 ¹ ; Reijnders et al, 1993 ² ; Rice, 1998 ³ ; Thomas & Schulein, 1988 ¹
Subantarctic fur seal	mainly coast.-up. cont. slope to deep wat.		no assoc. with ice edge, but season. close to areas of max. ice extent	S hemisphere - (Lon: > 20°W)	depth inferred based on Antarctic fur seals; Reijnders et al, 1993 ² ; Rice, 1998 ³
Antarctic fur seal	mainly coast.-up. cont. slope to deep wat.	polar-subpolar	reg. but not pref. in areas of max. ice extent	S hemisphere - (Lon: > 80°W)	Bonnadonna et al, 2000 ¹ ; Boyd et al, 1998 ¹ ; C. Bradshaw pers. comm ³ ; Guinet et al, 2001 ¹ ; Reijnders et al, 1993 ² ; Ribic et al, 1991 ^{1,2,3} ; Rice, 1998 ³
Juan Fernandez fur seal*	mainly low. cont. slope to v. deep wat.	narrow warm temperate only	no assoc. with ice edge, nowhere near ice at any time of the year	E Pacific - (Lat: > 0°N & Lon: > 100°W)	Francis & Ochoa-Acuna, 1998 ^{1,2} ; Ochoa-Acuna & Francis, 1995 ¹ ; Reijnders et al, 1993 ² ; Rice, 1998 ³

Appendix 2 (cont.).

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
New Zealand fur seal*	mainly coast.-cont. shelf to deep wat.	subpolar-warm temperate	no assoc. with ice edge, but season. close to areas of max. ice extent	S hemisphere - (Lon: > 180°E & < 150°E)	Bradshaw et al, 2002a ¹ ; Jefferson et al, 1993 ² ; Lalas & Bradshaw, 2001 ¹ ; Reijnders et al, 1993 ¹ ; Rice, 1998 ³
Northern fur seal	mainly cont. slope to deep wat.	subpolar-warm temperate	reg. but not pref. in areas of max. ice extent	N Pacific	Antonelis et al, 1990 ¹ ; Gentry, 1981 ^{1,2} ; Gentry, 2002 ² ; Jefferson et al, 1993 ¹ ; Loughlin & Ingraham, 1999 ¹ ; Rice, 1998 ³
Steller's sea lion	mainly coast.-cont. shelf to end of cont. slope	subpolar-cold temperate	no assoc. with ice edge, but season. close to areas of max. ice extent	N Pacific	Baba et al, 2000 ^{1,2,3} ; Merrick & Loughlin, 1997 ¹ ; Loughlin et al, 1987 ¹ ; Loughlin, 2002 ¹ ; Rice, 1998 ^{2,3} ; Trites, pers. comm ³
Australian sea lion	mainly coast.-up. cont. shelf to up. cont. slope	warm temperate-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	S hemisphere - (Lon: > 155°E & < 75°E)	Costa, 1991 ¹ ; Gales et al, 1994 ² ; Jefferson et al, 1993 ¹ ; Ling, 2002 ² ; Rice, 1998 ³
South (American) sea lion*	mainly estuar. to end of cont. shelf	polar-subtropical	no assoc. with ice edge, but season. close to areas of max. ice extent	S hemisphere - (Lat: > 60°S & Lon: < 40°W & > 120°W)	Campagna et al, 2001 ¹ ; Jefferson et al, 1993 ² ; Reijnders et al, 1993 ² ; Rice, 1998 ³ ; Thompson et al, 1998 ¹ ; Werner & Campagna, 1995 ¹
Hooker's or New Zealand sea lion	mainly coast.-cont. shelf to end of cont. slope	subpolar-cold temperate	reg. but not pref. in areas of max. ice extent	W Pacific - (Lat: > 0°N)	Costa & Gales, 2000 ¹ ; Crocker et al, 2001 ¹ ; Gales, 2002 ^{1,2} ; Jefferson et al, 1993 ² ; Rice, 1998 ^{1,3}
Galapagos sea lion*	mainly coast.-cont. shelf to deep wat.	full tropical only	no assoc. with ice edge, nowhere near ice at any time of the year	E Pacific - (Lat: > 10°N & Lon: > 100°W)	Dellinger & Trillmich, 1999 ² ; Heath, 2002 ¹ ; Jefferson et al, 1993 ¹ ; Rice, 1998 ³
California sea lion*	mainly up. cont. slope to deep wat.	warm temperate-tropical	no assoc. with ice edge, nowhere near ice at any time of the year	N Pacific - (Lat: < 10°N & Lon: > 150°W)	Antonellis et al, 1990 ¹ ; Heath, 2002 ² ; Jefferson et al, 1993 ¹ ; Rice, 1998 ^{1,3}
Hooded seal	mainly low. cont. slope to v. deep wat.	polar-cold temperate	mainly around edge of pack-ice, but also elsewhere	N Atlantic	Folkow & Blix, 1995 ^{1,3} ; Folkow et al, 1996 ^{1,3} ; Folkow & Blix, 1999 ¹ ; Kovacs & Lavigne, 1986 ^{1,2,3} ; Reijnders et al, 1993 ² ; Rice, 1998 ³
Bearded seal	mainly coast.-up. cont. shelf to up. cont. slope	polar-subpolar	mainly around edge of pack-ice, but also elsewhere	N hemisphere - (Baltic)	Gjertz et al, 2000 ¹ ; Kingsley et al, 1985 ¹ ; Krafft et al, 2000 ¹ ; Kovacs, 2002 ^{1,2,3} ; Lund et al, 1997 ³ ; Reijnders et al, 1993 ² ; Rice, 1998 ³ ; Wiig, 1995 ³
Gray seal	mainly estuar. to beyond shelf break	subpolar-cold temperate	reg. but not pref. in areas of max. ice extent	N Atlantic - (Hudson's Bay & Strait)	Hall, 2002 ³ ; Jefferson et al, 1993 ^{1,2} ; McConnell et al, 1999 ¹ ; Rice, 1998 ³ ; Sjöberg & Ball, 2000 ¹ ; Thompson et al, 1996 ¹

Appendix 2 (cont.).

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
Ribbon seal	mainly coast.-cont. slope to deep wat.	polar-subpolar	mainly in areas of max. ice extent, but also elsewhere	N Pacific	Fedoseev, 2002 ^{1,2} ; Jefferson et al, 1993 ^{1,2} ; Mizuno et al, 2002 ^{1,2} ; Reijnders et al, 1993 ¹ ; Rice, 1998 ³
Leopard seal	mainly up. cont. slope to deep wat.	polar-warm temperate	mainly around edge of pack-ice, but also elsewhere	S hemisphere	Jefferson et al, 1993 ² ; King, 1983 ² ; Knox, 1994 ³ ; Laws, 1984 ^{1,2,3} ; Rice, 1998 ³ ; Rogers, 2002 ³
Weddell seal	mainly coast.-cont. slope to v. deep wat.	polar-subpolar	mainly restricted to fast & deep pack-ice	S hemisphere	Hindell et al, 2003 ¹ ; Jefferson et al, 1993 ² ; Kooyman, 1981 ² ; Lake et al, 2003 ¹ ; Rice, 1998 ³ ; Stirling, 1971 ³ ; Thomas, 2002b ^{1,3} ; Wantabe et al, 2003 ¹
Crabeater seal	mainly coast.-cont. shelf to deep wat.	polar-cold temperate	mainly around edge of pack-ice, but also elsewhere	S hemisphere	Bengtson, 1997 ¹ ; Bengtson, 2002 ¹ ; Jefferson et al, 1993 ² ; Nordoy et al, 1995 ¹ ; Ribic et al, 1991 ^{1,2,3} ; Rice, 1998 ³
Southern elephant seal	mainly cont. slope-abyss. plains to v. deep wat.	polar-tropical	mainly around edge of pack-ice, but also elsewhere	S hemisphere	Bennet et al, 2002 ¹ ; Bornemann et al, 2000 ³ ; Boyd & Arnborn, 1991 ² ; Bradshaw et al, 2002b ² ; Campagna et al, 1998 ³ ; Hindell et al, 1991 ¹ ; Hindell et al, 1999 ² ; Hindell, 2002 ¹ ; Ling & Bryden, 1992 ² ; McConnell et al, 1992 ¹ ; Rice, 1998 ³
Northern elephant seal	mainly low. cont. slope-abyss. plains to v. deep wat.	subpolar-subtropical	no assoc. with ice edge, nowhere near ice at any time of the year	NE Pacific - (Lat: < 10°N)	DeLong et al, 1992 ¹ ; Hakoyama et al, 1994 ² ; Hindell, 2002 ¹ ; Rice, 1998 ³ ; Stewart & Hubert, 1993 ^{1,2}
Hawaiian monk seal*	mainly coast.-cont. shelf to deep wat.	subtropical-tropical	no assoc. with ice edge, nowhere near ice at any time of the year	NE Pacific - (Lat: < 10°N & Lon: < 140°W)	Gilmartin & Forcada, 2002 ¹ ; Parrish et al, 2000 ¹ ; Parrish et al, 2002 ¹ ; Reijnders et al, 1993 ^{2,3} ; Schmelzer, 2000 ²
Mediterranean monk seal	mainly coast.-up. cont. shelf to up. cont. slope	subtropical only	no assoc. with ice edge, nowhere near ice at any time of the year	N hemisphere - (Pacific, Indian O.; Lon: > 20°W)	Duguay, 1975 ¹ ; Kenyon, 1981 ¹ ; Reijnders et al, 1993 ^{1,2,3}
Ross seal	mainly coast.-cont. slope to deep wat.	polar only	mainly restricted to fast & deep pack-ice	S hemisphere	Bengtson & Steward, 1997 ¹ ; Bester et al, 1995 ³ ; Jefferson et al, 1993 ² ; Knox, 1994 ³ ; Rice, 1998 ³ ; Spletstoesser et al, 2000 ¹ ; Thomas, 2002a ³
Harp seal	mainly up. cont. slope to deep wat.	polar-cold temperate	mainly around edge of pack-ice, but also elsewhere	N hemisphere - (Baltic, Hudson's Bay & Strait, Black S.; Lon: > 95°W)	Joiris et al, 1996 ³ ; Kovacs & Lavigne, 1986 ¹ ; Lawson et al, 1998 ¹ ; Lacoste & Stenson, 2000 ¹ ; Lavigne, 2002 ^{1,3} ; Reijnders et al, 1993 ² ; Rice, 1998 ³

Appendix 2 (cont.).

Common name	Depth range preference	Temperature range preference	Distance to ice edge preference	General area - (excluded areas)	Sources
Harp seal	mainly up. cont. slope to deep wat.	polar-cold temperate	mainly around edge of pack-ice, but also elsewhere	N hemisphere - (Baltic, Hudson's Bay & Strait, Black S.; Lon: > 95°W)	Joiris et al, 1996 ³ ; Kovacs & Lavigne, 1986 ¹ ; Lawson et al, 1998 ¹ ; Lacoste & Stenson, 2000 ¹ ; Lavigne, 2002 ^{1,3} ; Reijnders et al, 1993 ² ; Rice, 1998 ³
Largha or spotted seal	mainly coast.-cont. shelf to deep wat.	polar-warm temperate	predom. in areas of max. ice extent, but also elsewhere	N Pacific	Burns, 2002 ² ; Jefferson et al, 1993 ¹ ; Lowry et al, 2000 ^{1,3} ; Mizuno, 2002 ¹ ; Reijnders et al, 1993 ¹
Harbour seal	mainly coast.-up. cont. shelf to up. cont. slope	subpolar-warm temperate	reg. but not pref. in areas of max. ice extent	N hemisphere - (Med., Black S.)	Bjørge et al, 1995 ¹ ; Burns, 2002 ^{1,2} ; Gjertz et al, 2001 ¹ ; Lowry et al, 2001 ¹ ; Rice, 1998 ³
Ringed seal	mainly coast.-cont. shelf to deep wat.	polar-subpolar	mainly in fast & deep pack-ice, but also elsewhere	N hemisphere	Kingsley et al, 1985 ¹ ; Lund et al, 1997 ³ ; Miyazaki, 2002 ² ; Reeves, 1998 ^{1,3} ; Rice, 1998 ³ ; Stirling et al, 1982 ¹ ; Wiig et al, 1999 ³

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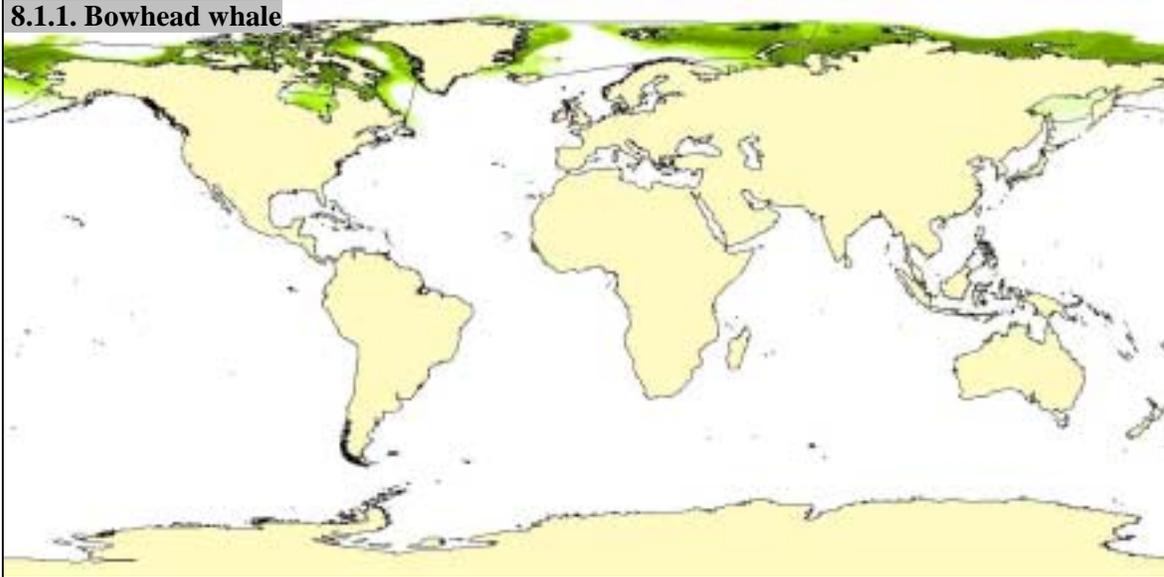
8. Appendix 3

Appendix 3. RES model outputs for 115 marine mammal species: Predicted relative environmental suitability in each raster cell (ranging from less suitable (light) to very suitable (dark)) based on habitat preference information for all baleen whales (Section 8.1.), odontocetes (Section 8.2) and pinniped species (Section 8.3) Outlines of proposed maximum range extent (Jefferson et al, 1993) are included for comparison, whenever possible. For all beaked whale species, known ‘at-sea’ (sightings, bycatch, whaling: ○ = high certainty; ◐ = tentative records) and stranding locations (◻ = high certainty; ◑ = tentative records) were included (D’Amico et al, 2003).

Note that, when viewed on a global scale, RES predictions for many coastal species are difficult to see in narrower shelf areas, such as along the western coast of South America and east coast of Africa and apparent absences from certain areas may just be artefacts of viewing scale. RES maps can be viewed at higher resolutions online at www.seararoundus.org/distribution/search.aspx. Please refer also to website for more information about model parameter settings and known predicted absences and presences.

8.1. BALEEN WHALES

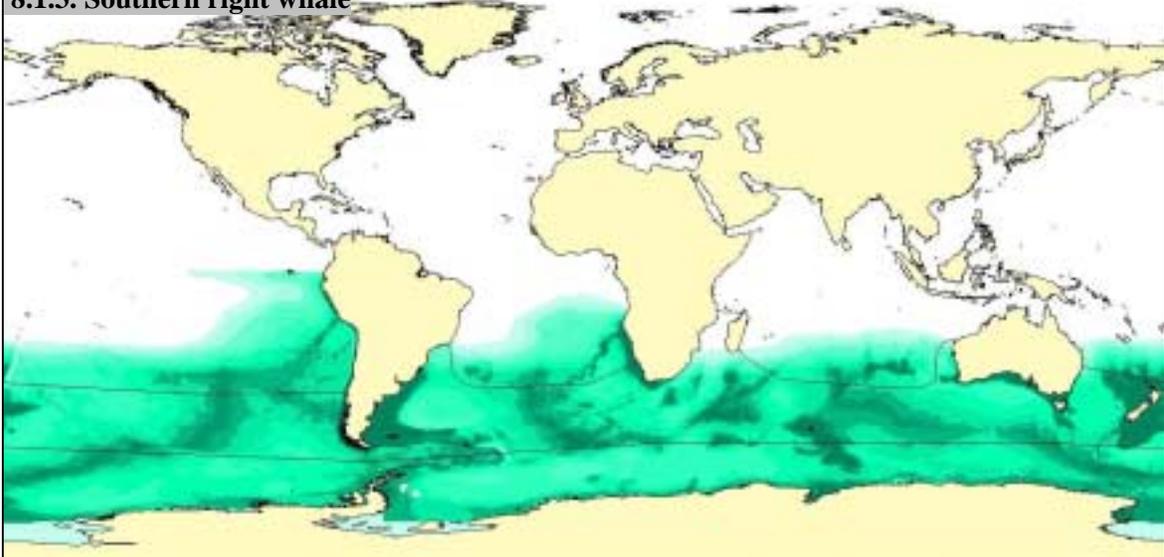
8.1.1. Bowhead whale



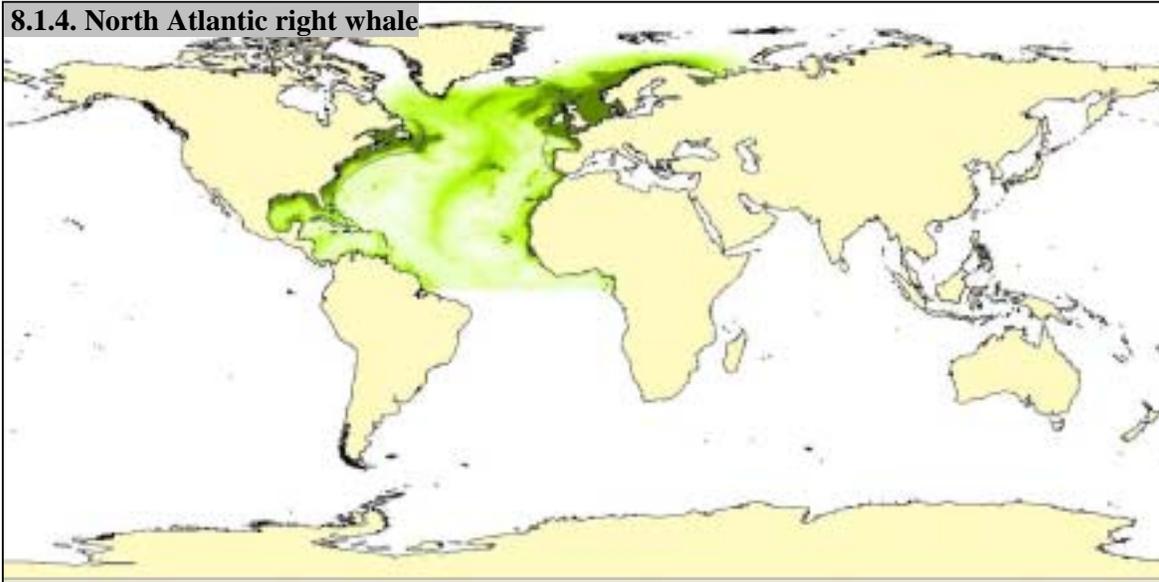
8.1.2. North Pacific right whale



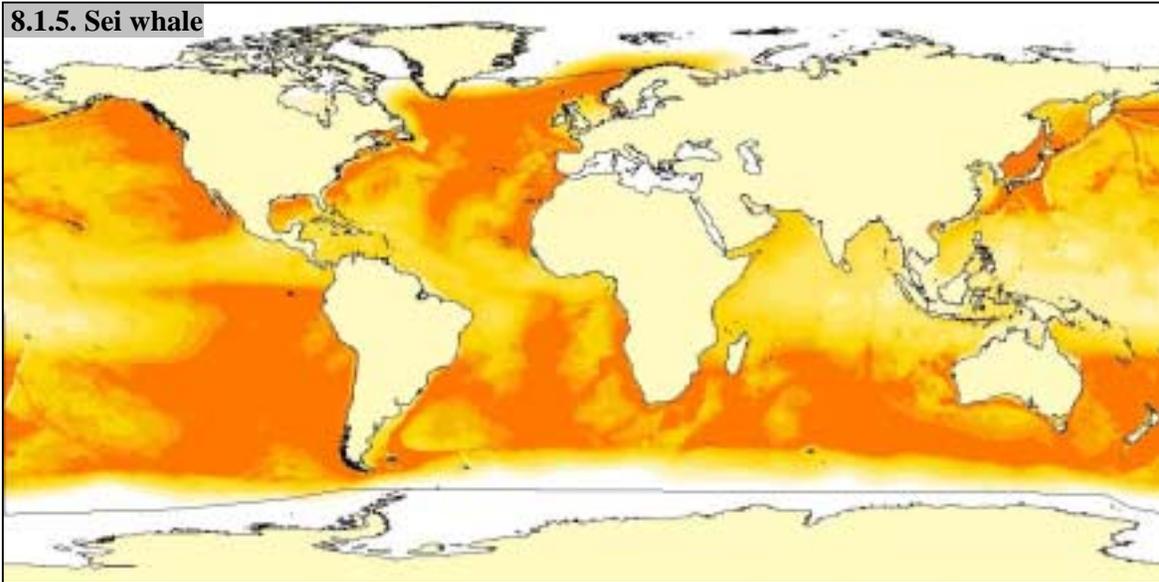
8.1.3. Southern right whale



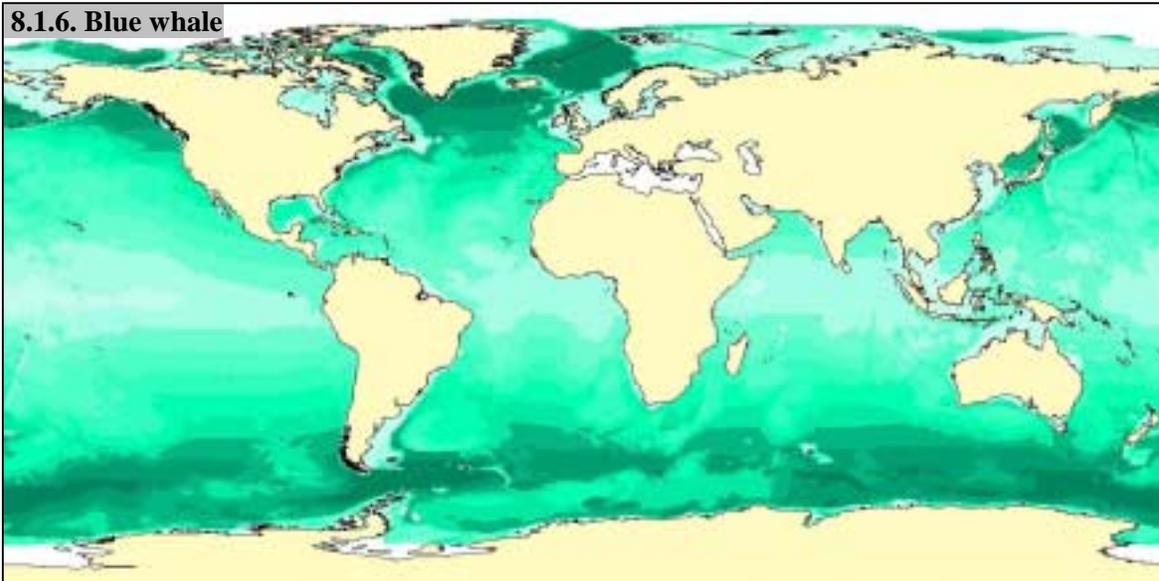
8.1.4. North Atlantic right whale



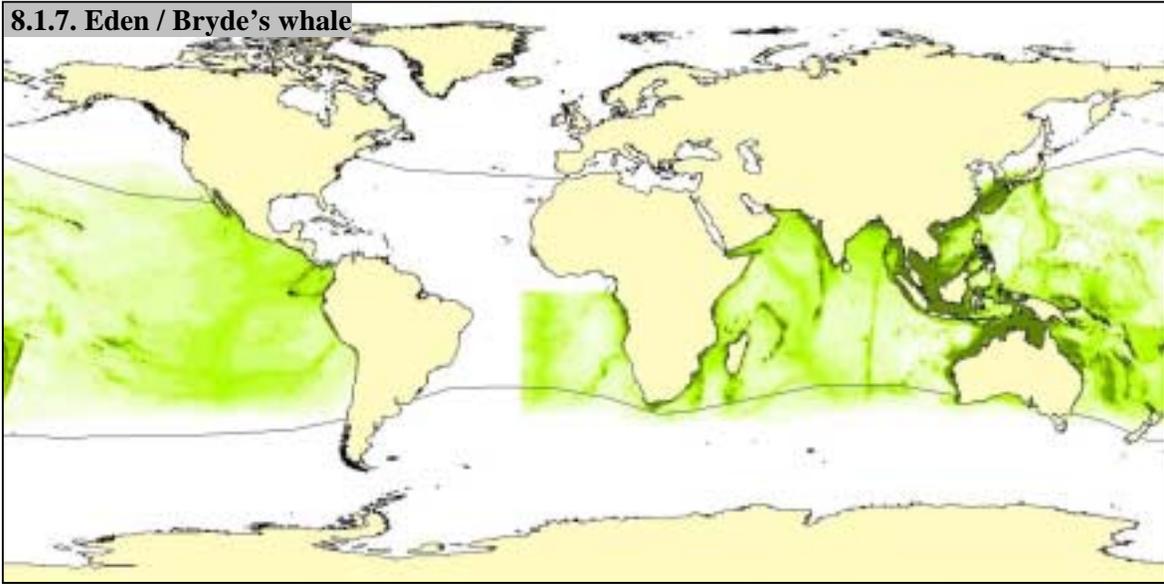
8.1.5. Sei whale



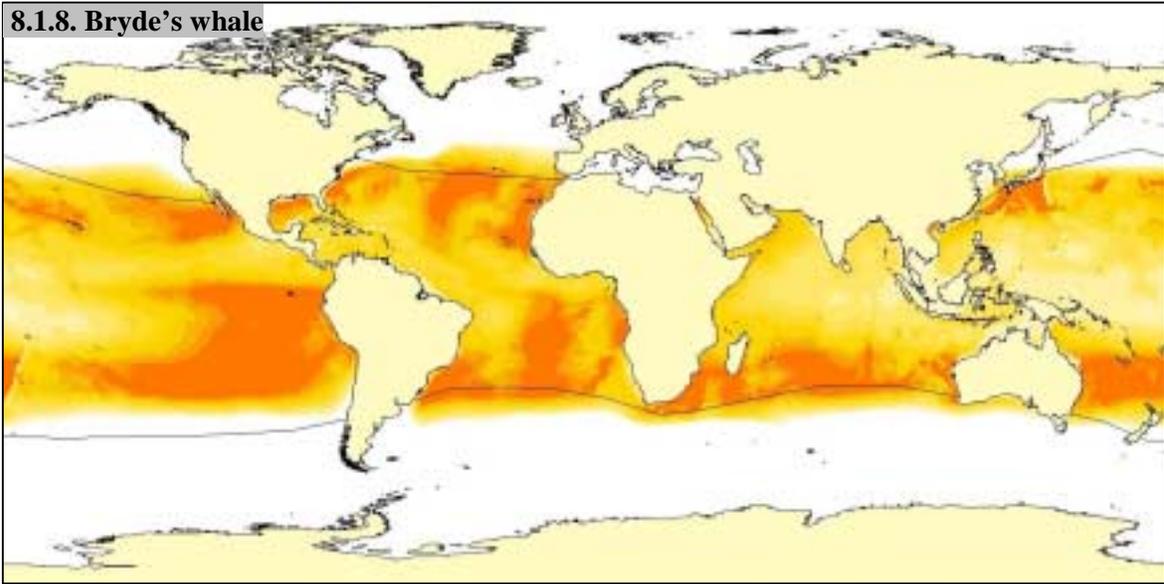
8.1.6. Blue whale



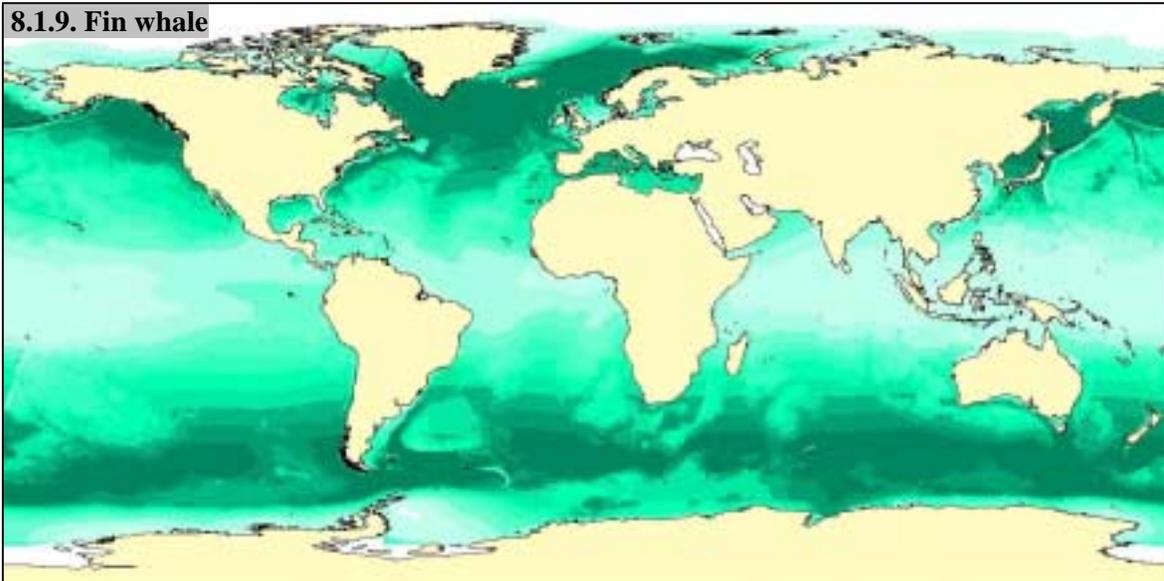
8.1.7. Eden / Bryde's whale



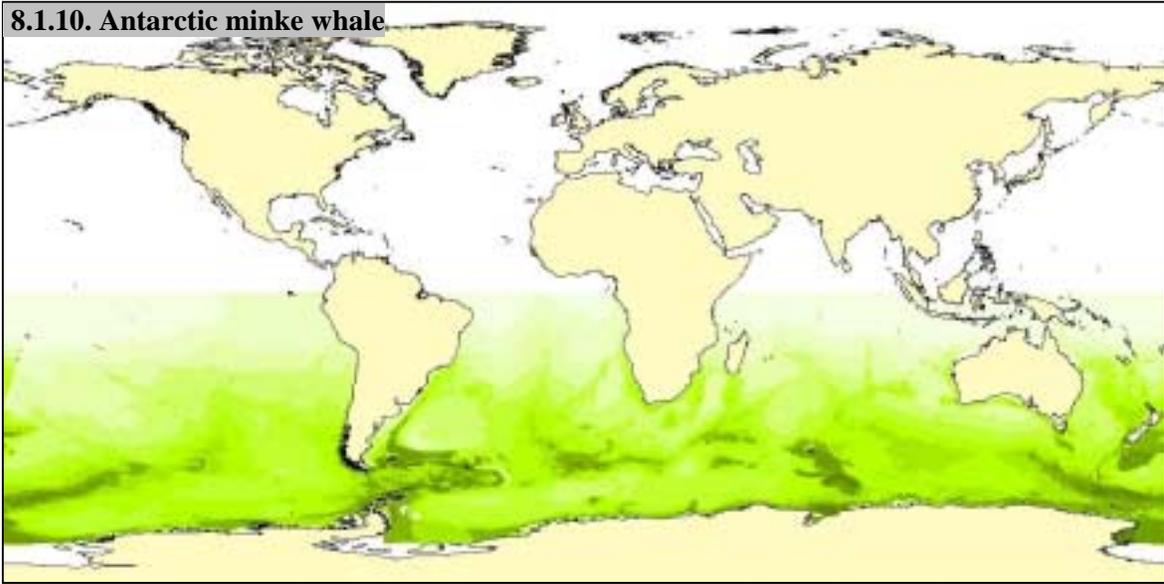
8.1.8. Bryde's whale



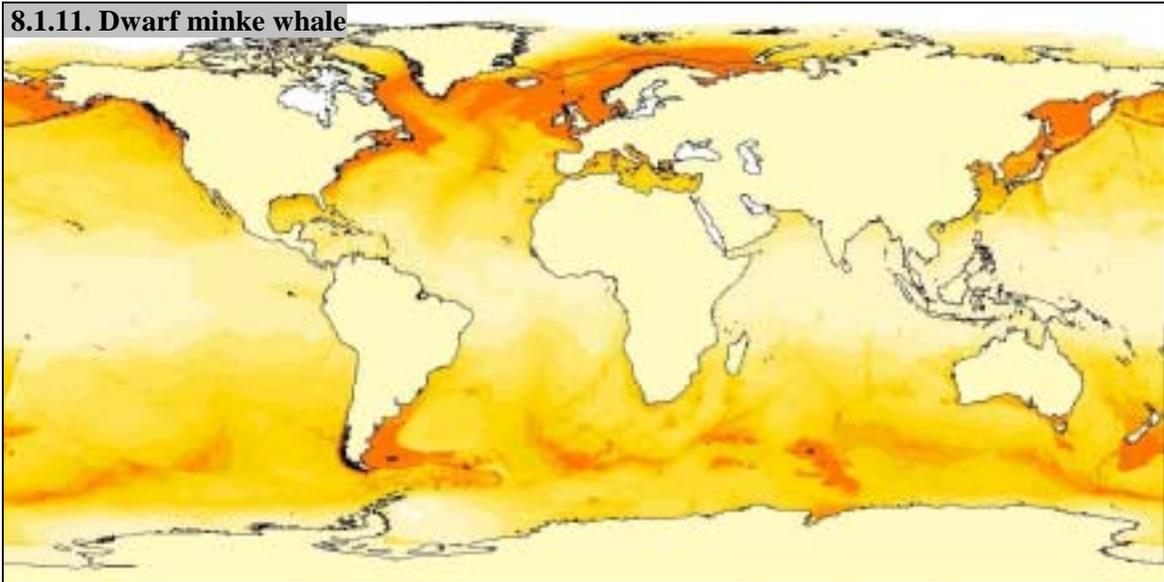
8.1.9. Fin whale



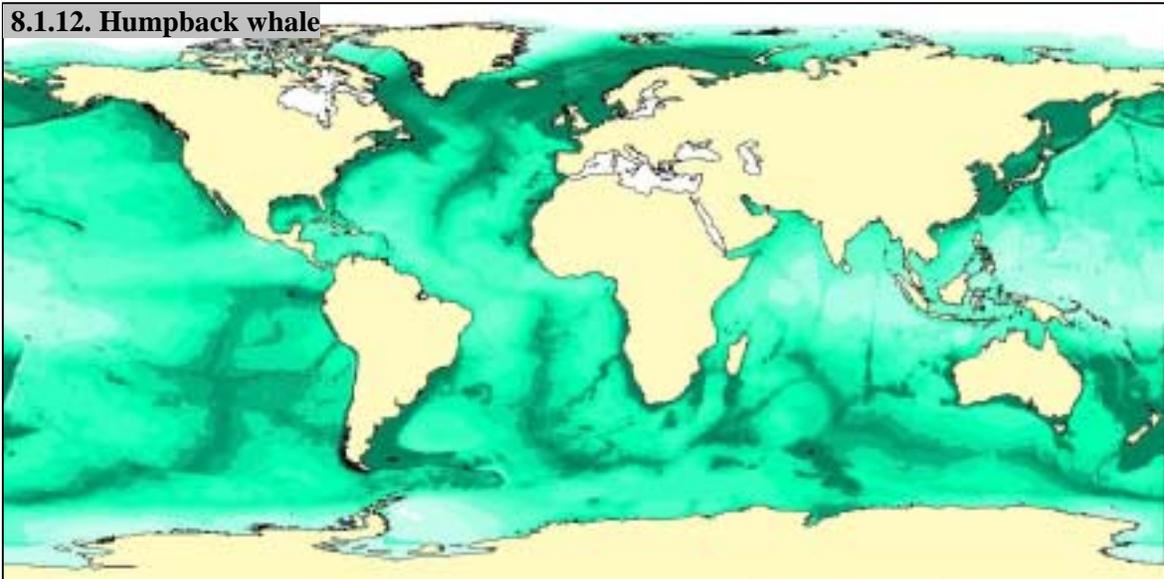
8.1.10. Antarctic minke whale



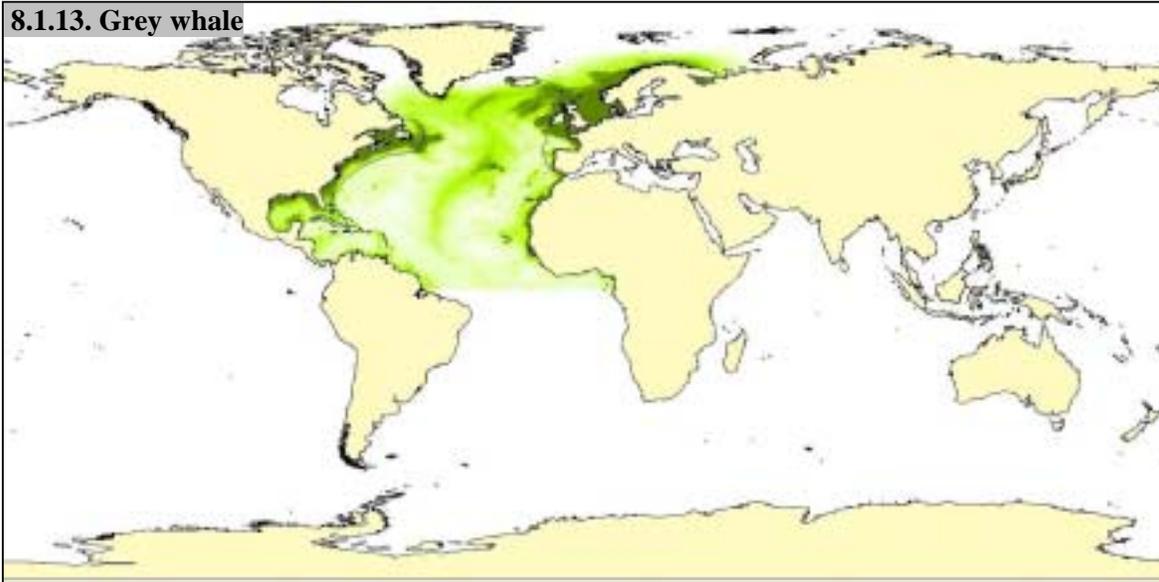
8.1.11. Dwarf minke whale



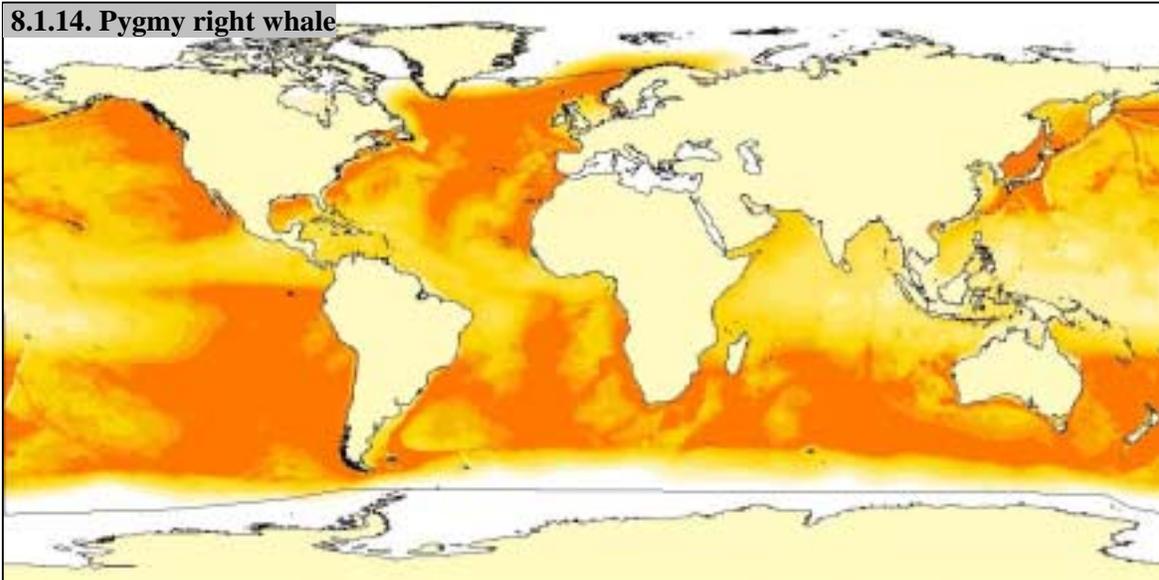
8.1.12. Humpback whale



8.1.13. Grey whale

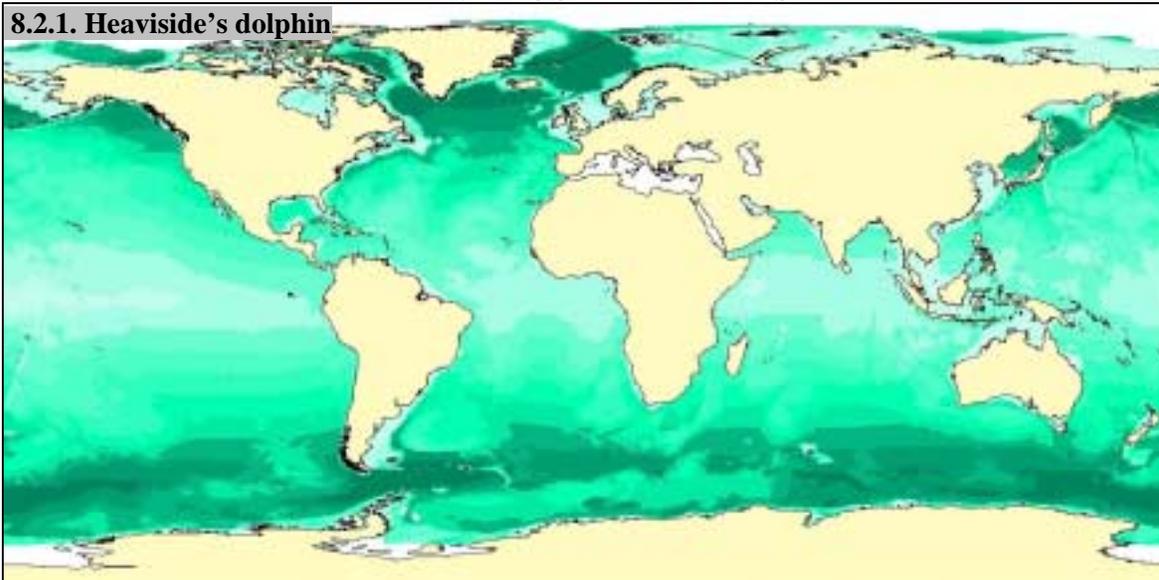


8.1.14. Pygmy right whale

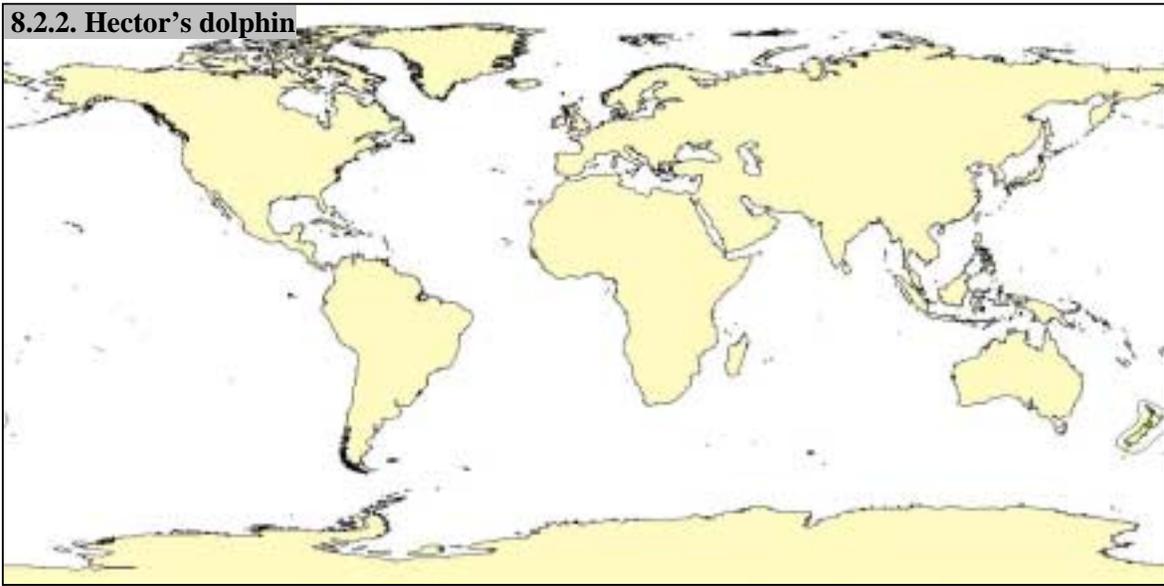


8.2. TOOTHED WHALES

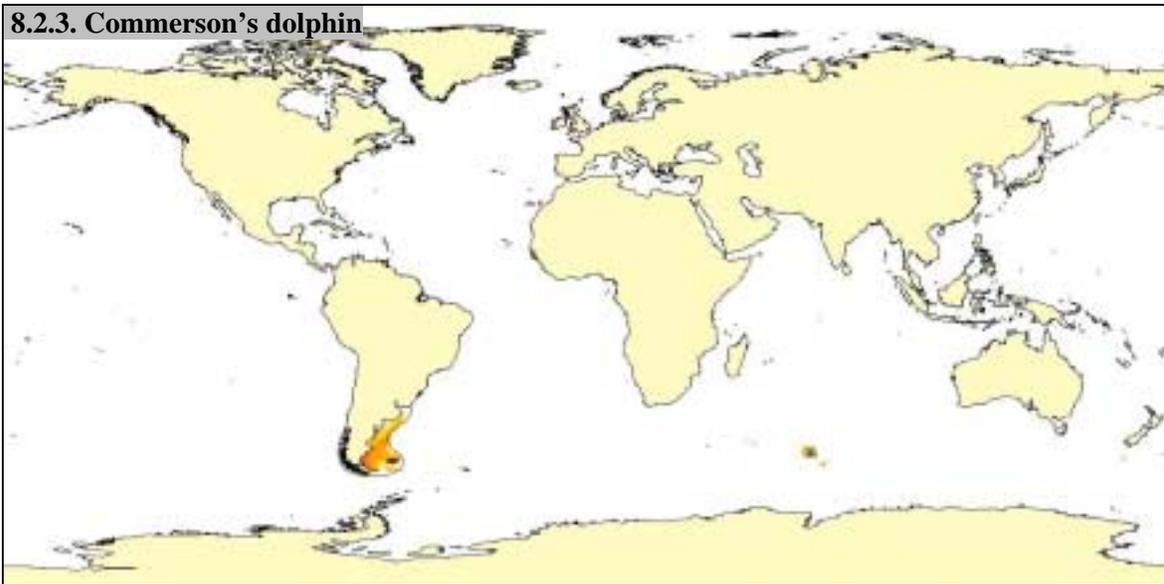
8.2.1. Heaviside's dolphin



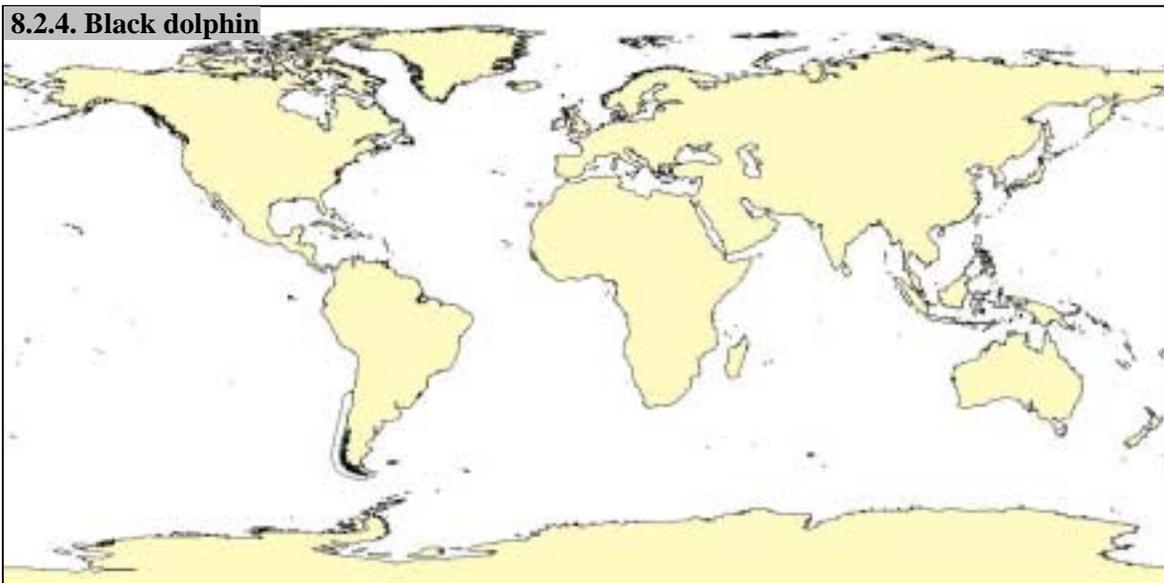
8.2.2. Hector's dolphin



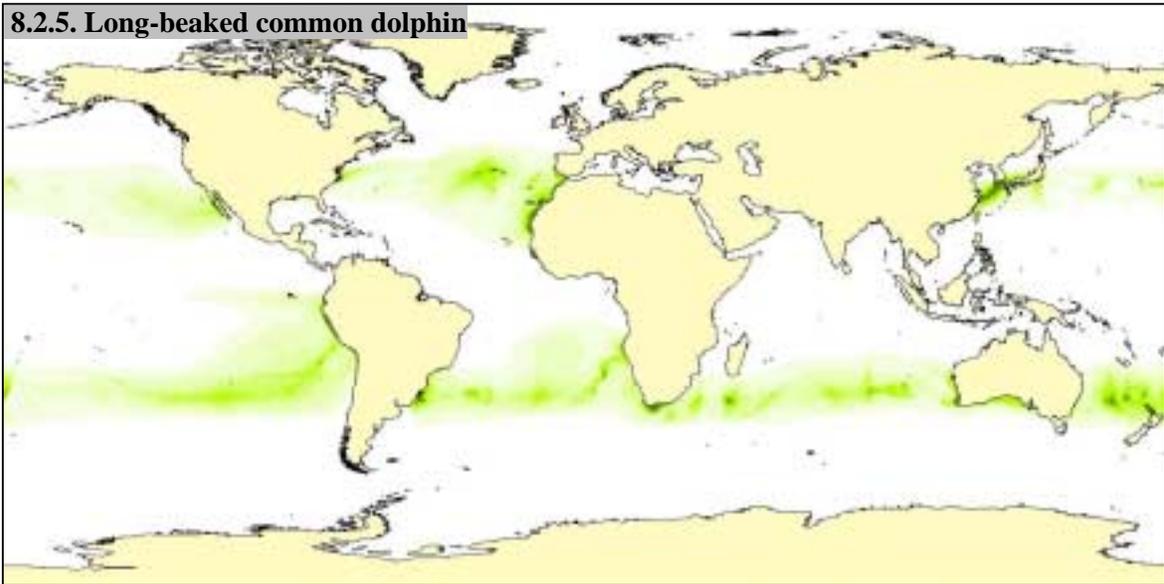
8.2.3. Commerson's dolphin



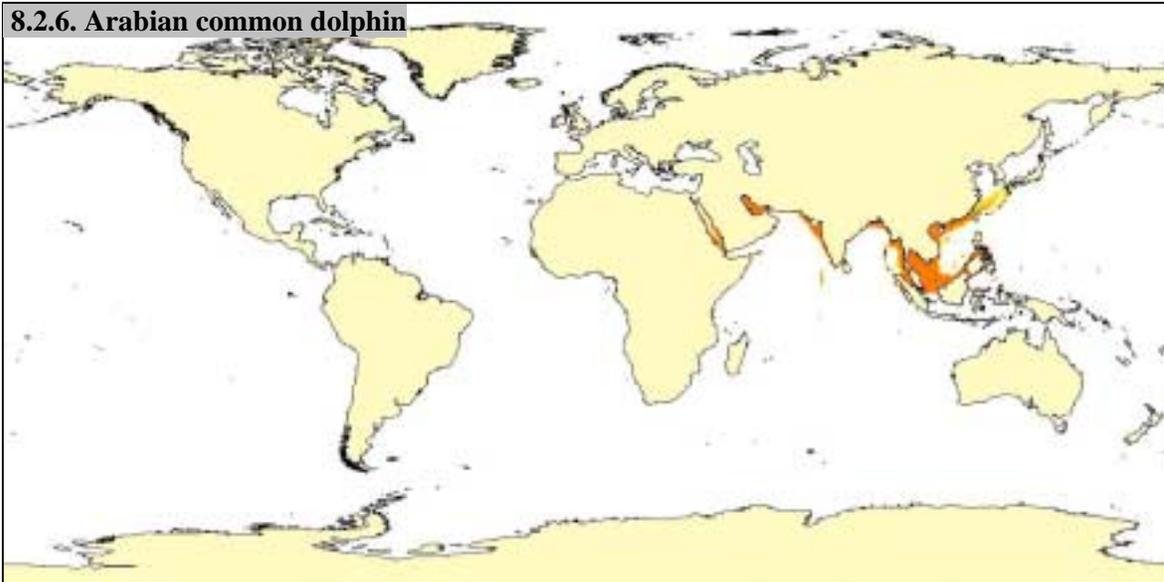
8.2.4. Black dolphin



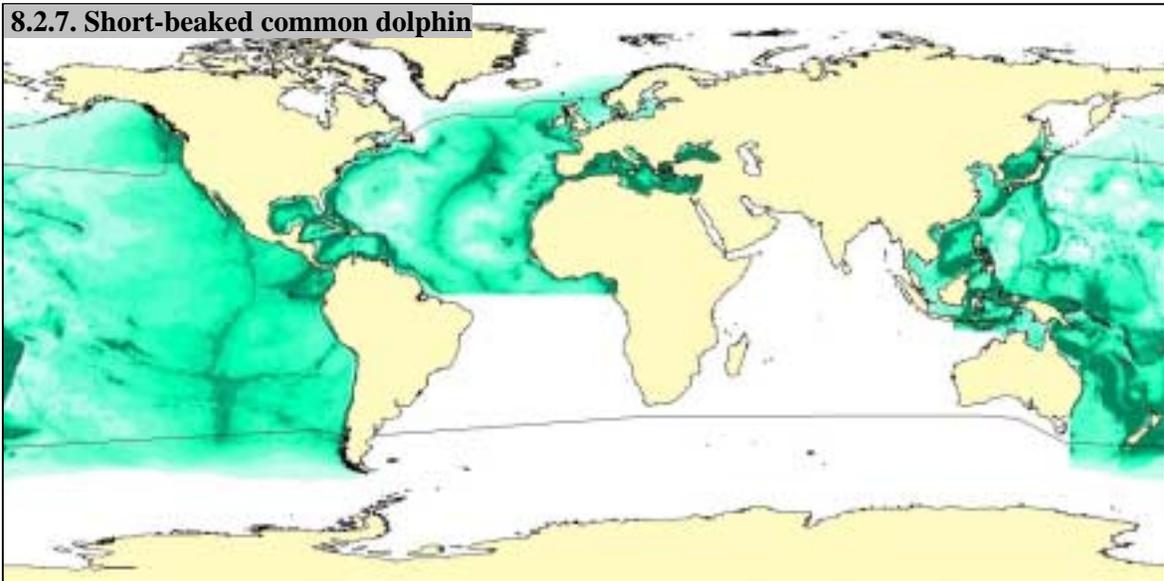
8.2.5. Long-beaked common dolphin



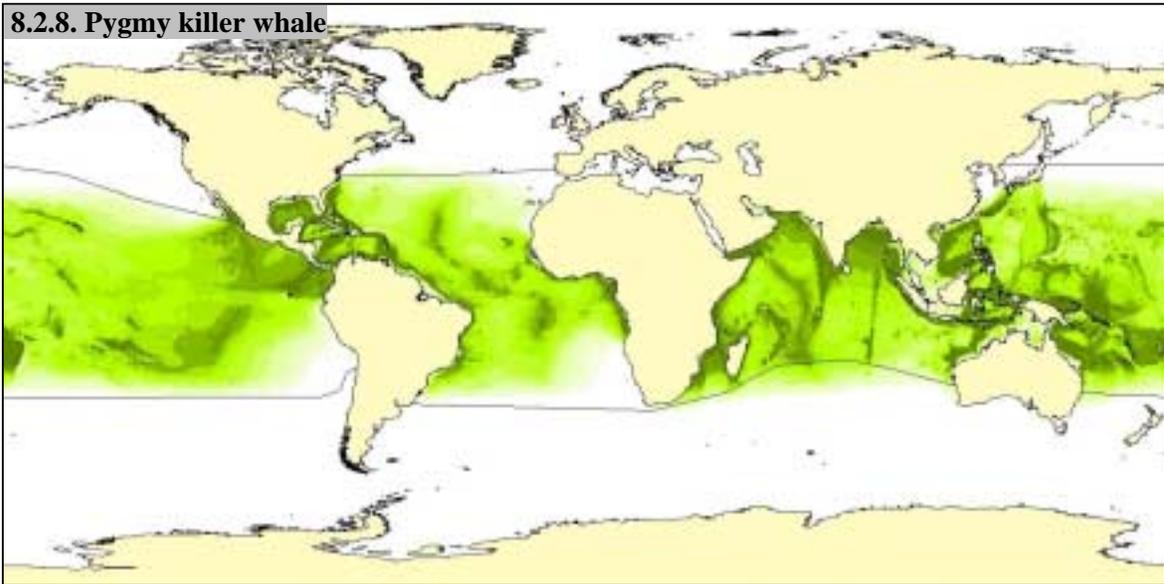
8.2.6. Arabian common dolphin



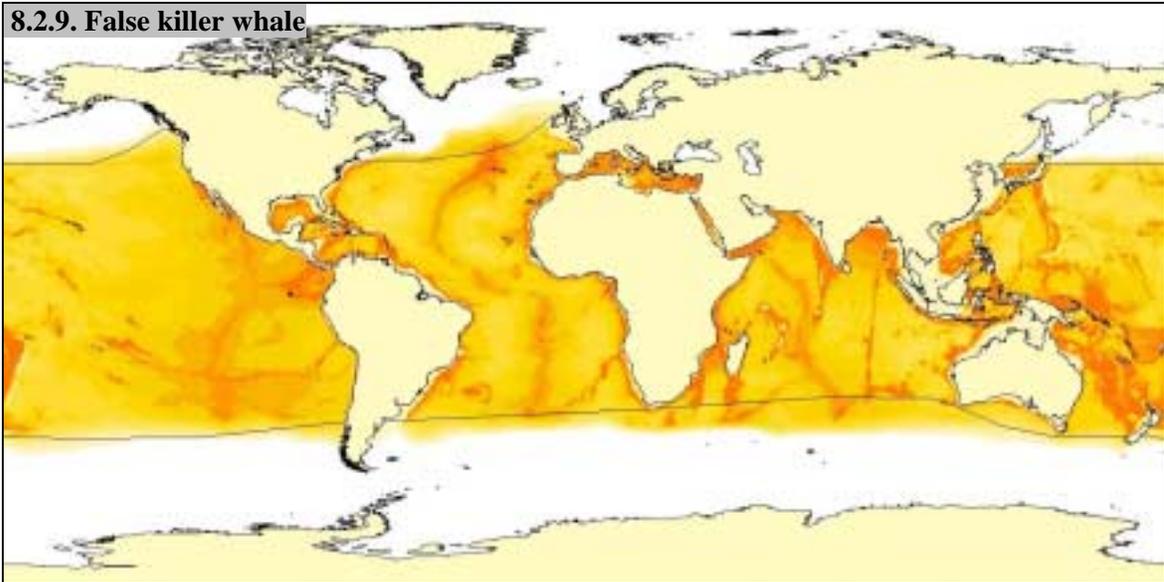
8.2.7. Short-beaked common dolphin



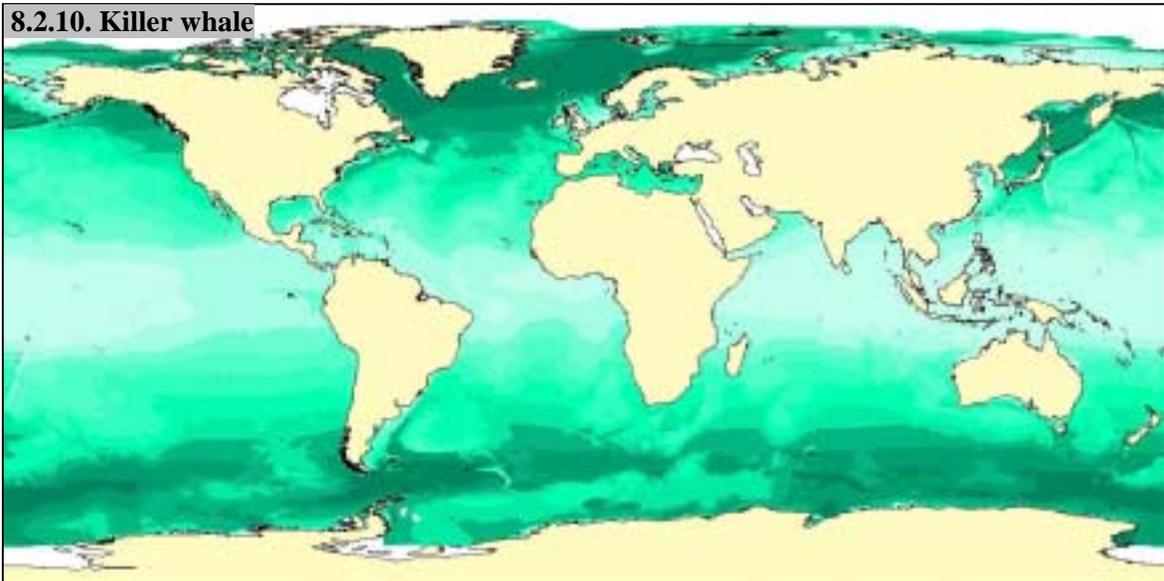
8.2.8. Pygmy killer whale



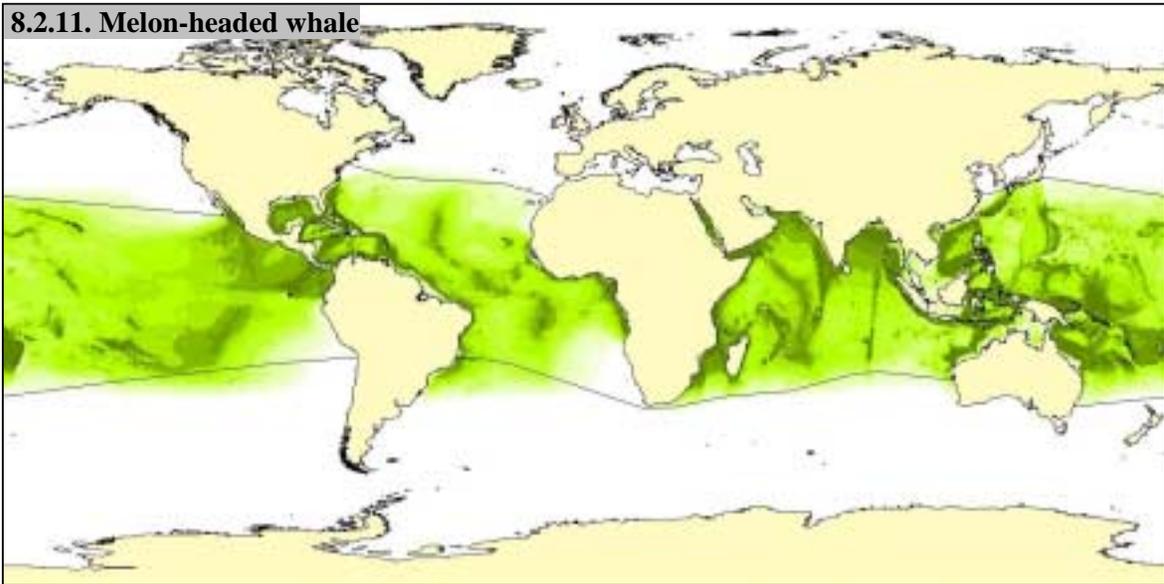
8.2.9. False killer whale



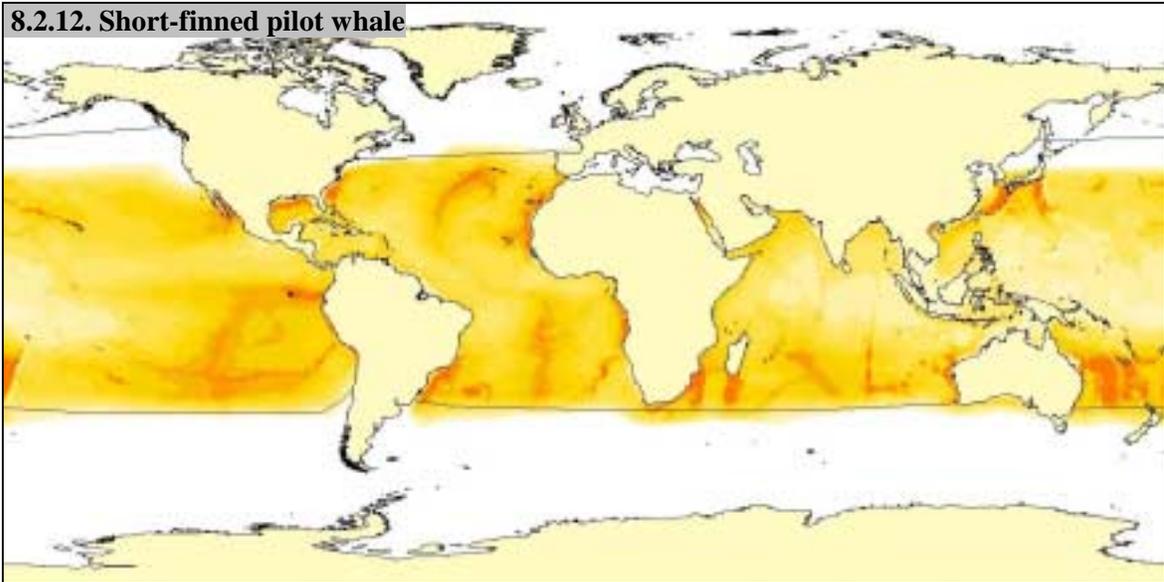
8.2.10. Killer whale



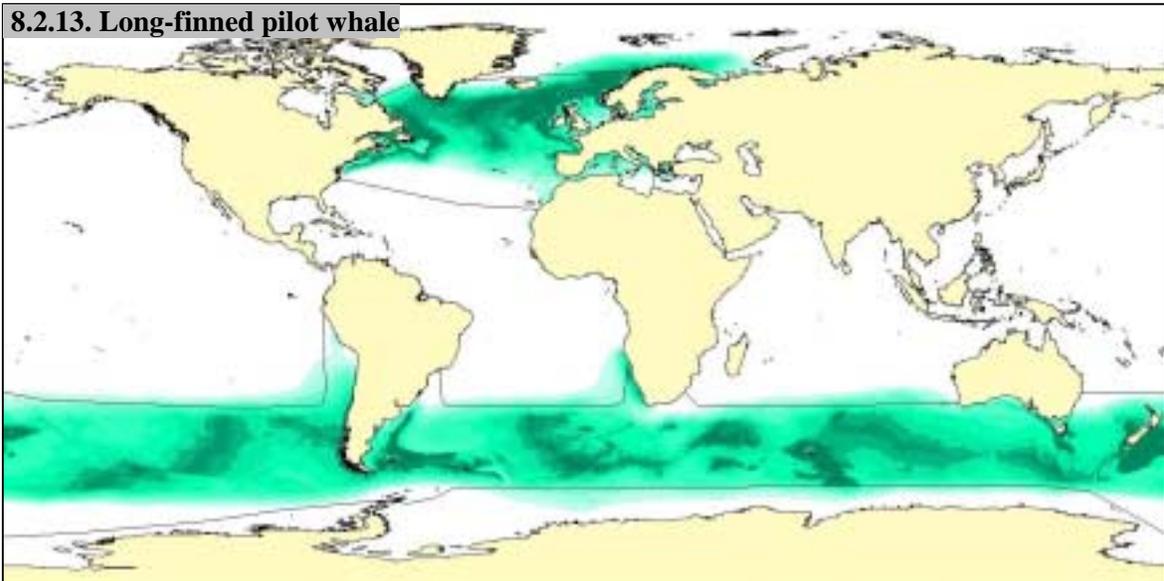
8.2.11. Melon-headed whale



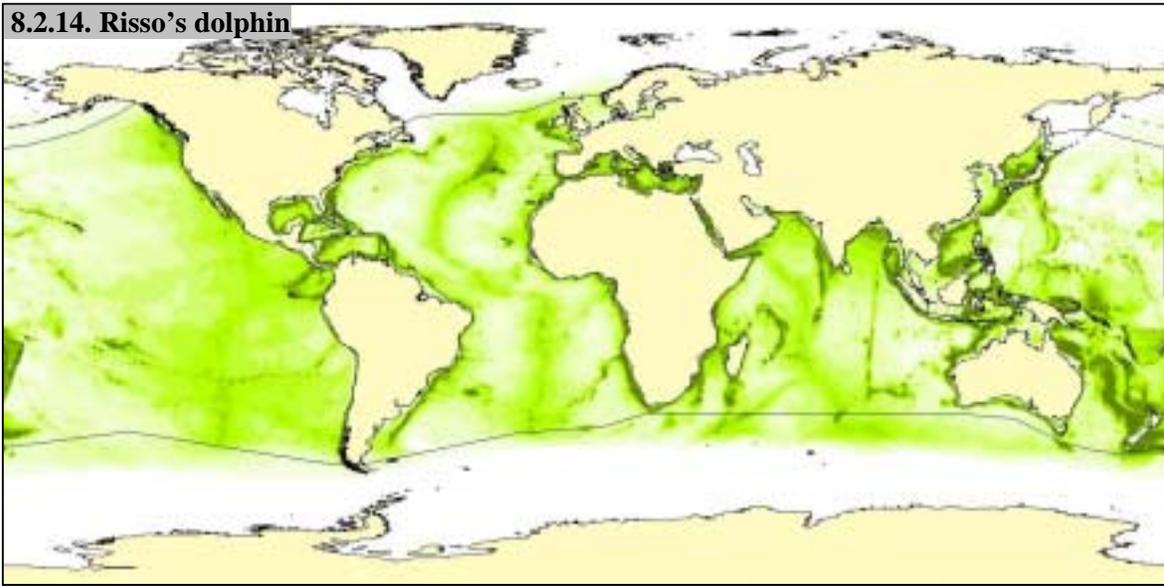
8.2.12. Short-finned pilot whale



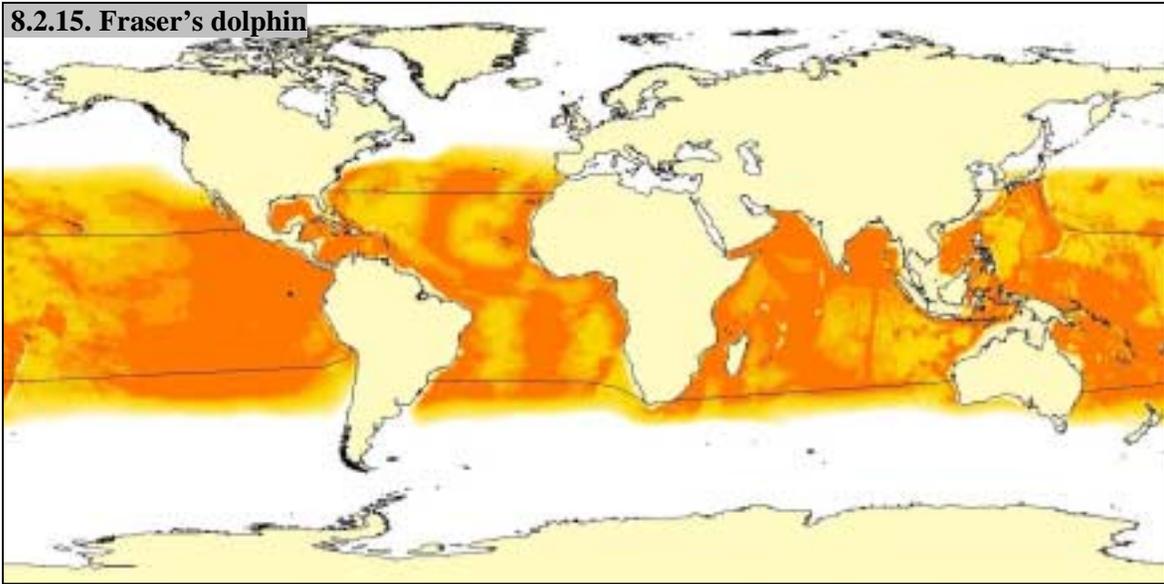
8.2.13. Long-finned pilot whale



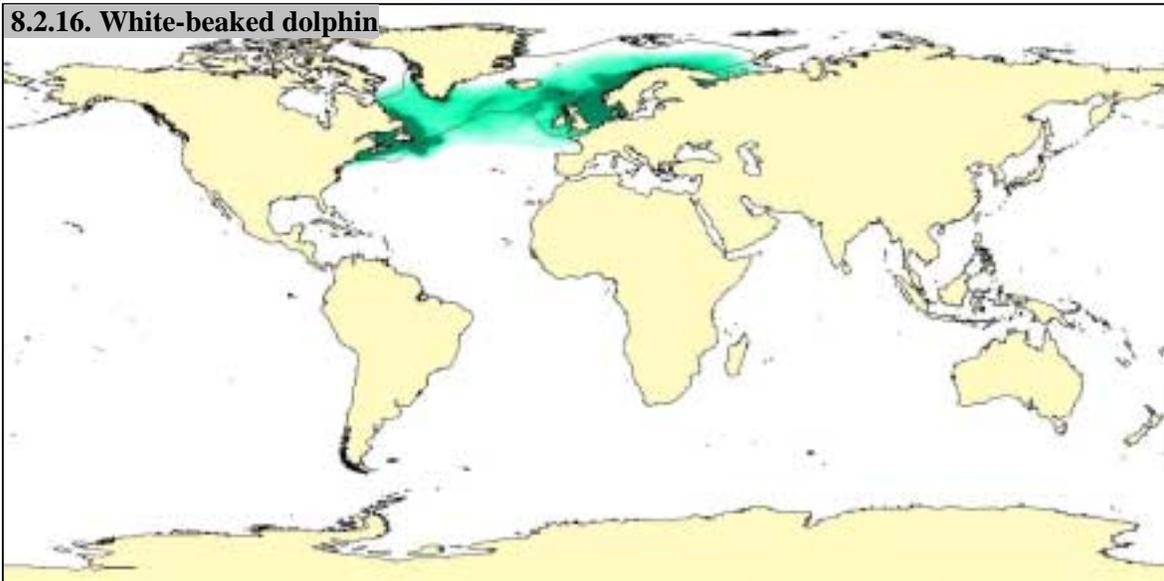
8.2.14. Risso's dolphin



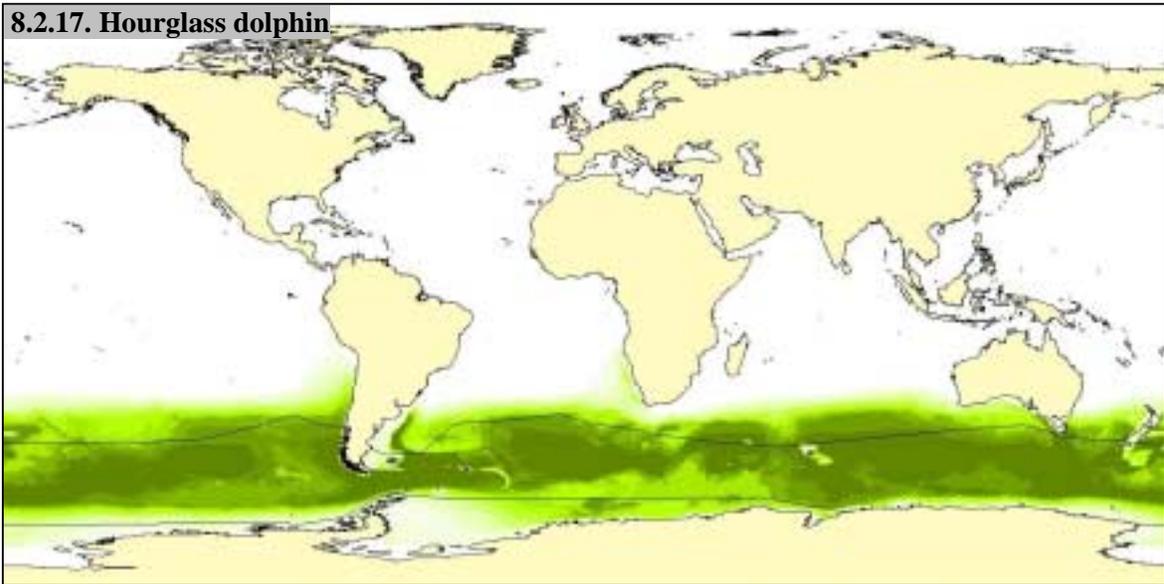
8.2.15. Fraser's dolphin



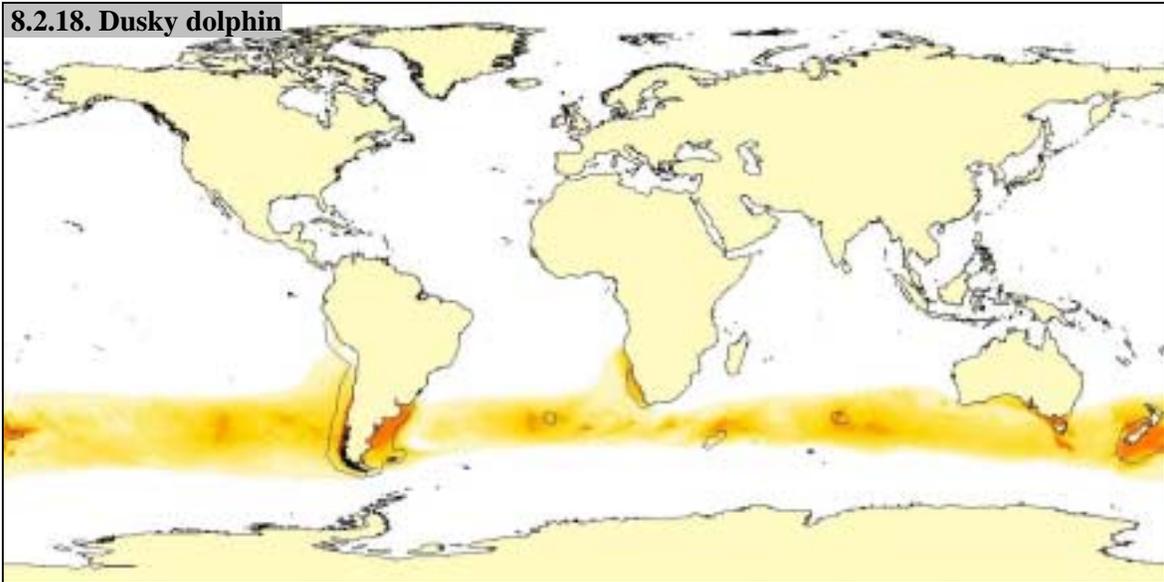
8.2.16. White-beaked dolphin



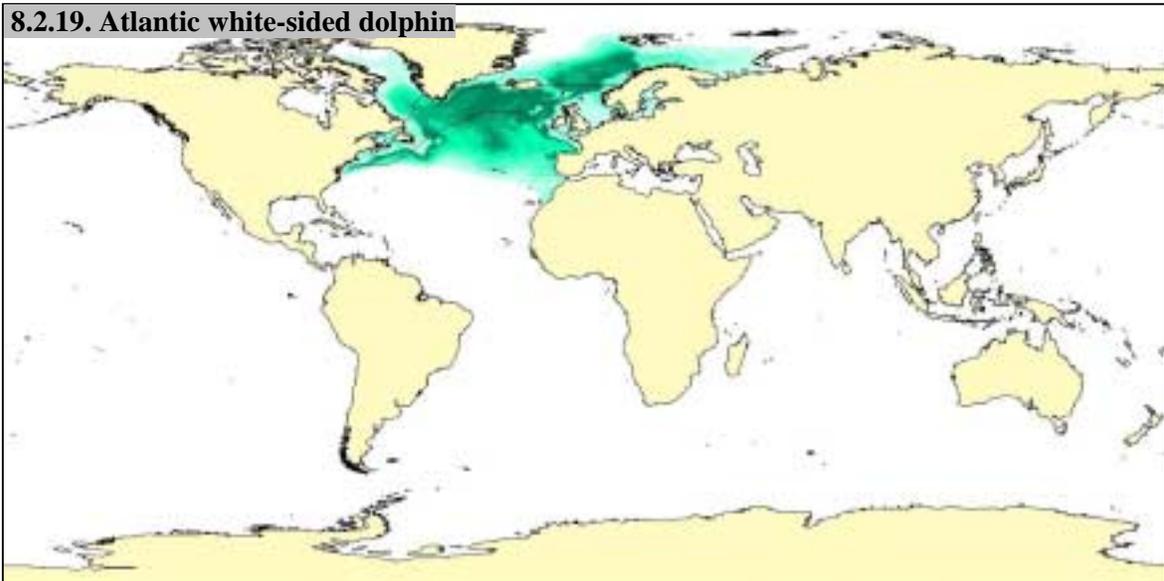
8.2.17. Hourglass dolphin



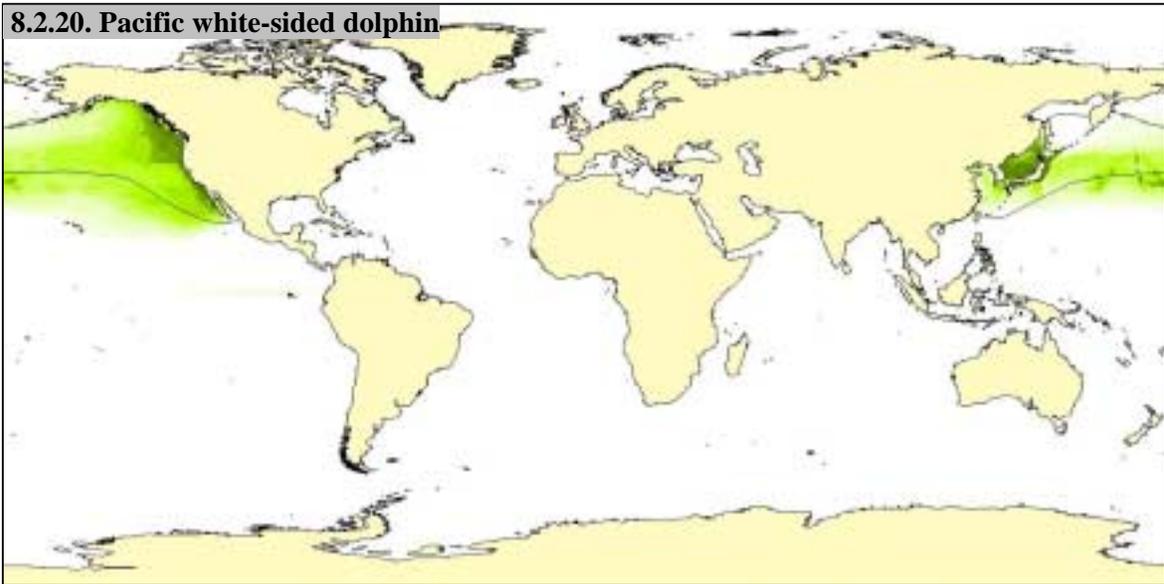
8.2.18. Dusky dolphin



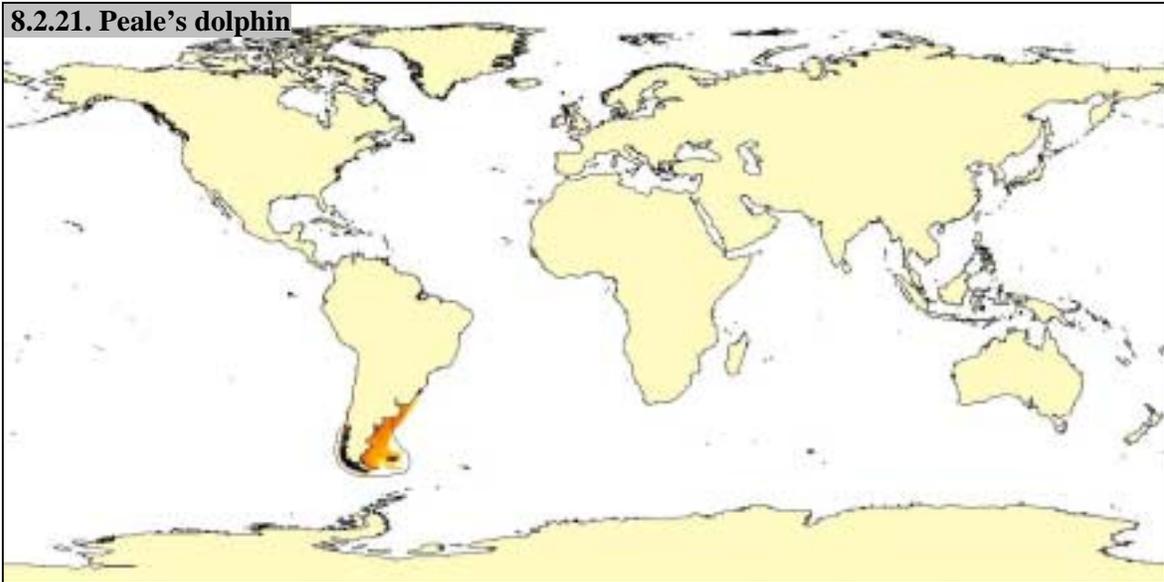
8.2.19. Atlantic white-sided dolphin



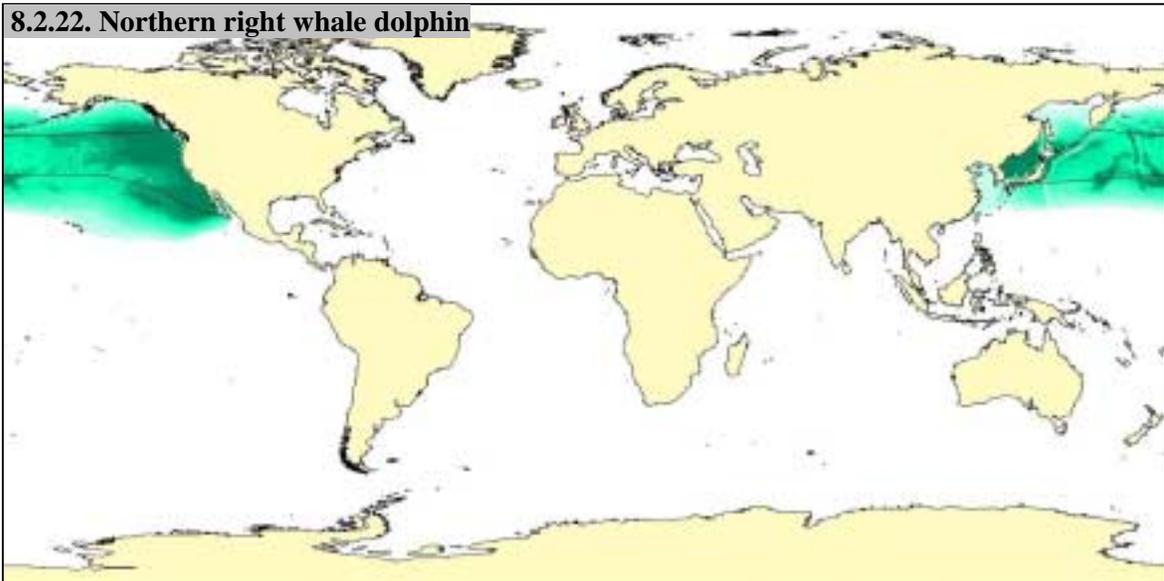
8.2.20. Pacific white-sided dolphin



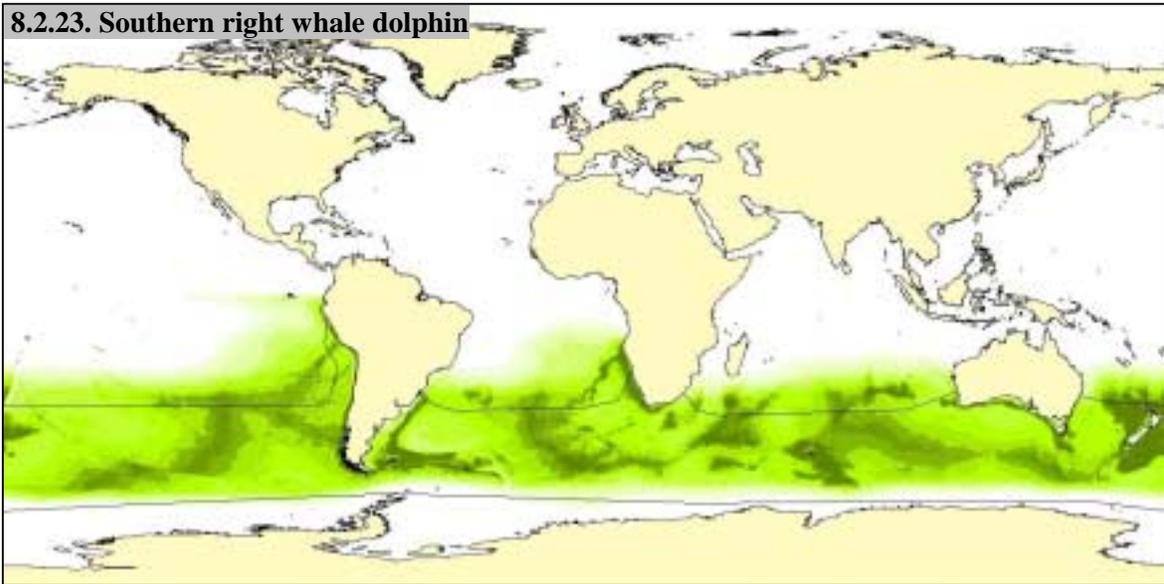
8.2.21. Peale's dolphin



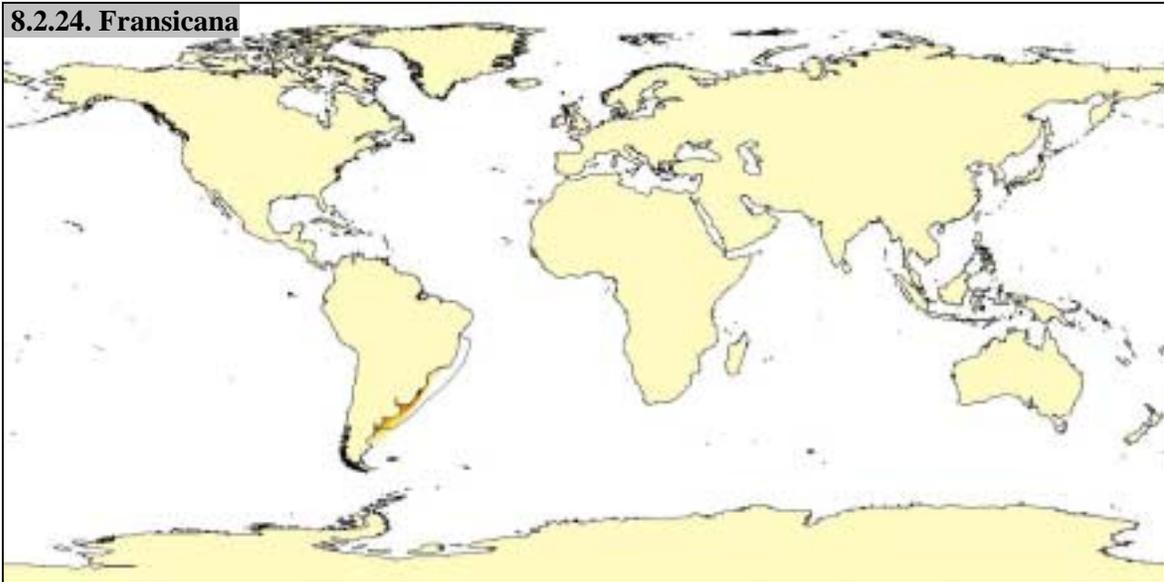
8.2.22. Northern right whale dolphin



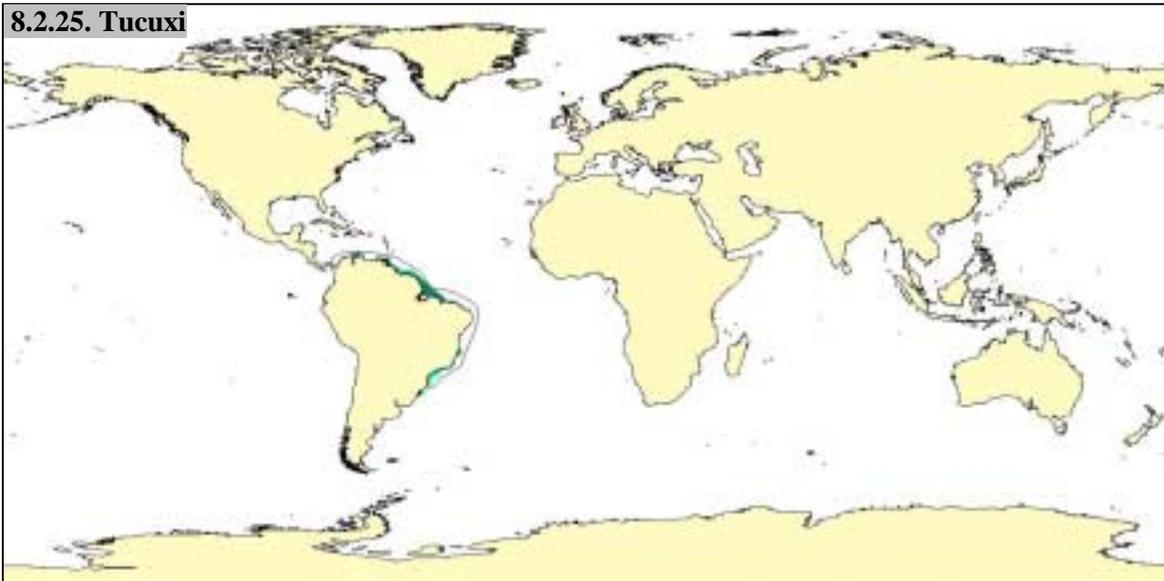
8.2.23. Southern right whale dolphin



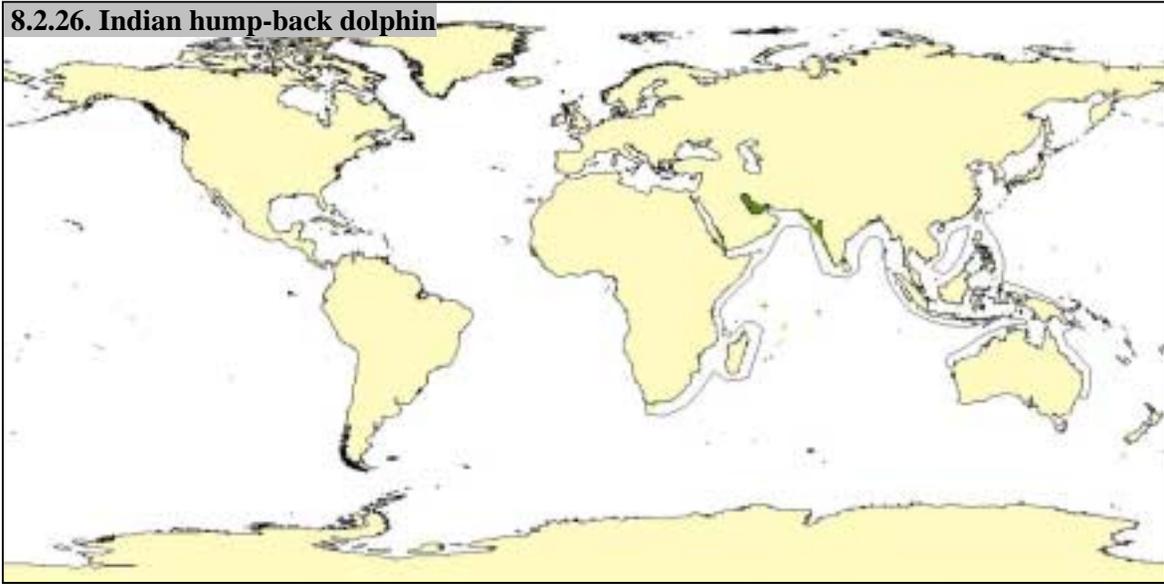
8.2.24. Fransicana



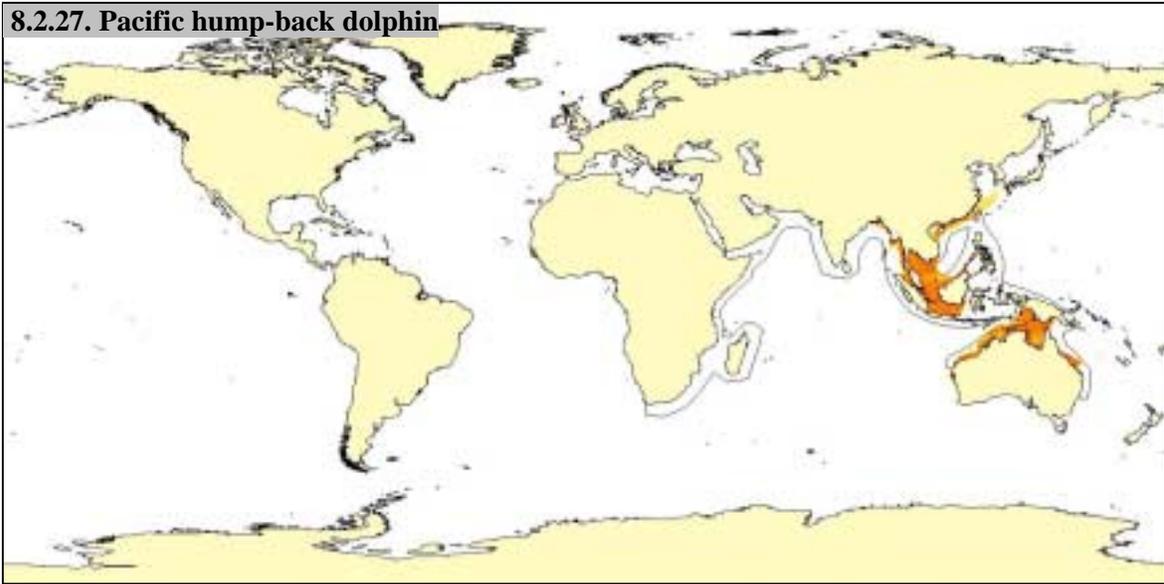
8.2.25. Tucuxi



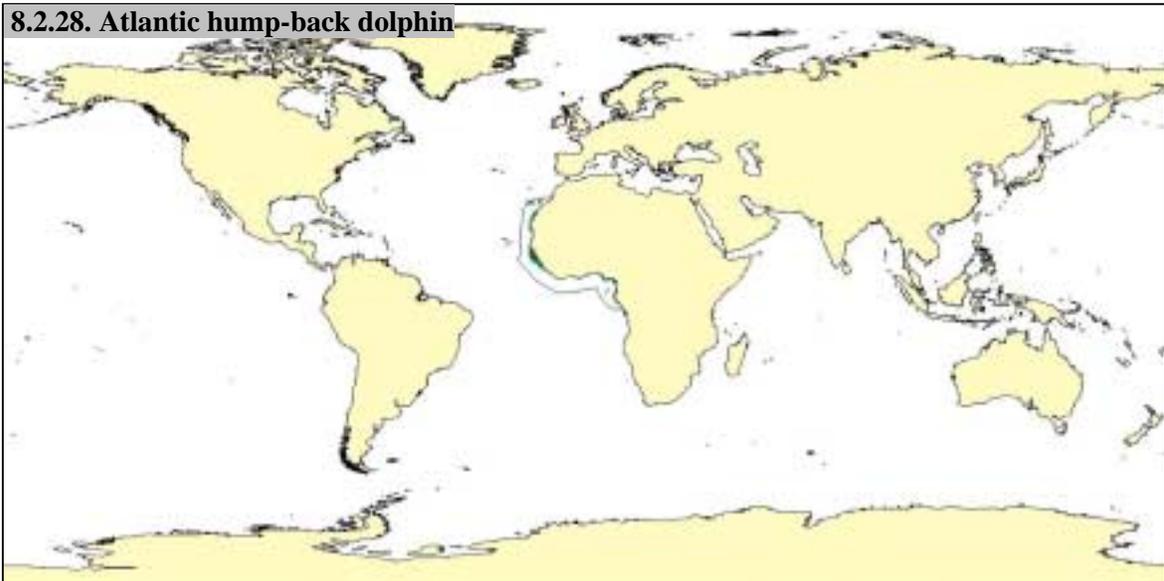
8.2.26. Indian hump-back dolphin



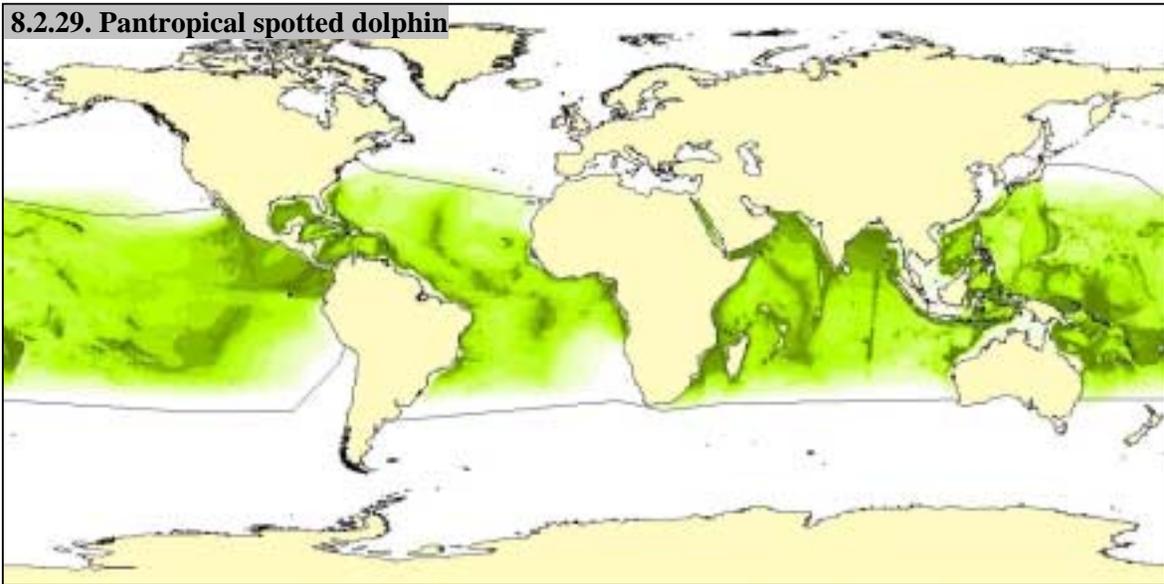
8.2.27. Pacific hump-back dolphin



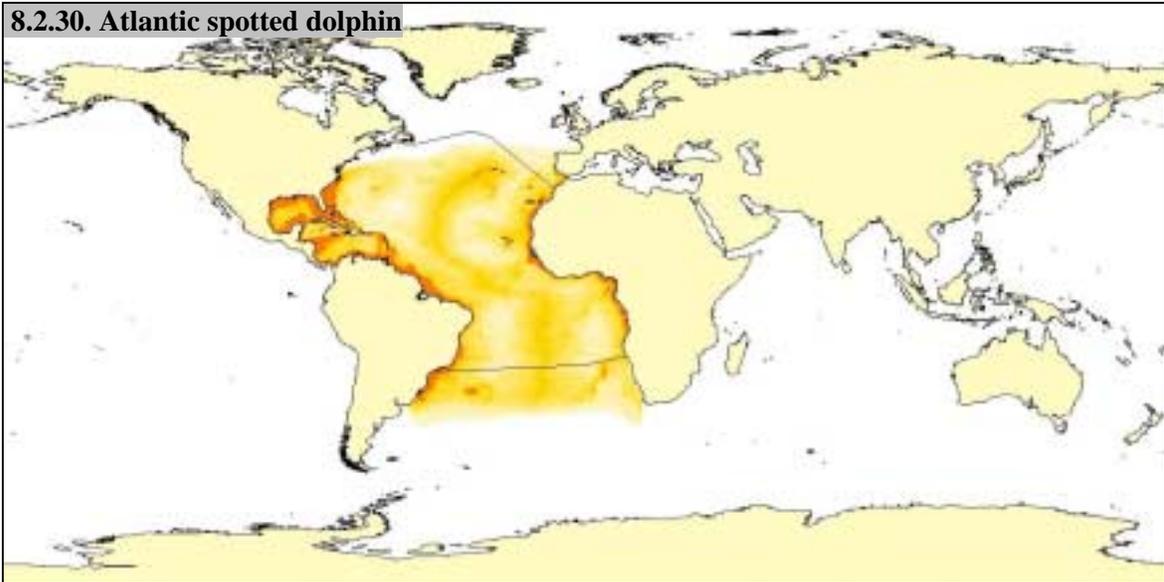
8.2.28. Atlantic hump-back dolphin



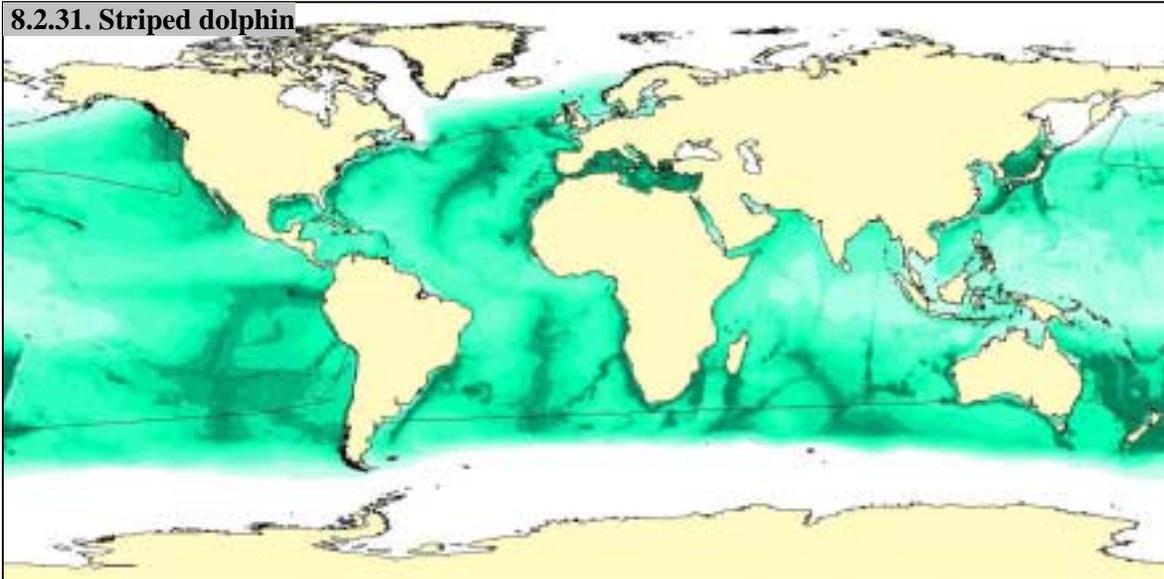
8.2.29. Pantropical spotted dolphin



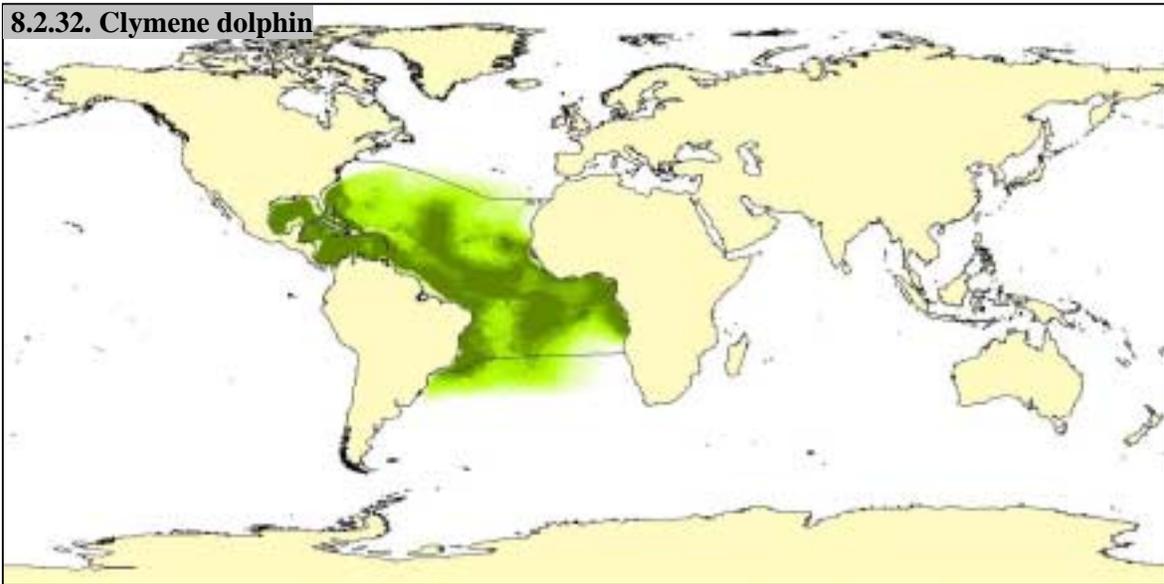
8.2.30. Atlantic spotted dolphin



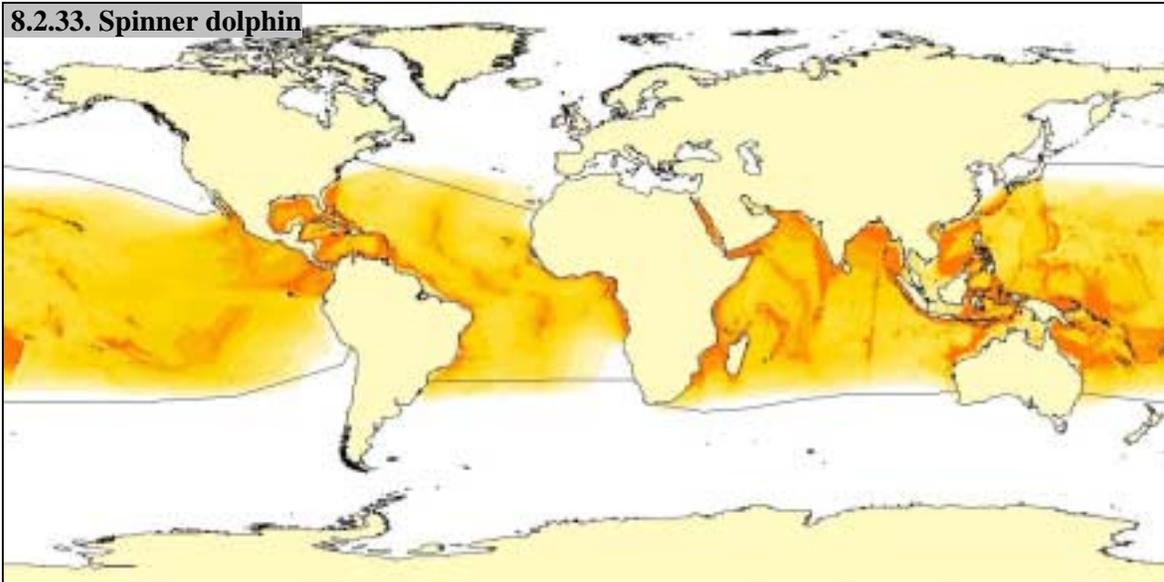
8.2.31. Striped dolphin



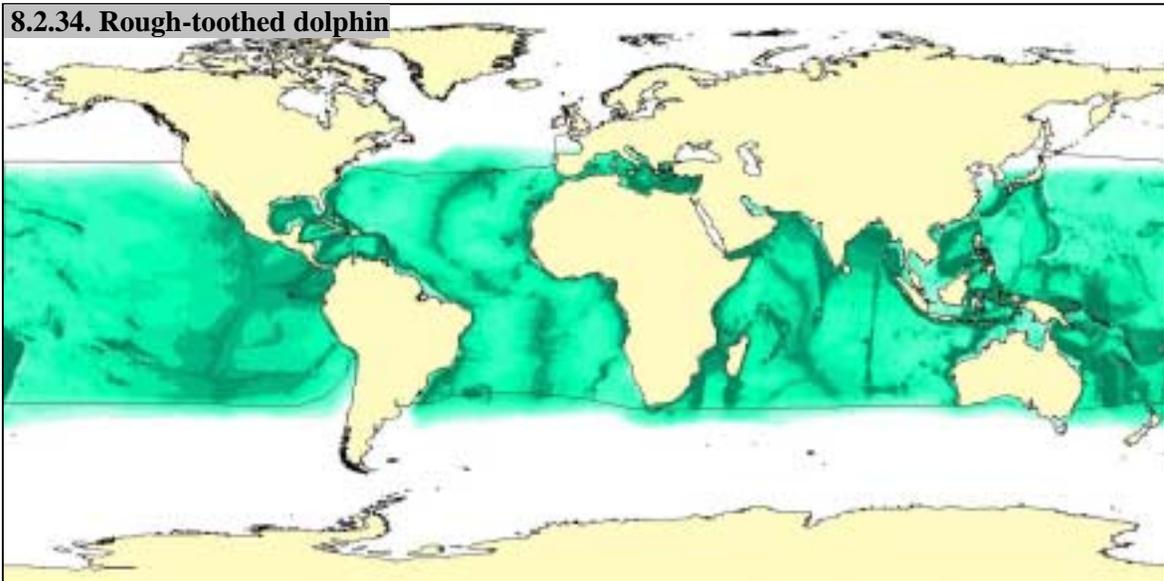
8.2.32. Clymene dolphin



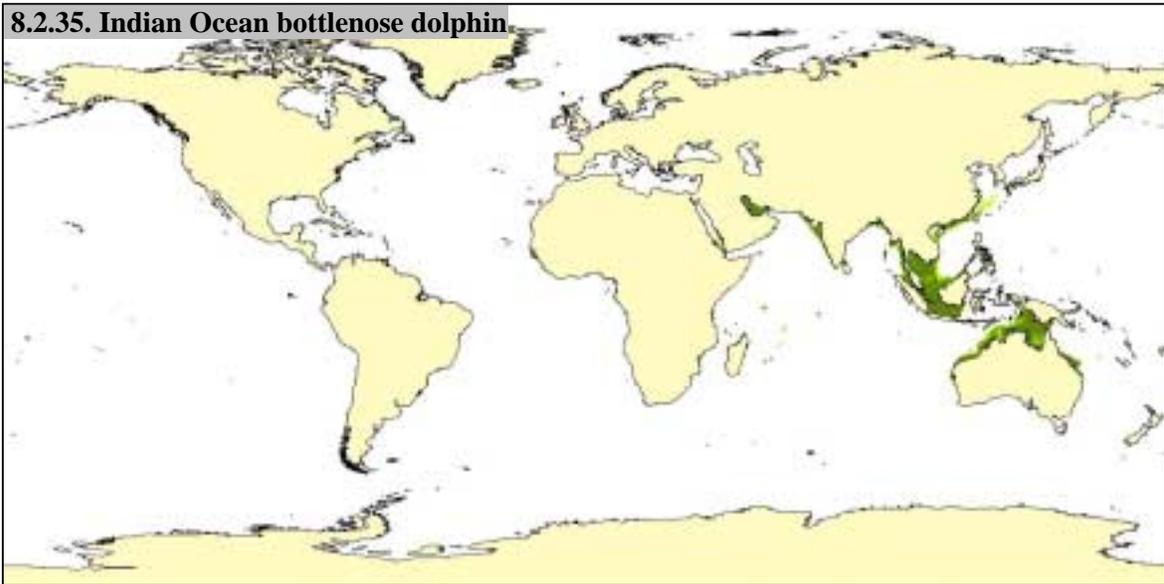
8.2.33. Spinner dolphin



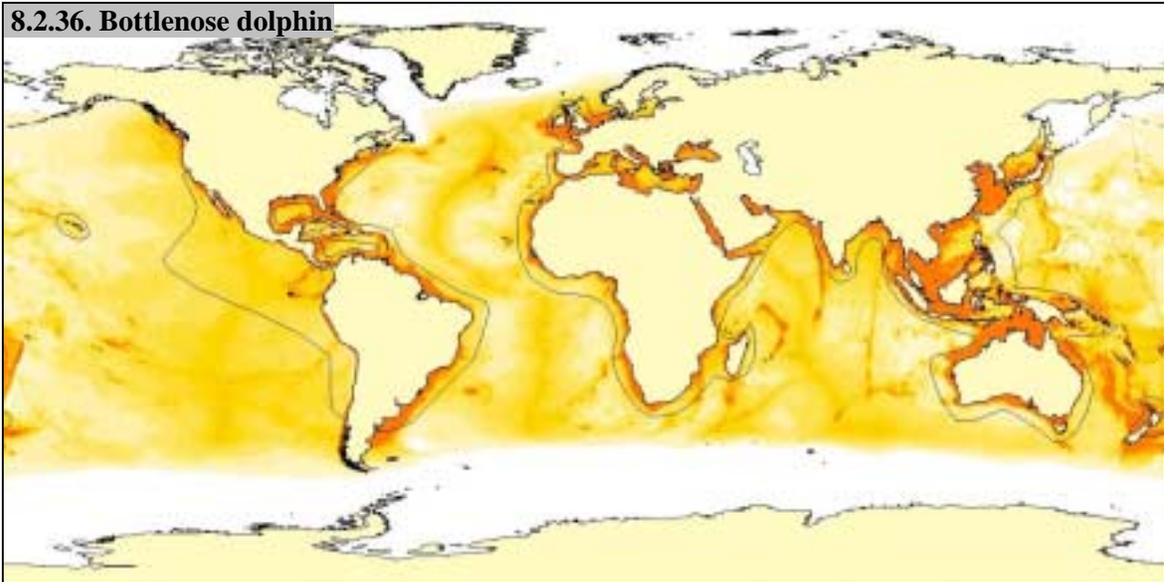
8.2.34. Rough-toothed dolphin



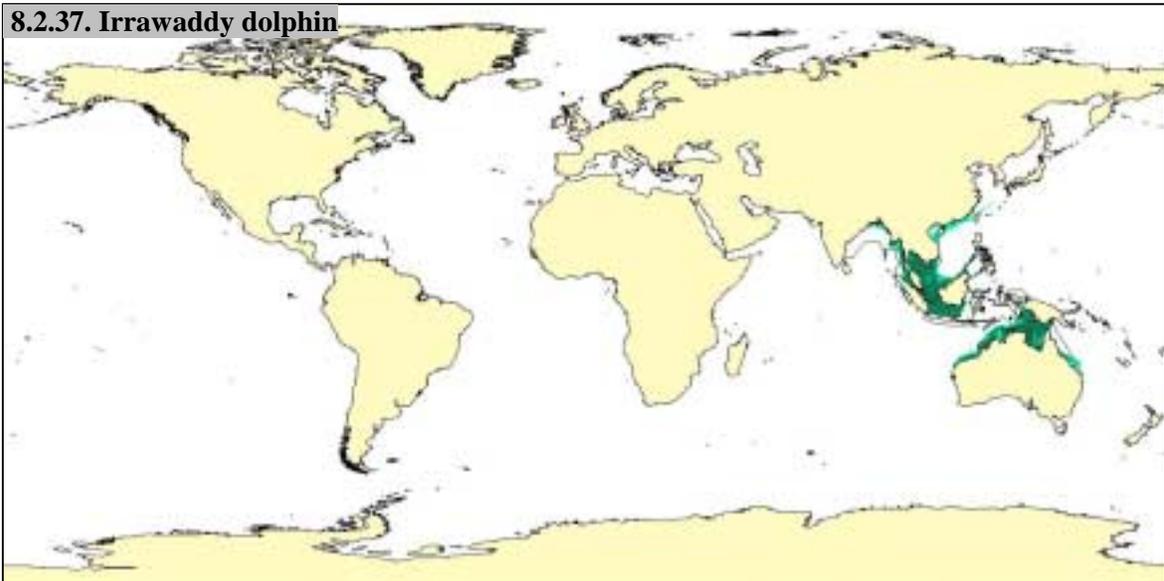
8.2.35. Indian Ocean bottlenose dolphin



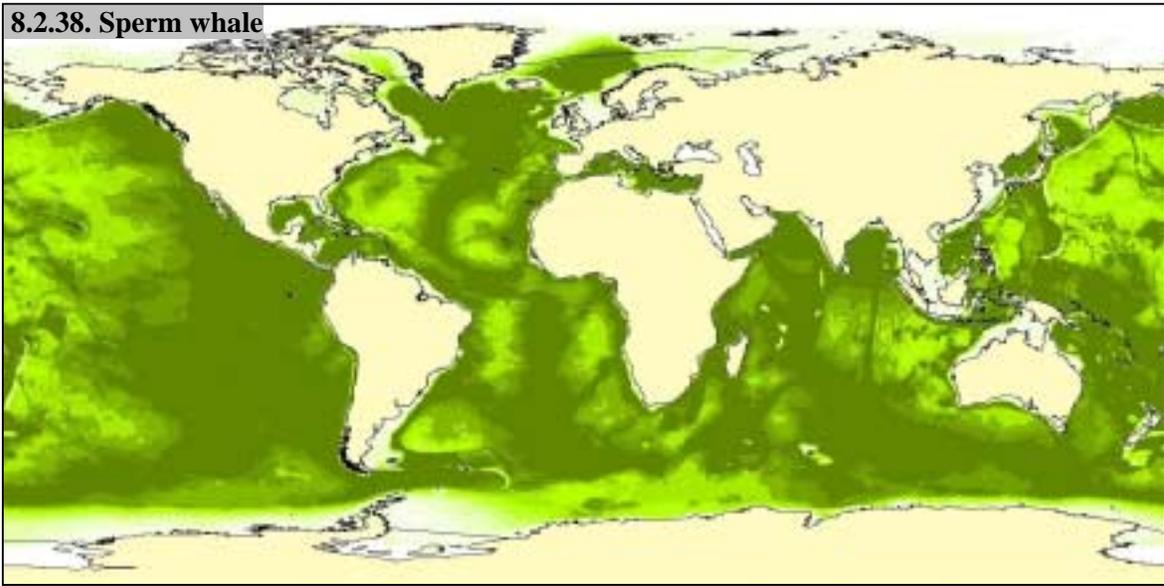
8.2.36. Bottlenose dolphin



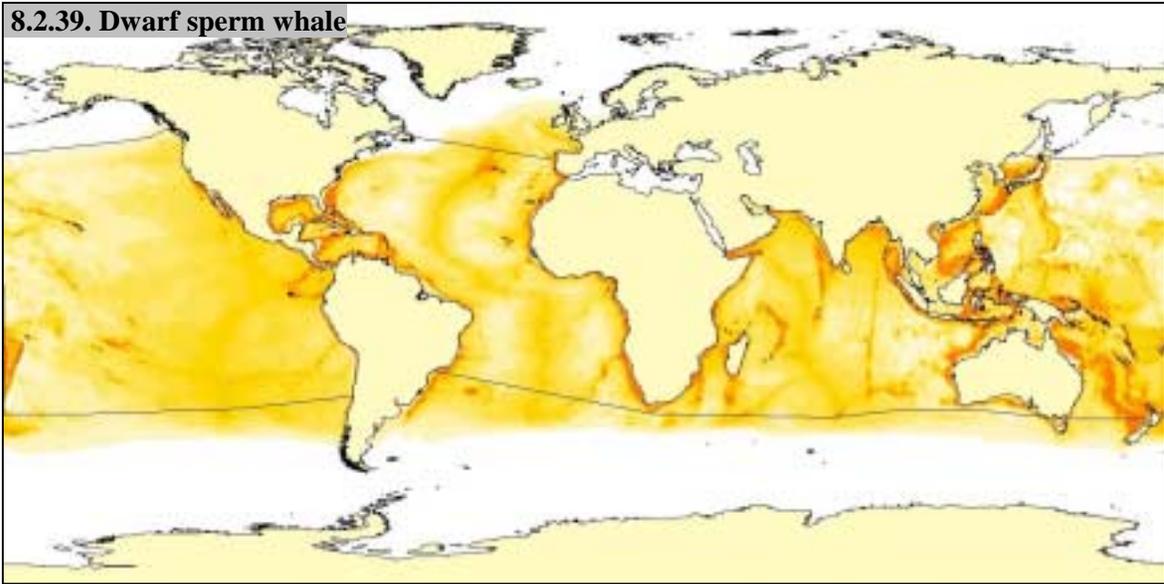
8.2.37. Irrawaddy dolphin



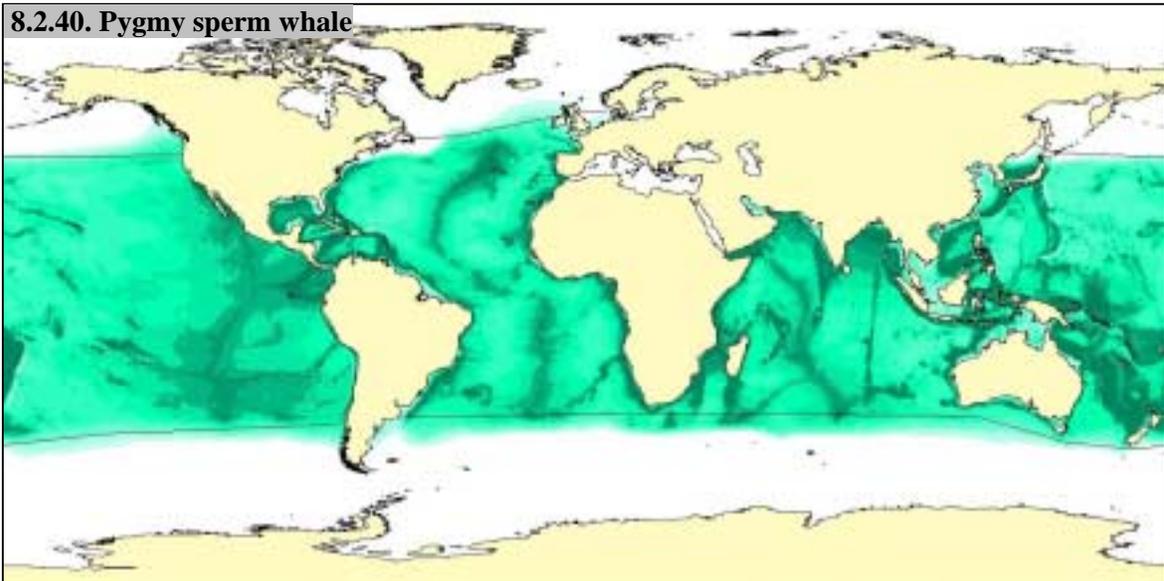
8.2.38. Sperm whale



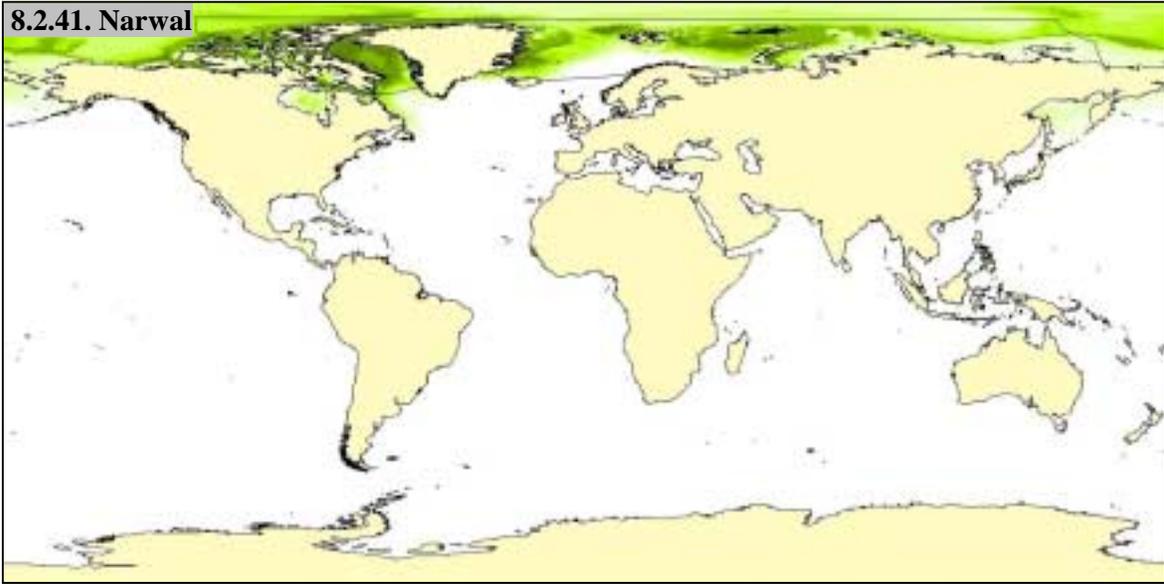
8.2.39. Dwarf sperm whale



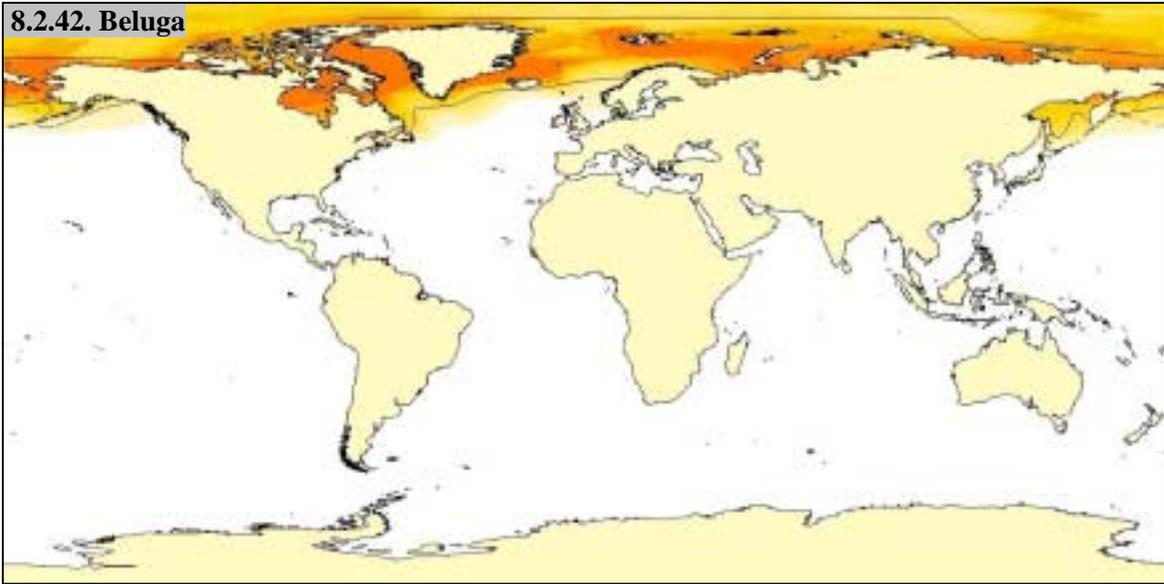
8.2.40. Pygmy sperm whale



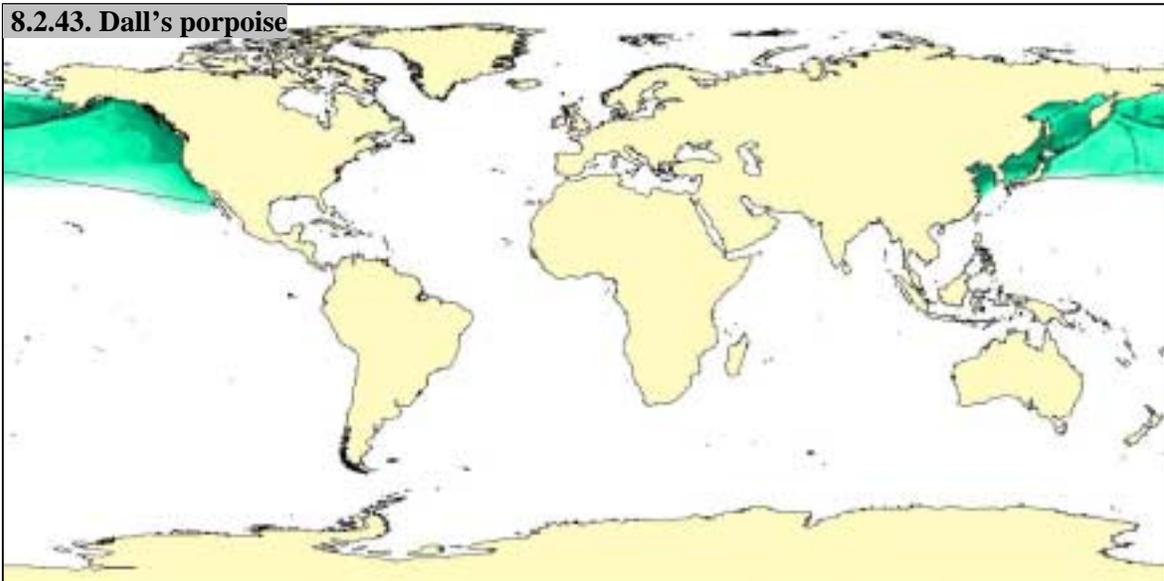
8.2.41. Narwal



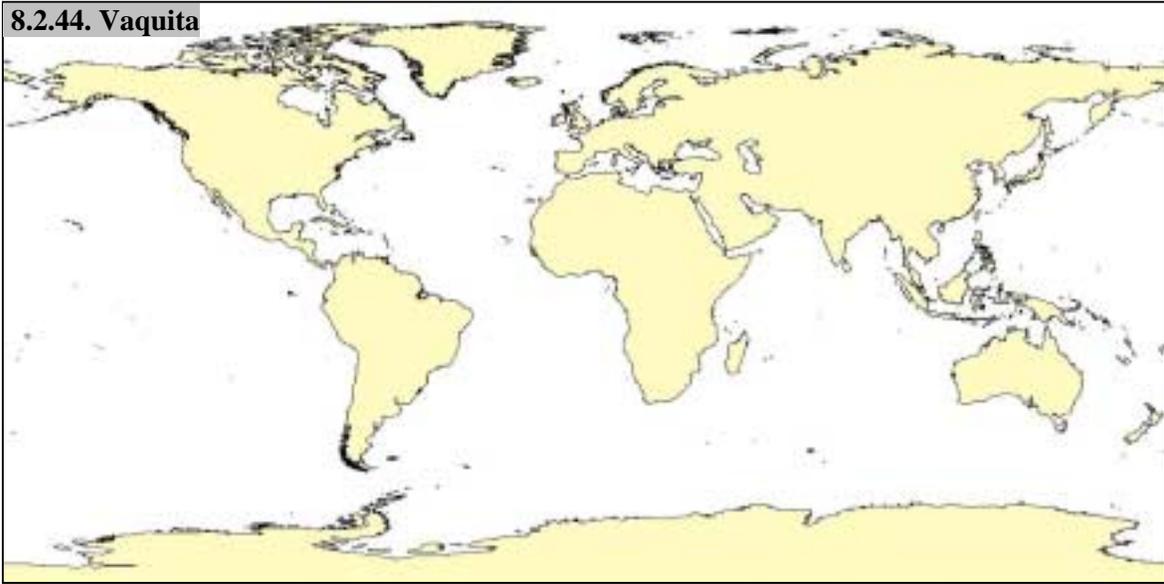
8.2.42. Beluga



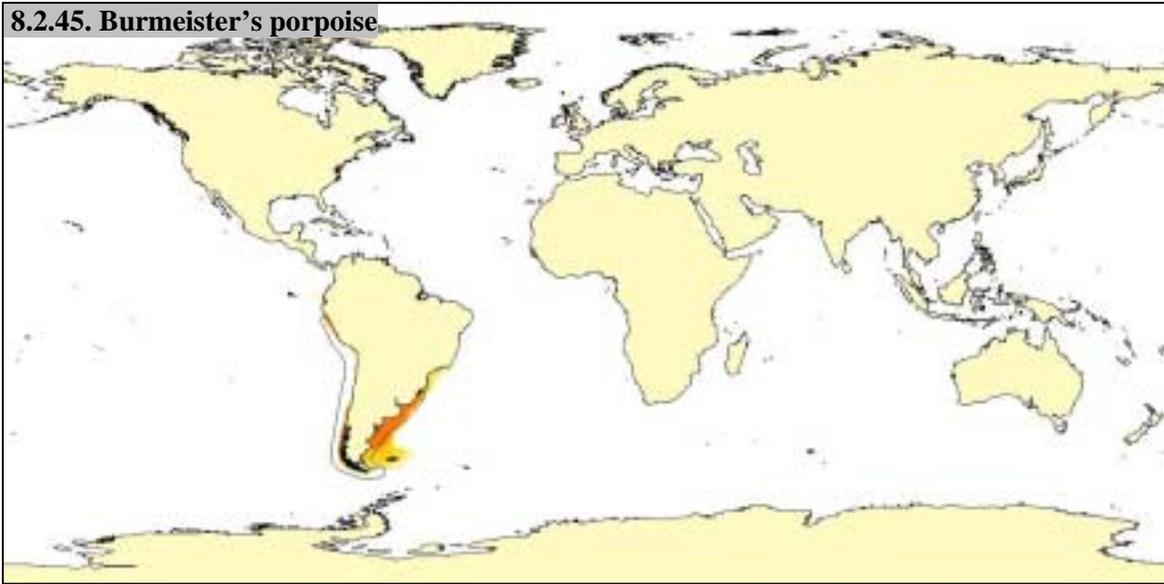
8.2.43. Dall's porpoise



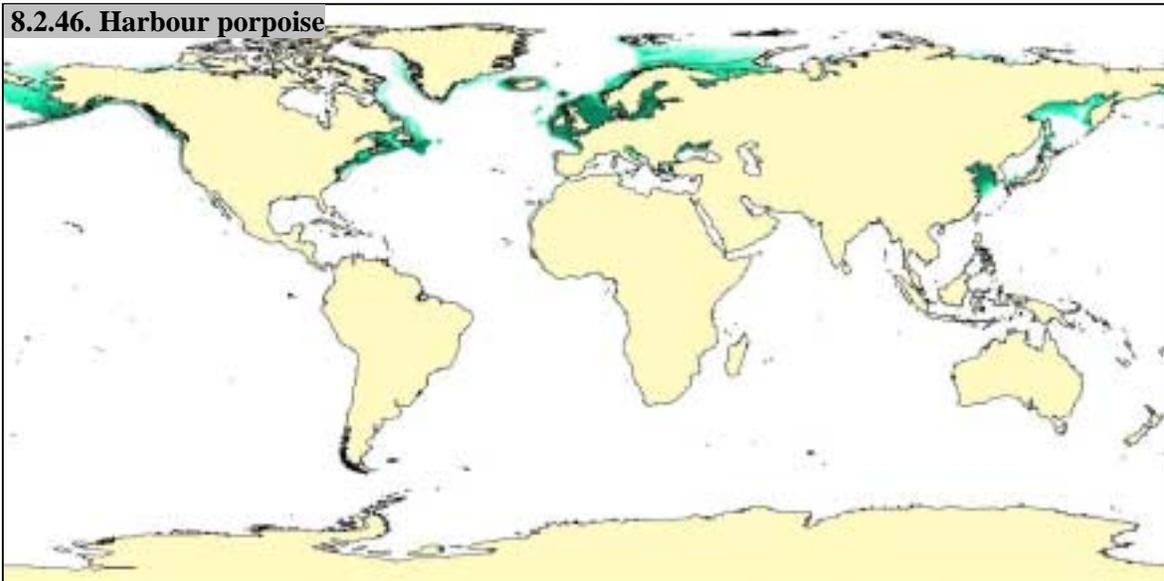
8.2.44. Vaquita



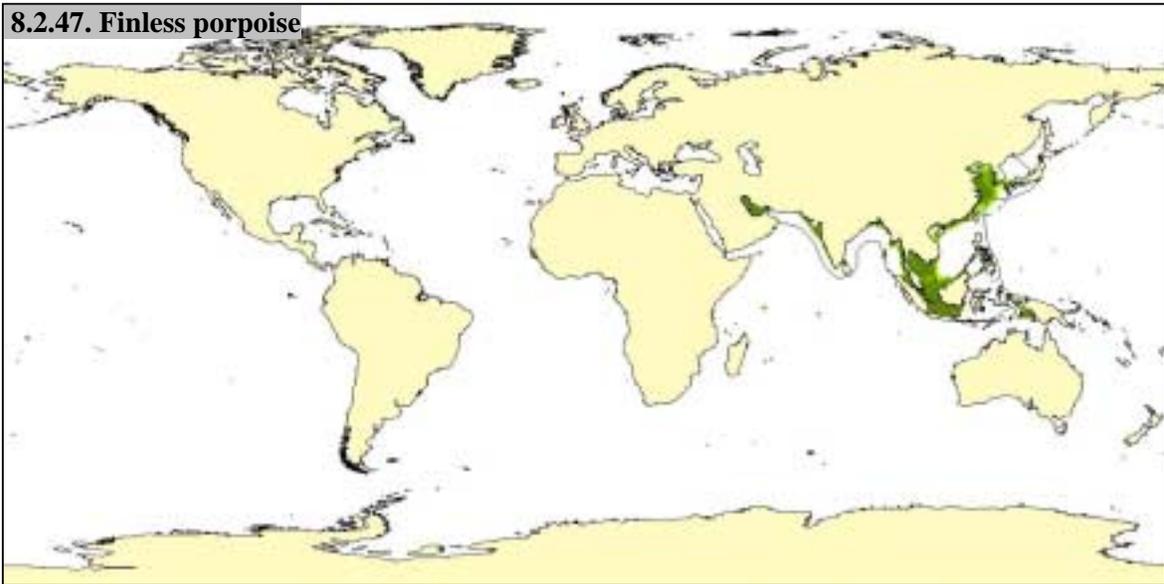
8.2.45. Burmeister's porpoise



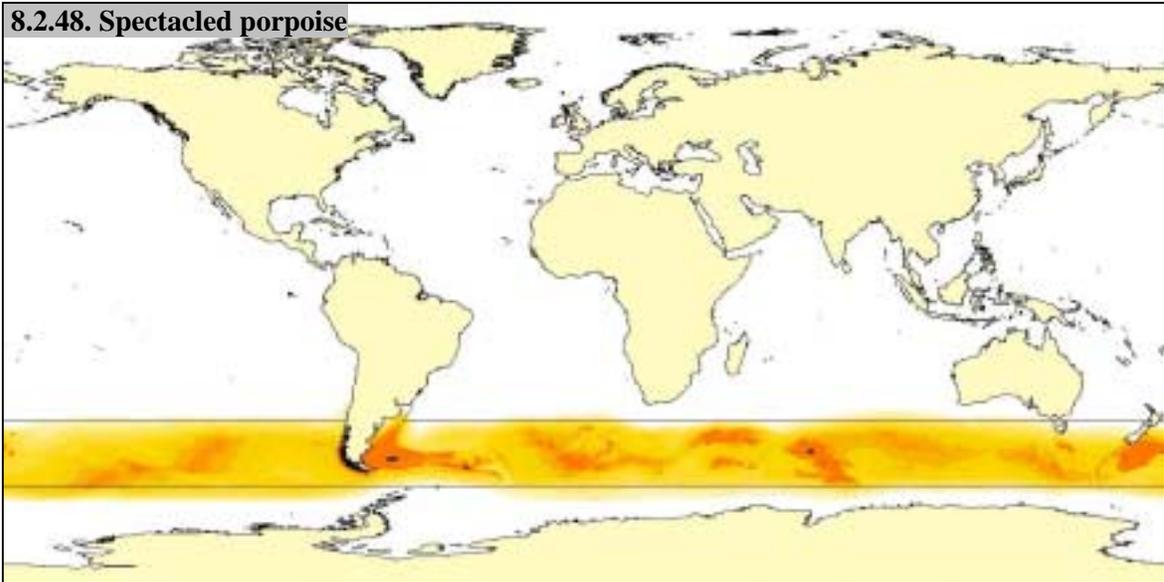
8.2.46. Harbour porpoise



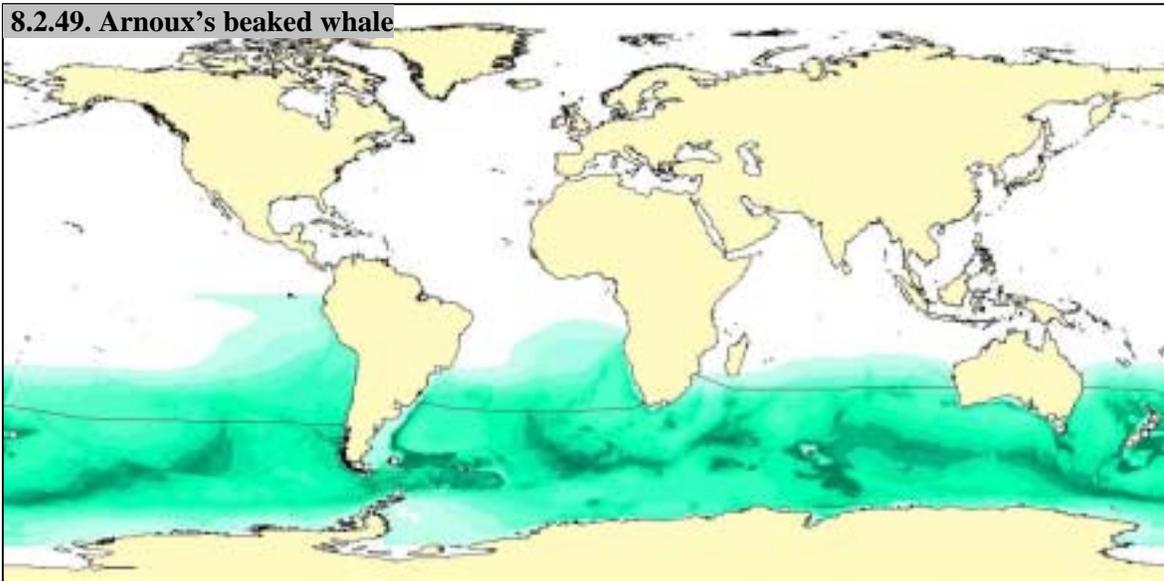
8.2.47. Finless porpoise



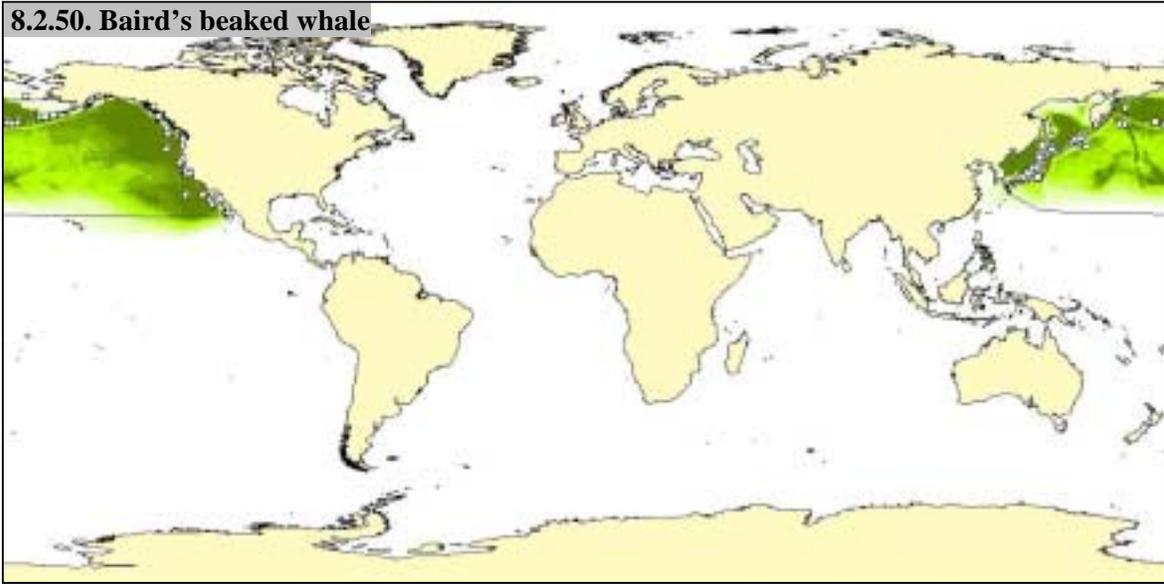
8.2.48. Spectacled porpoise



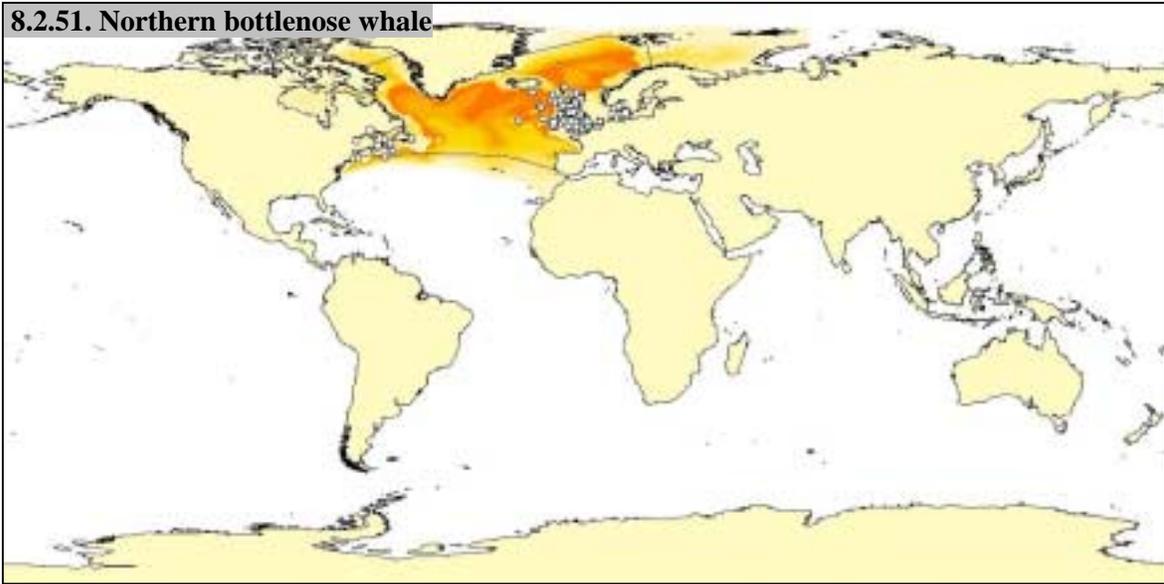
8.2.49. Arnoux's beaked whale



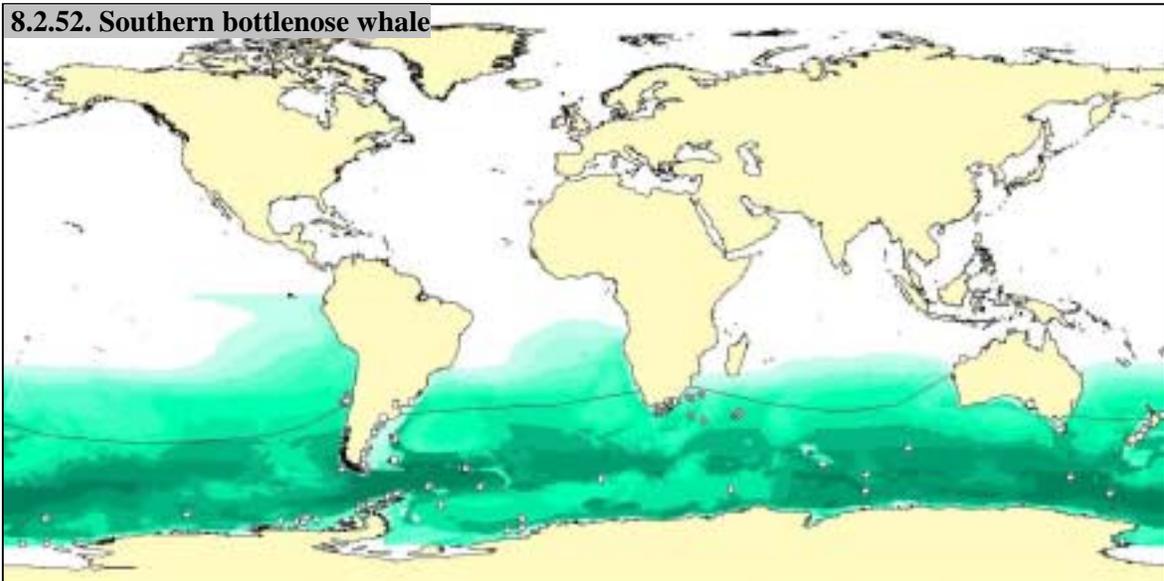
8.2.50. Baird's beaked whale



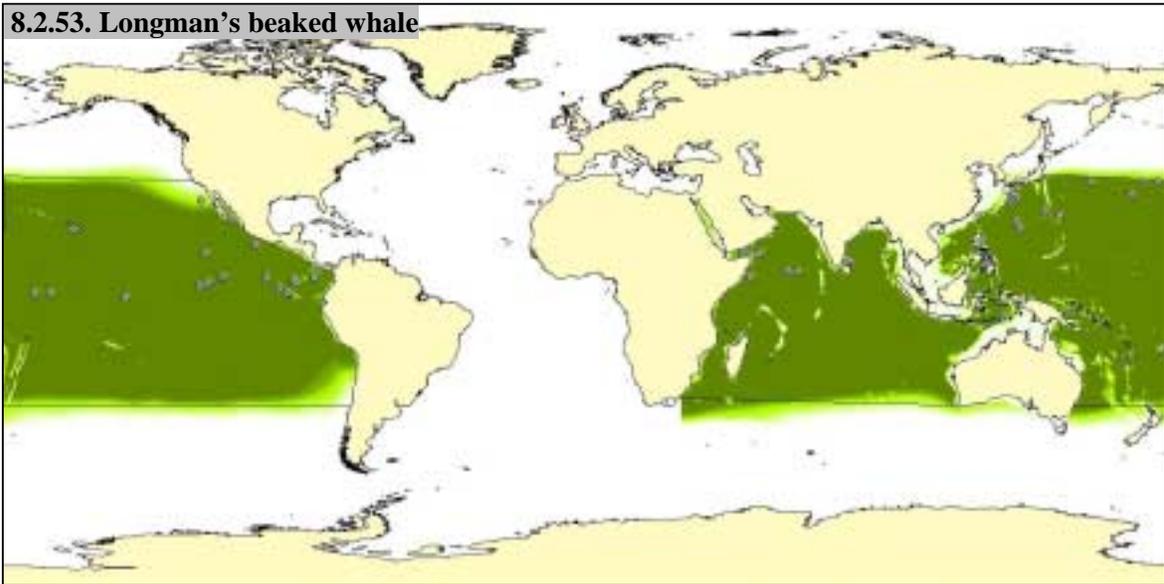
8.2.51. Northern bottlenose whale



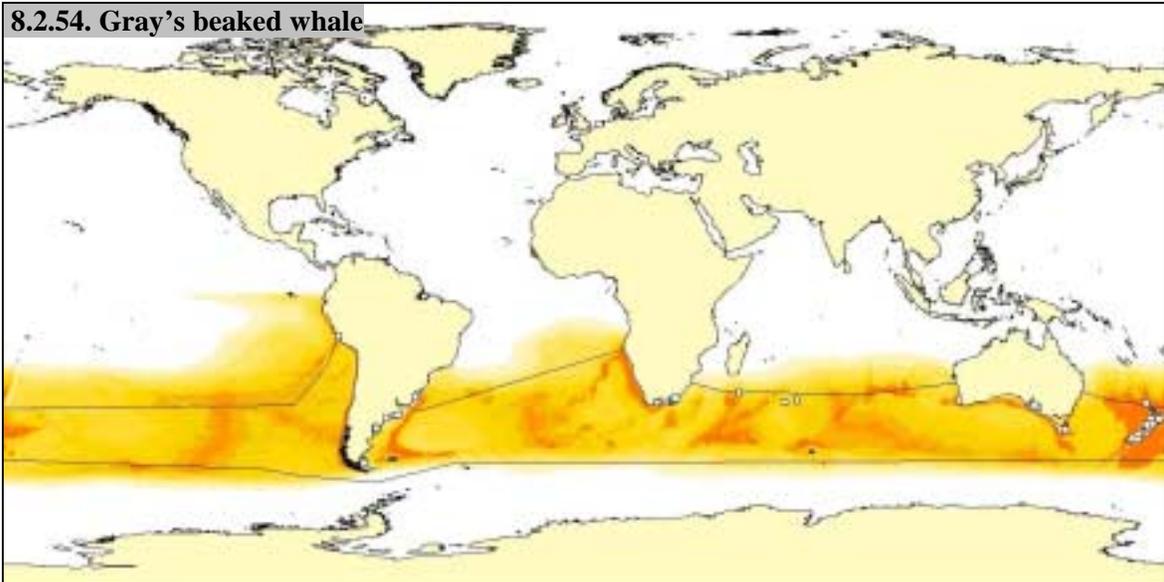
8.2.52. Southern bottlenose whale



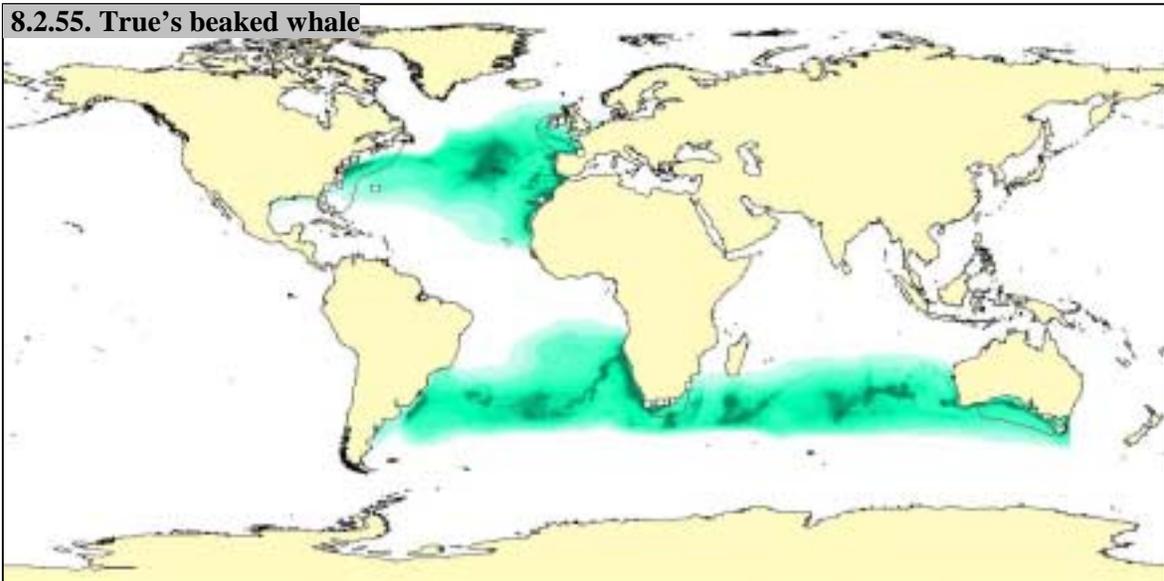
8.2.53. Longman's beaked whale



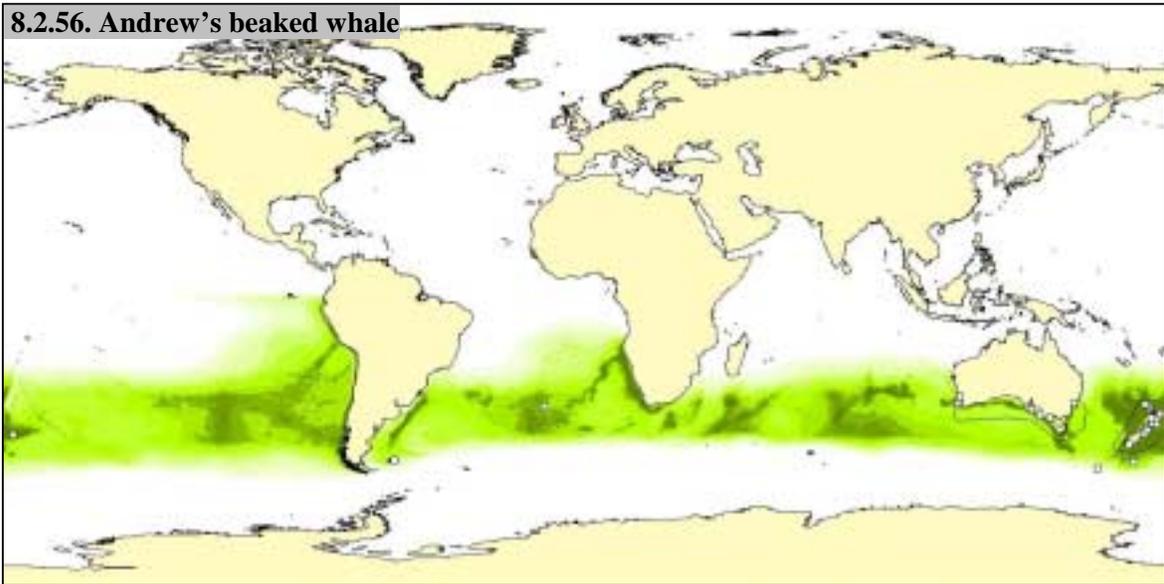
8.2.54. Gray's beaked whale



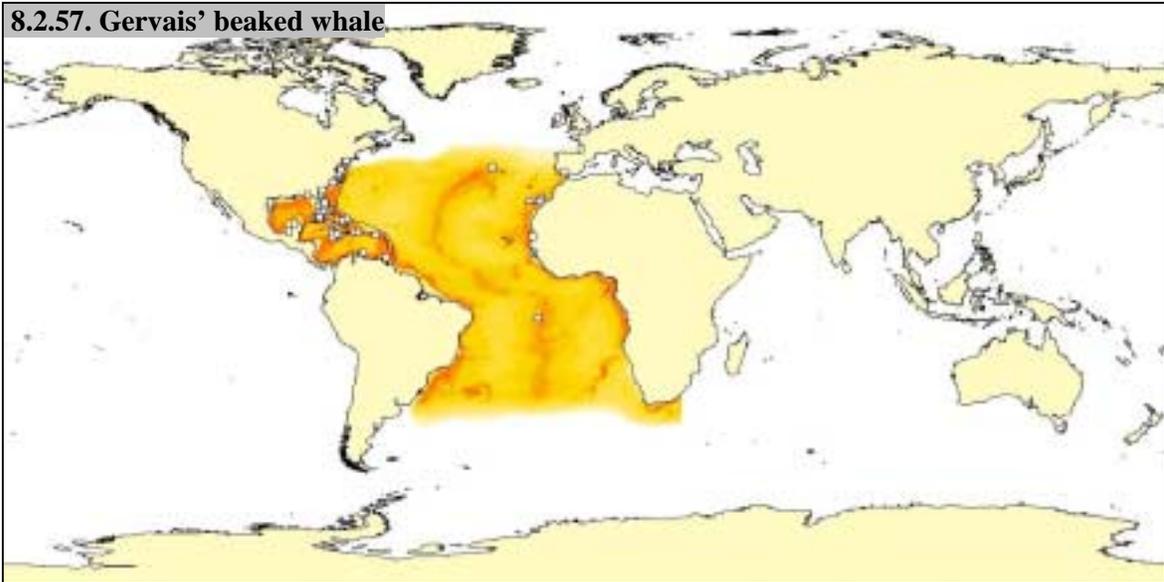
8.2.55. True's beaked whale



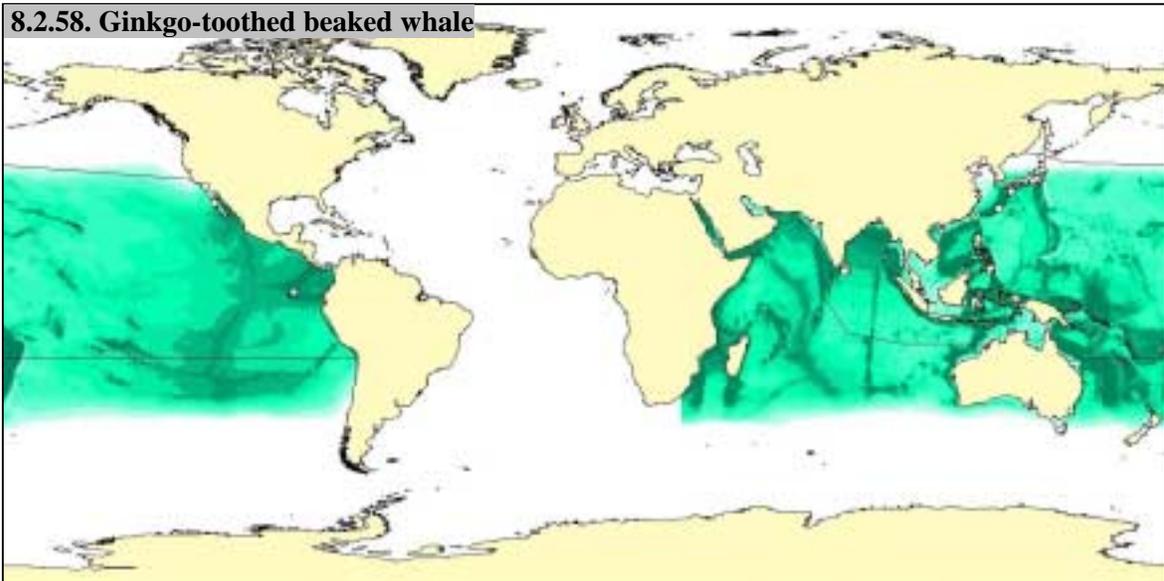
8.2.56. Andrew's beaked whale



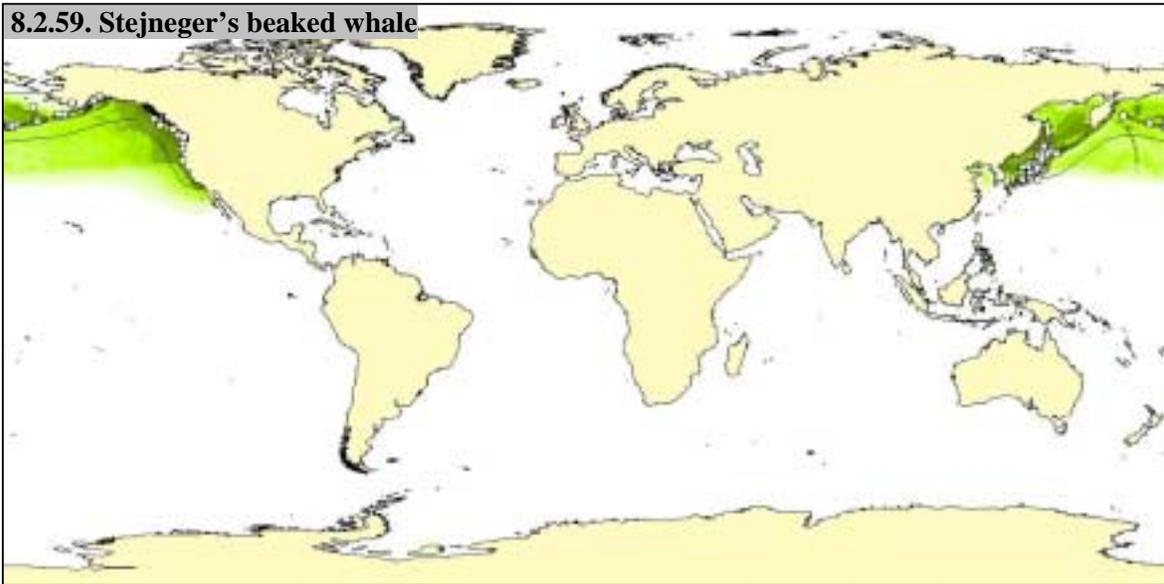
8.2.57. Gervais' beaked whale



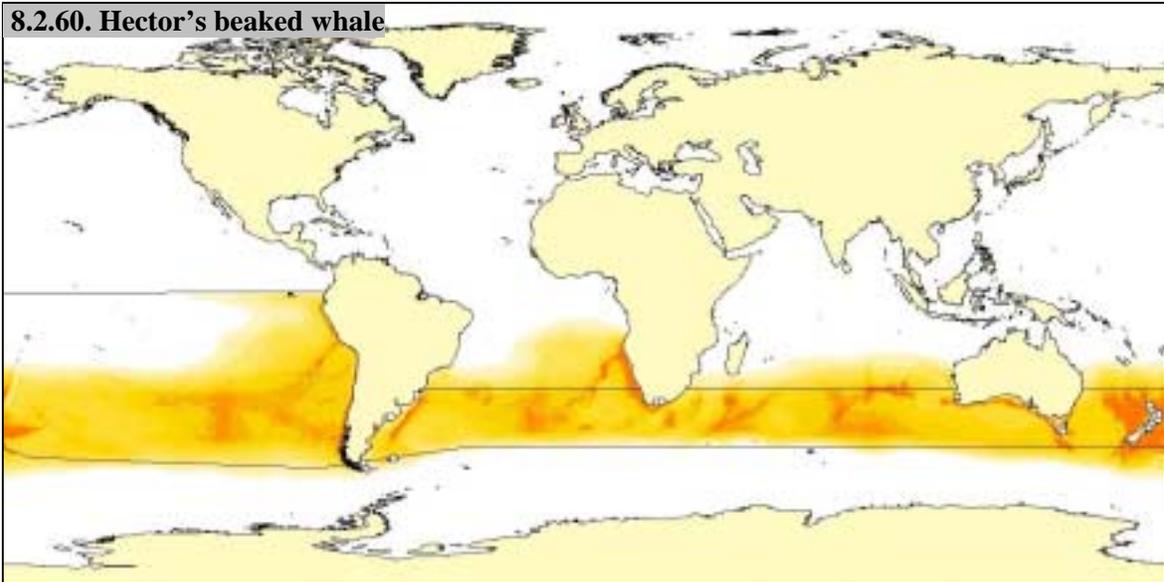
8.2.58. Ginkgo-toothed beaked whale



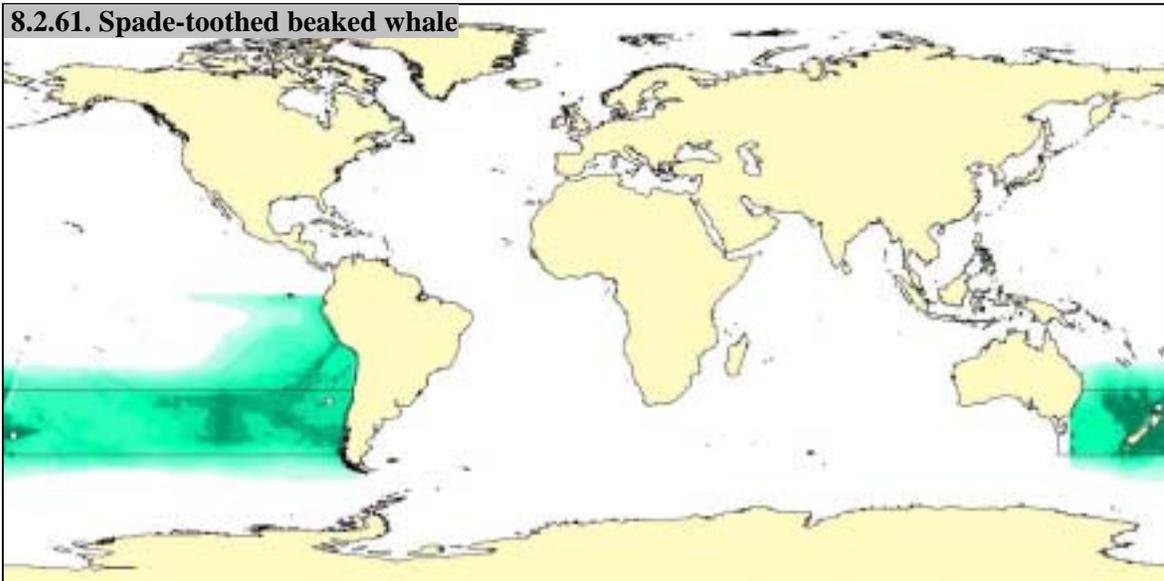
8.2.59. Stejneger's beaked whale



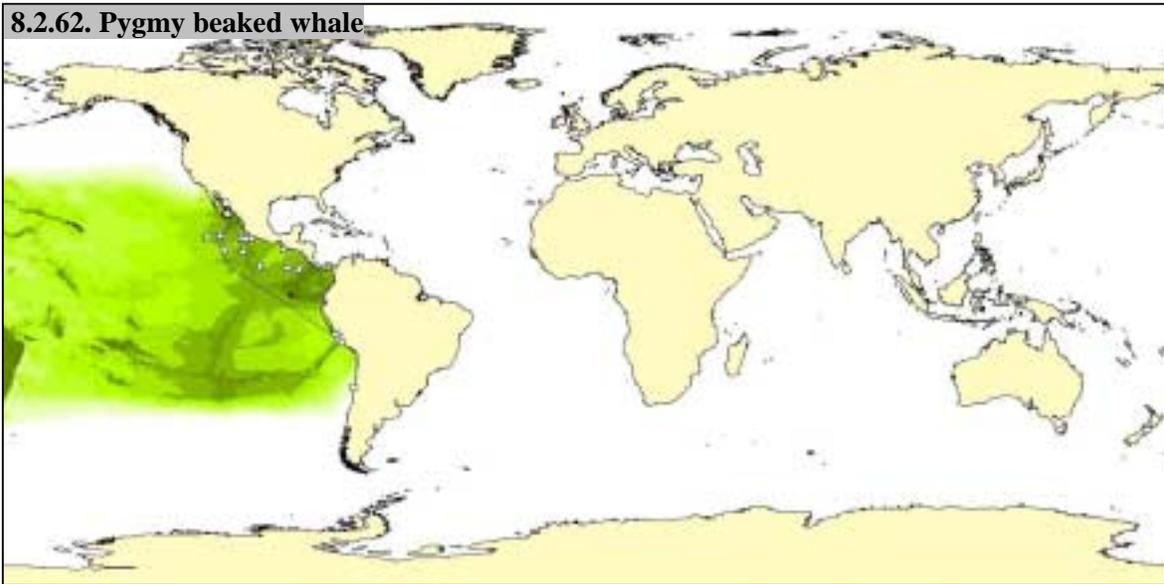
8.2.60. Hector's beaked whale



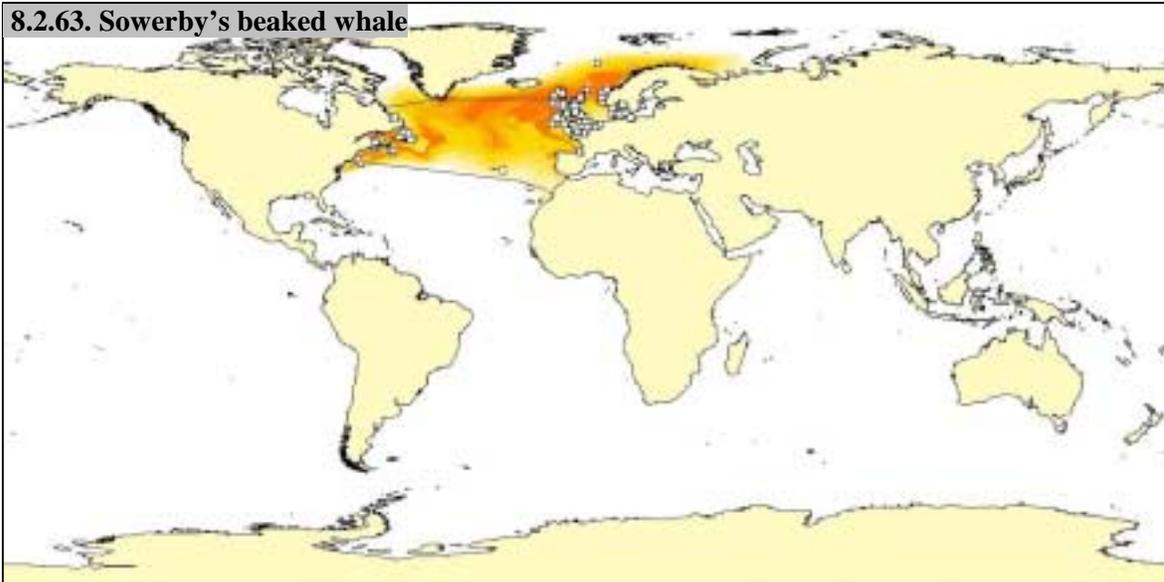
8.2.61. Spade-toothed beaked whale



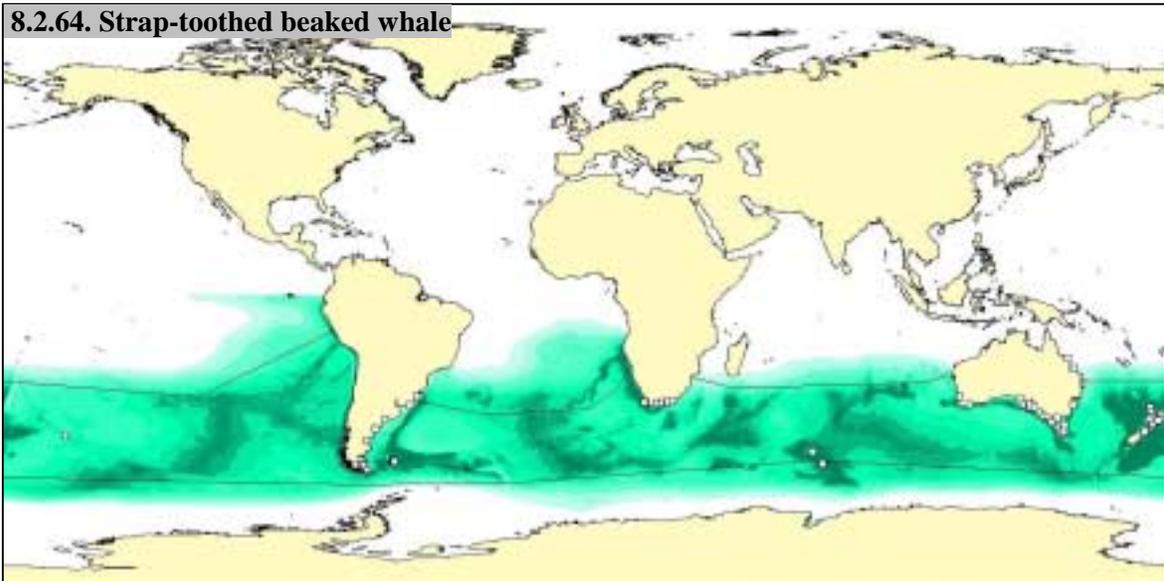
8.2.62. Pygmy beaked whale



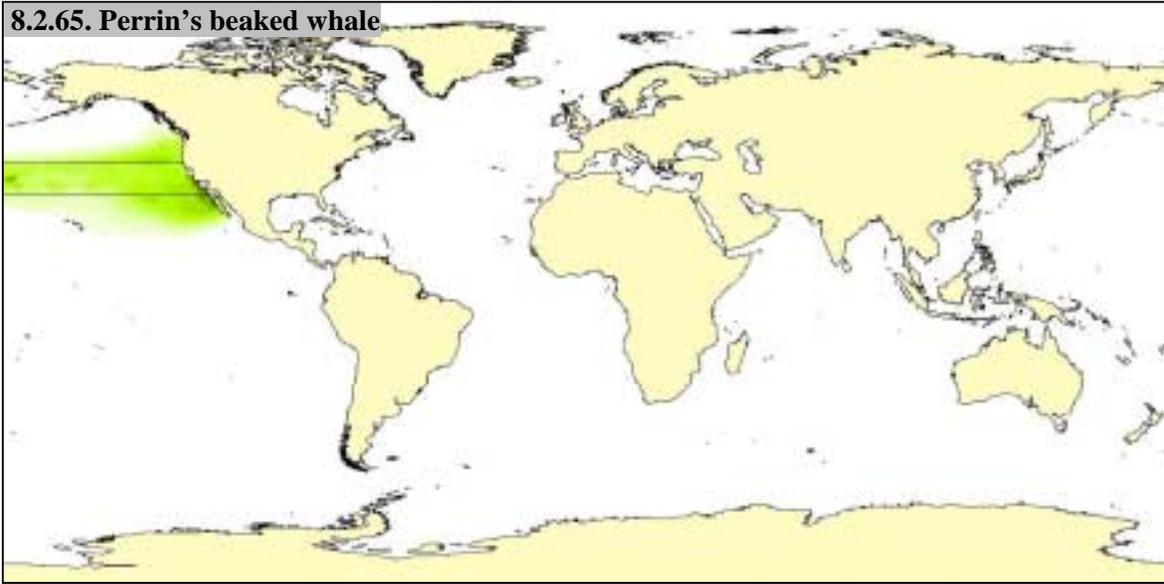
8.2.63. Sowerby's beaked whale



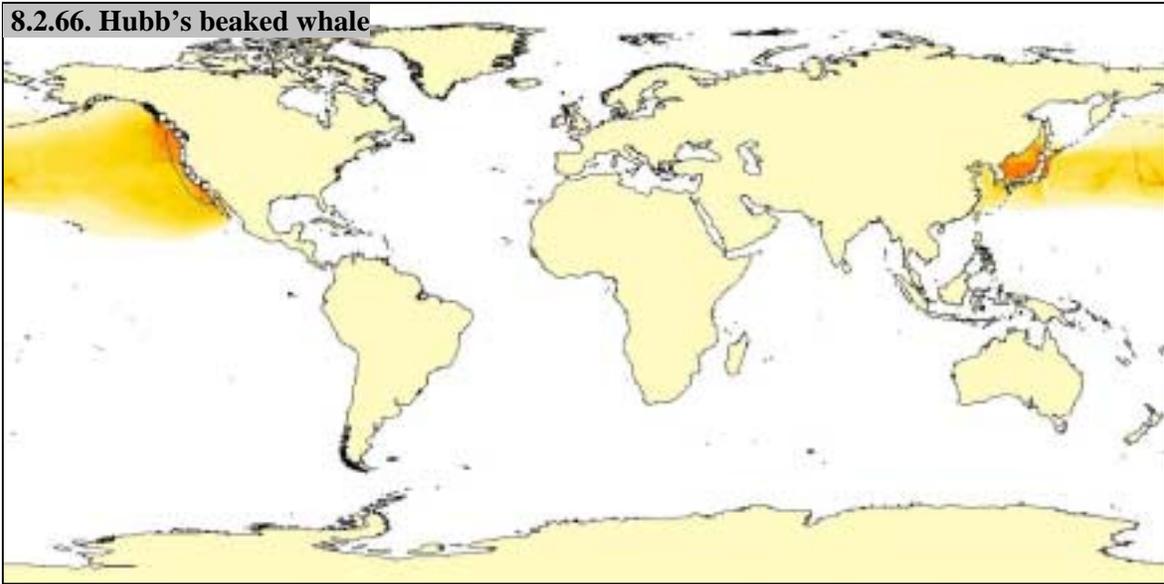
8.2.64. Strap-toothed beaked whale



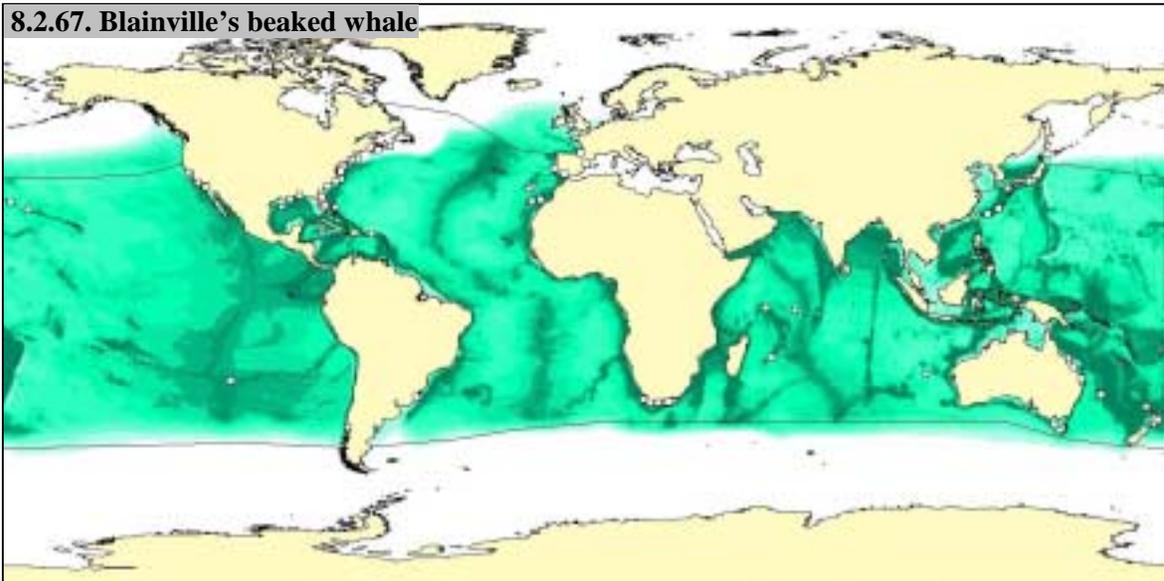
8.2.65. Perrin's beaked whale



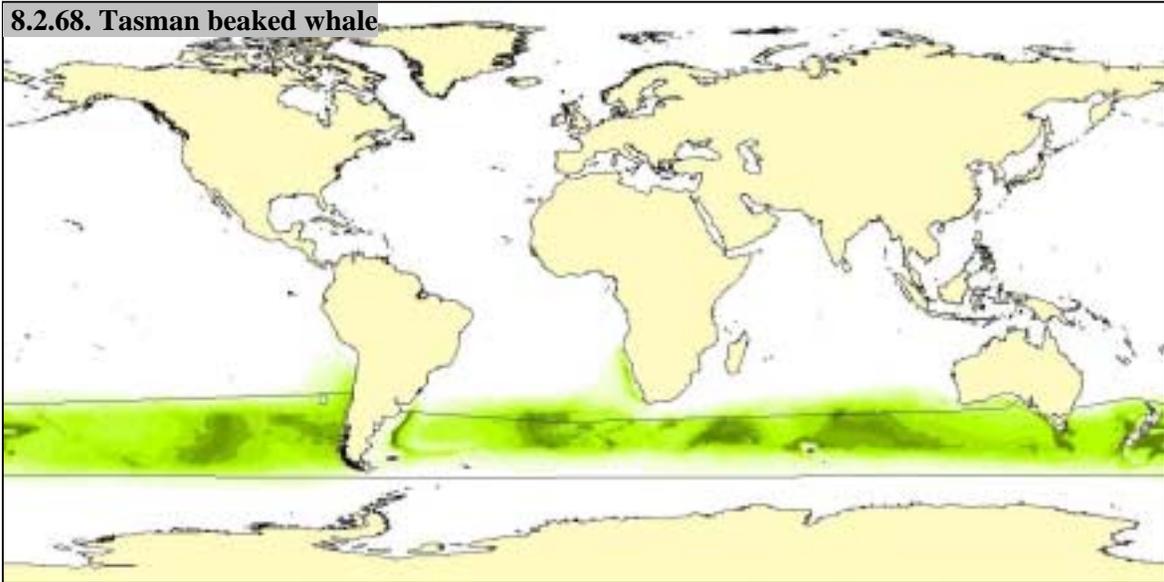
8.2.66. Hubb's beaked whale



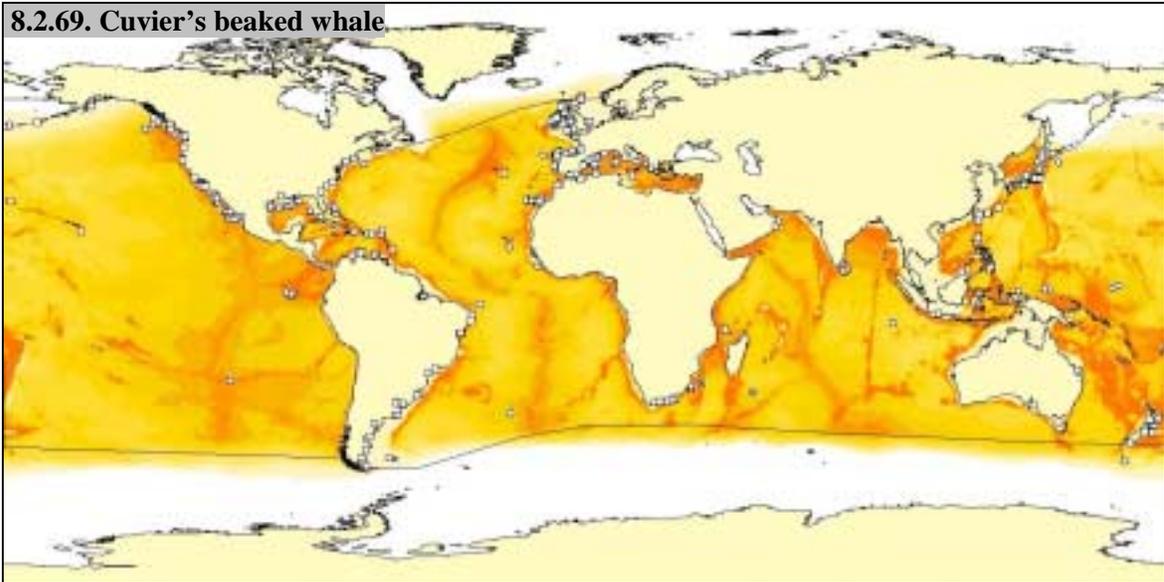
8.2.67. Blainville's beaked whale



8.2.68. Tasman beaked whale

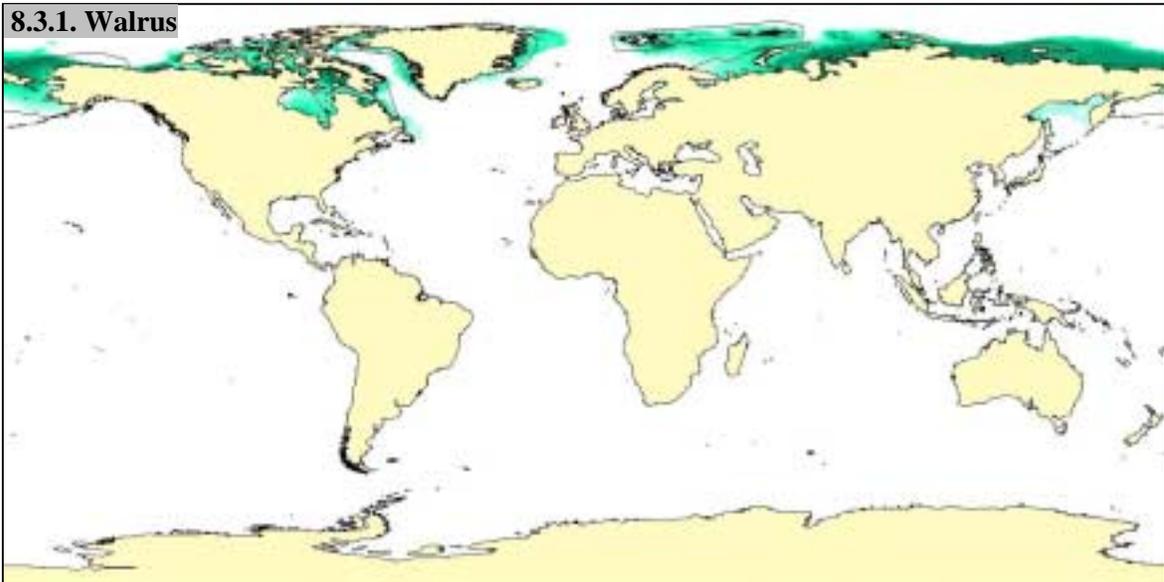


8.2.69. Cuvier's beaked whale

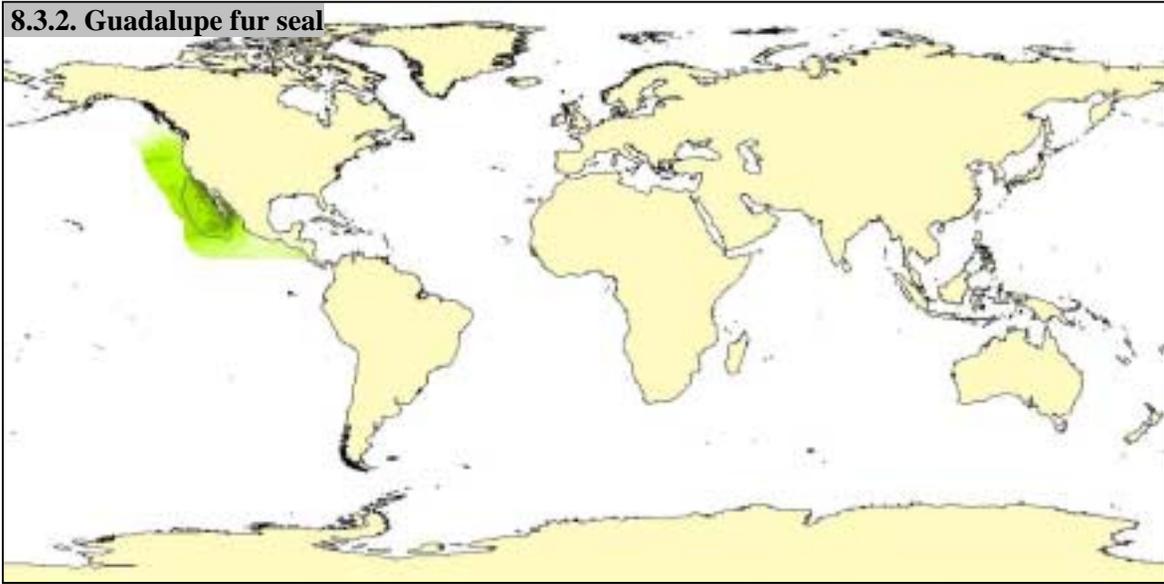


8.3. PINNIPEDS

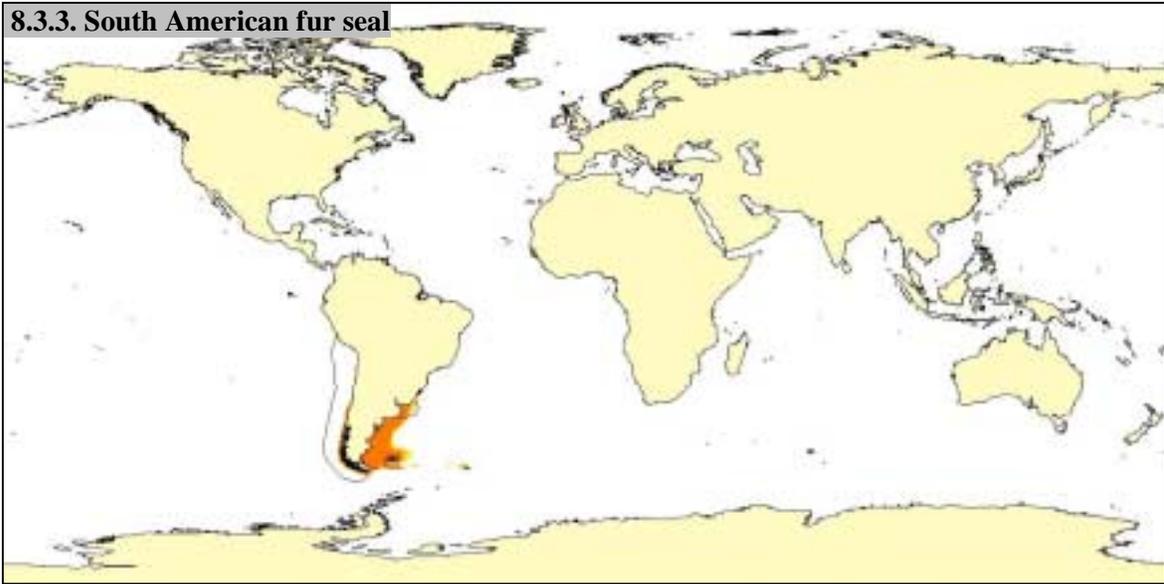
8.3.1. Walrus



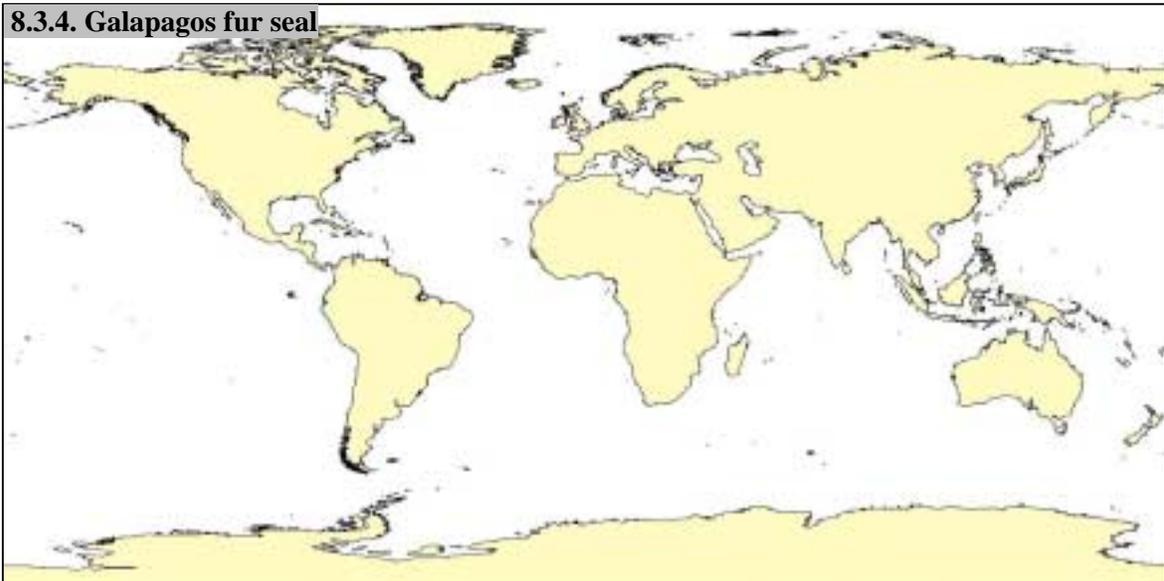
8.3.2. Guadalupe fur seal



8.3.3. South American fur seal



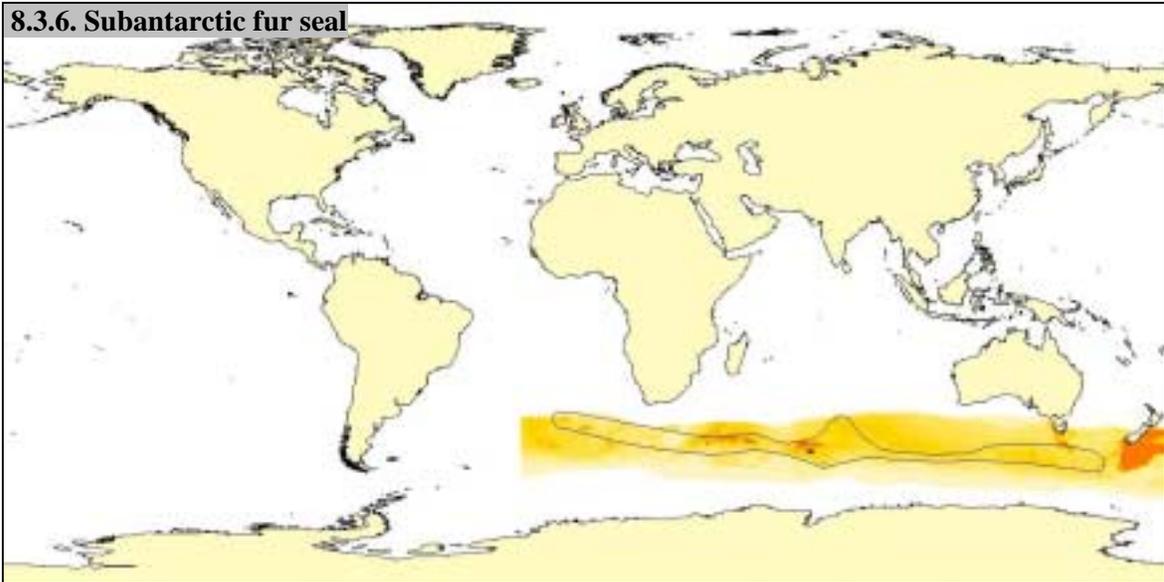
8.3.4. Galapagos fur seal



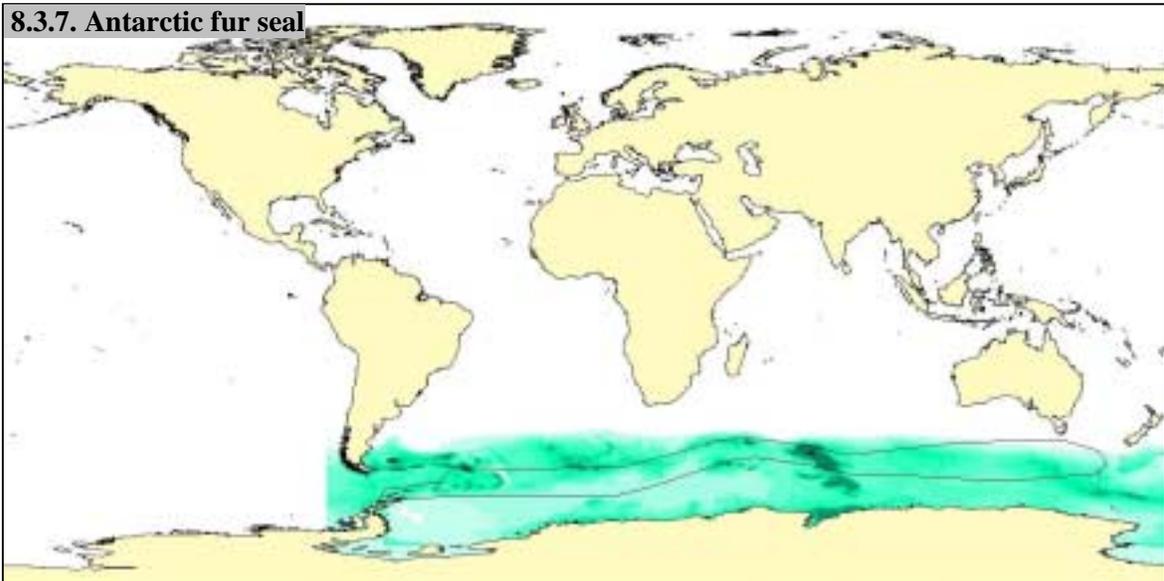
8.3.5. South African & Australian fur seal



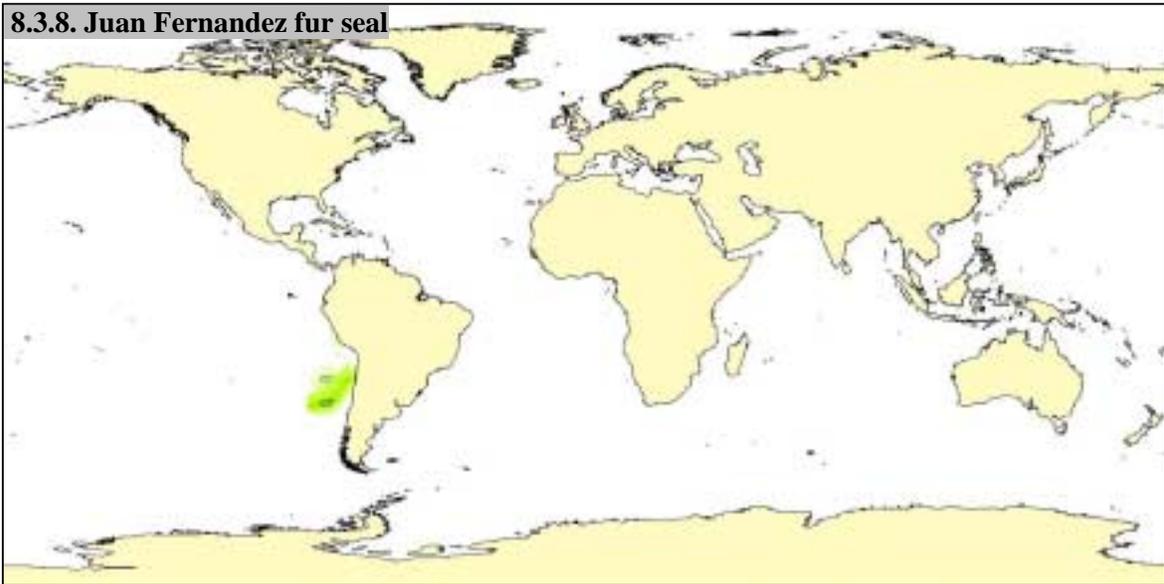
8.3.6. Subantarctic fur seal



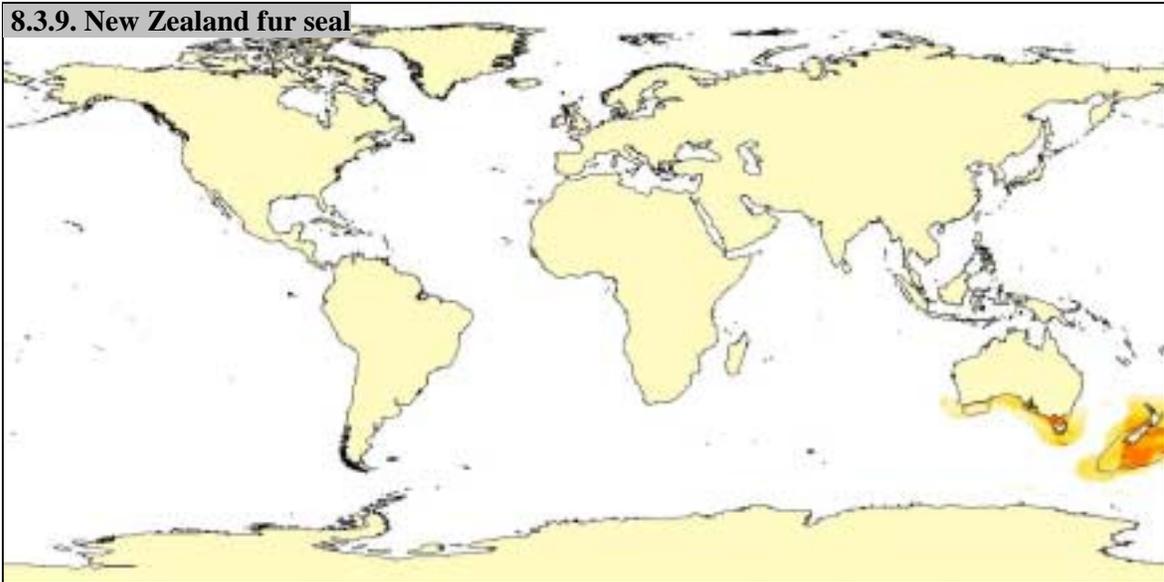
8.3.7. Antarctic fur seal



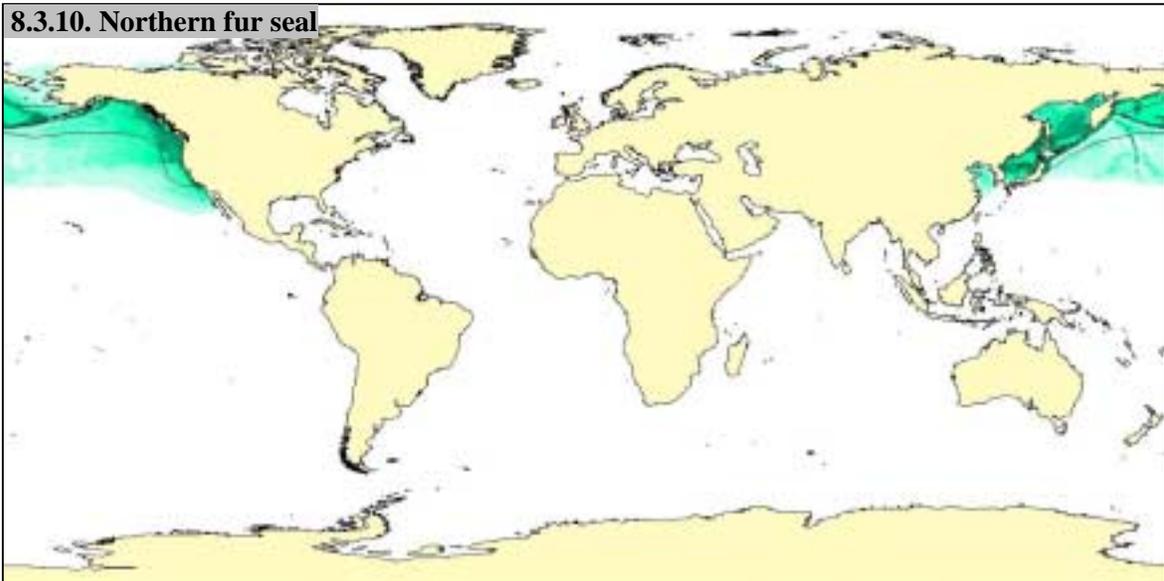
8.3.8. Juan Fernandez fur seal



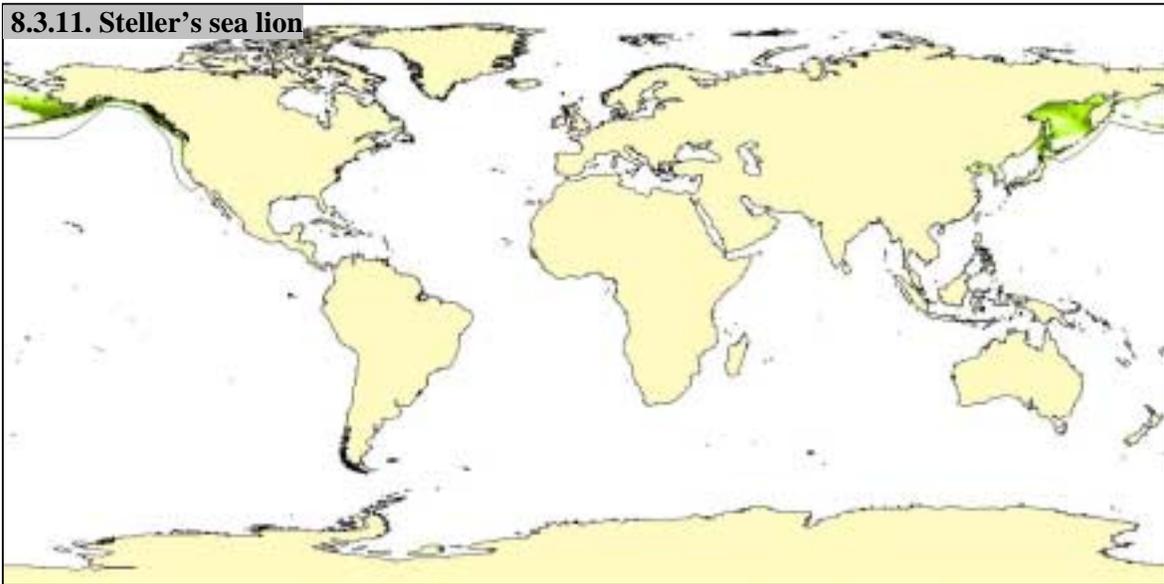
8.3.9. New Zealand fur seal



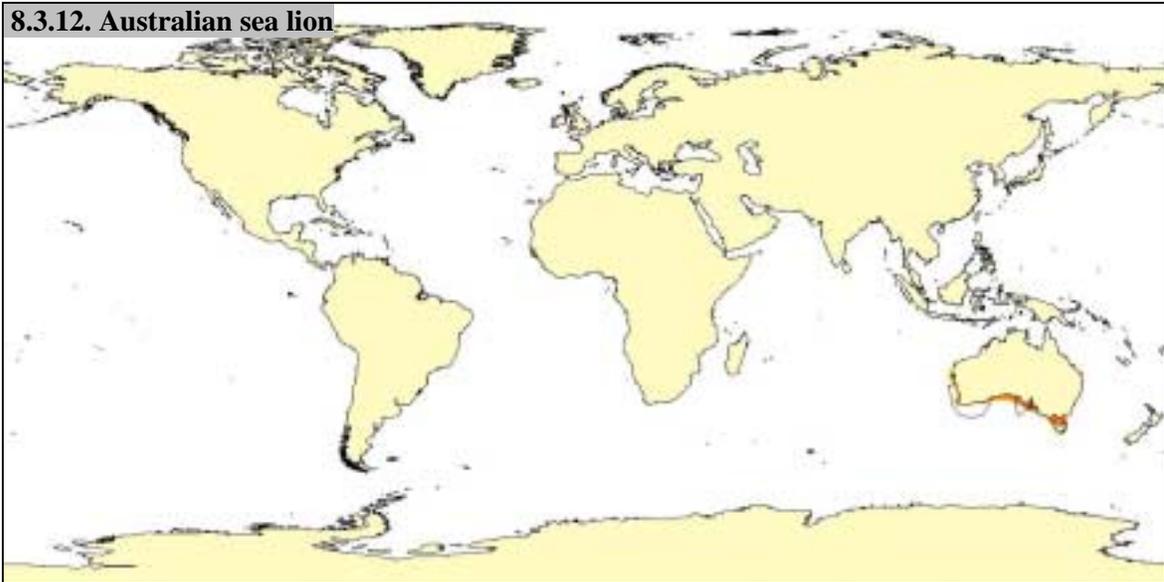
8.3.10. Northern fur seal



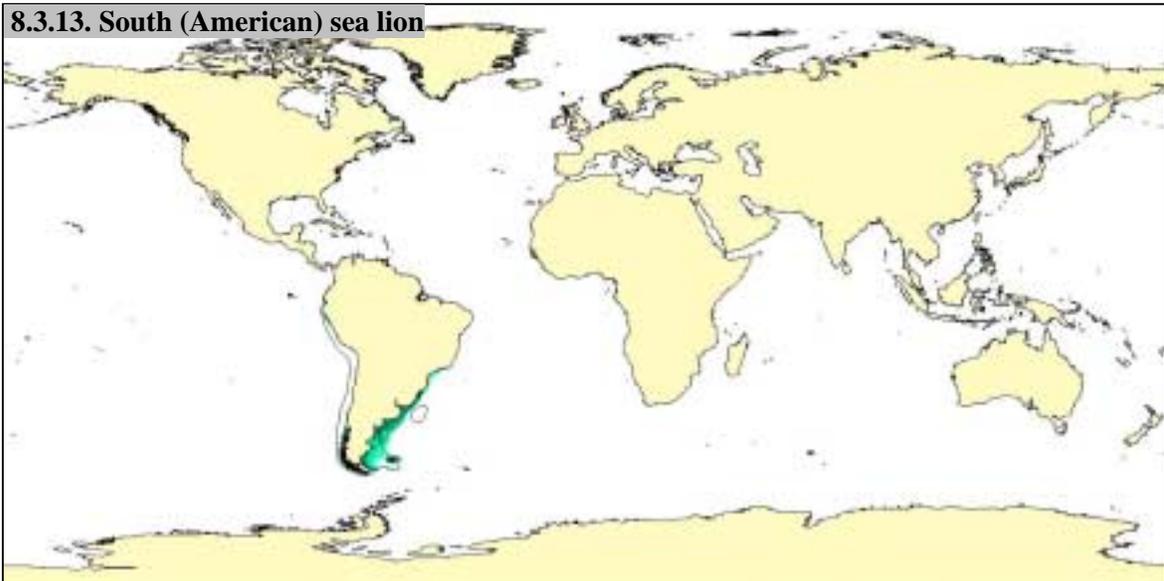
8.3.11. Steller's sea lion



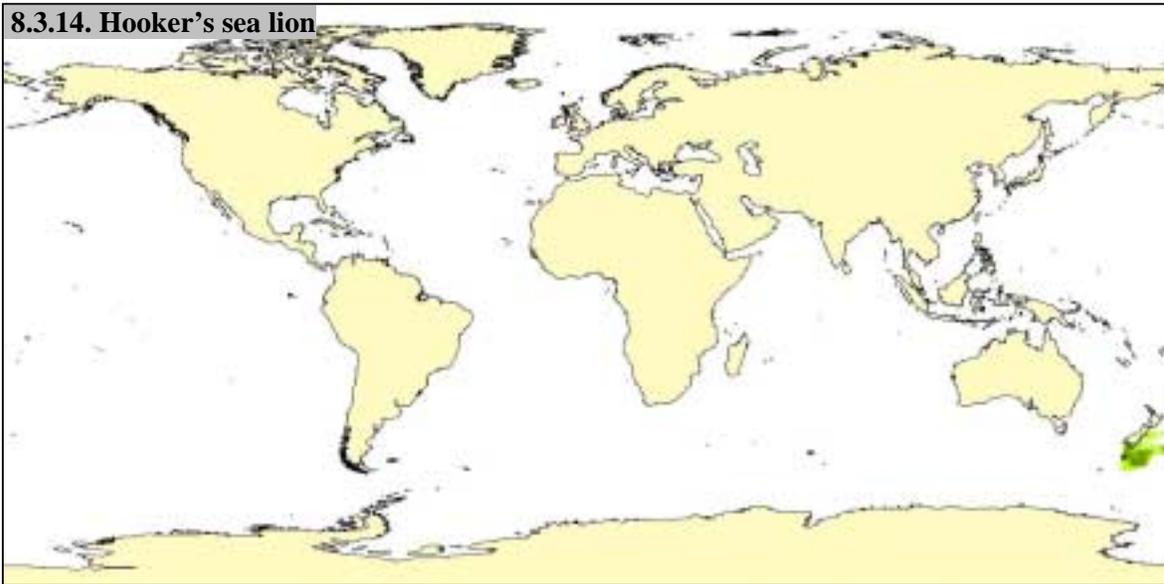
8.3.12. Australian sea lion



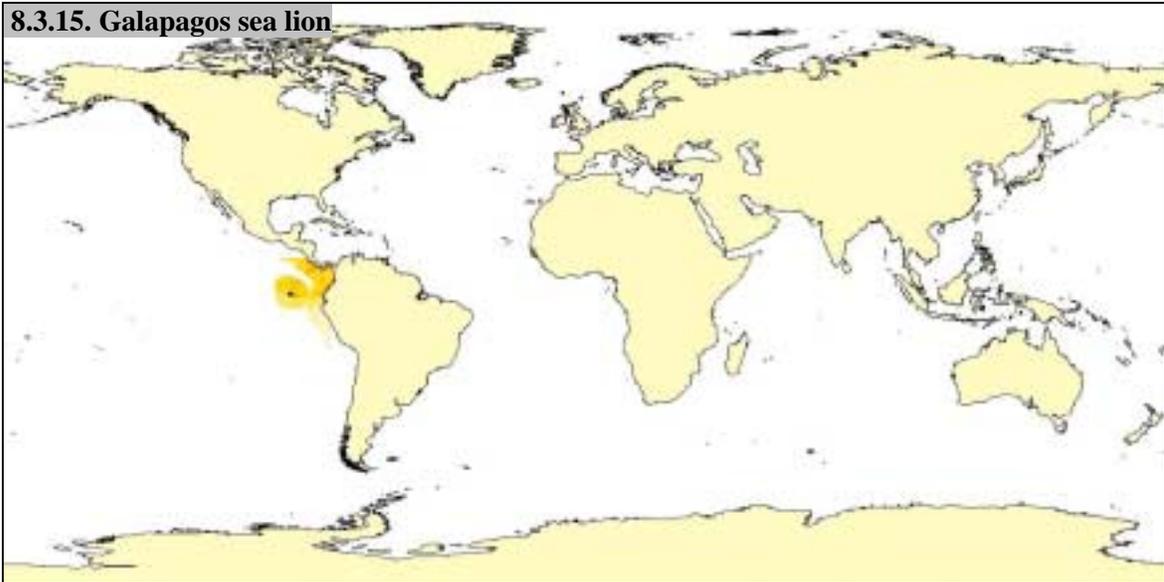
8.3.13. South (American) sea lion



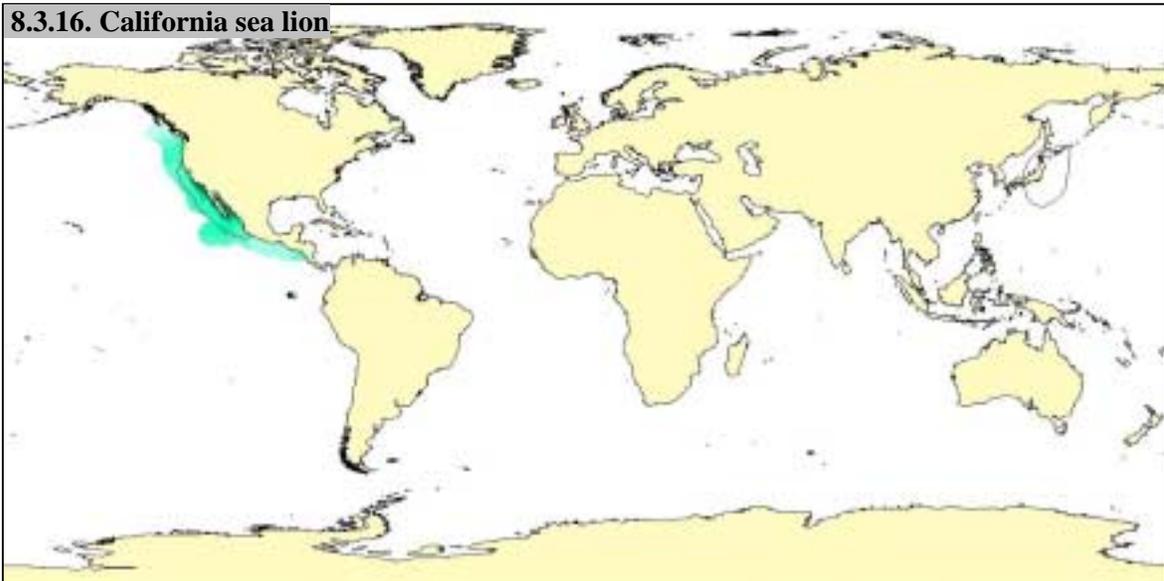
8.3.14. Hooker's sea lion



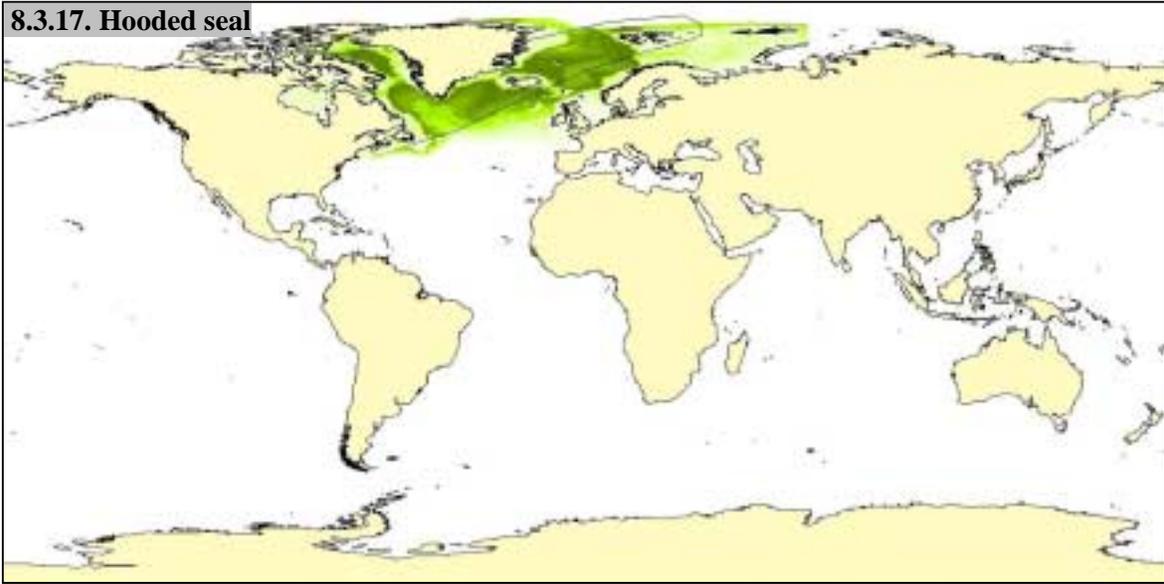
8.3.15. Galapagos sea lion



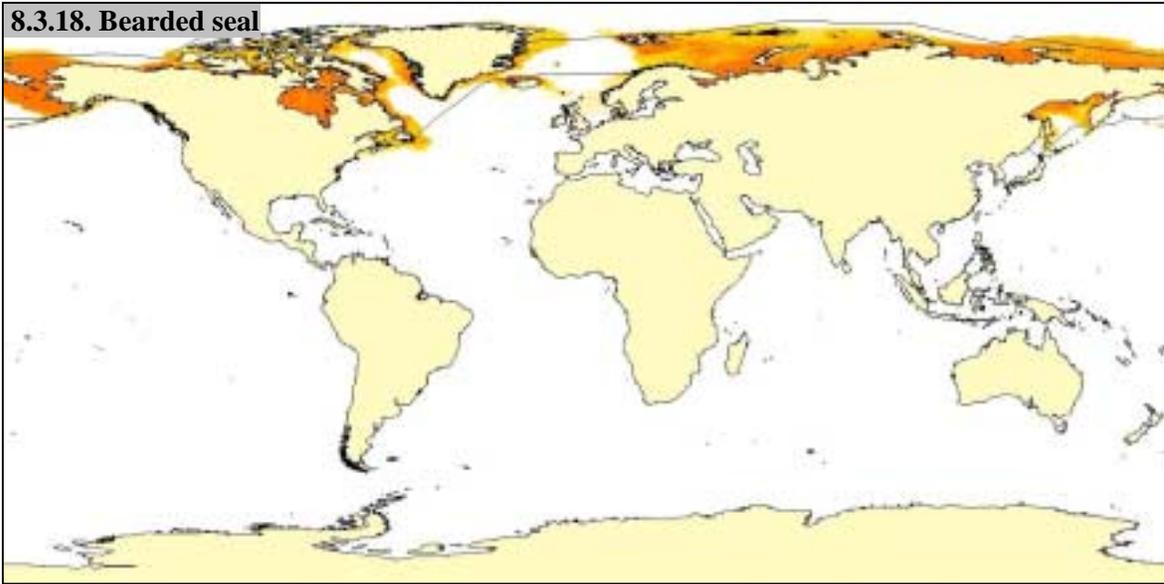
8.3.16. California sea lion



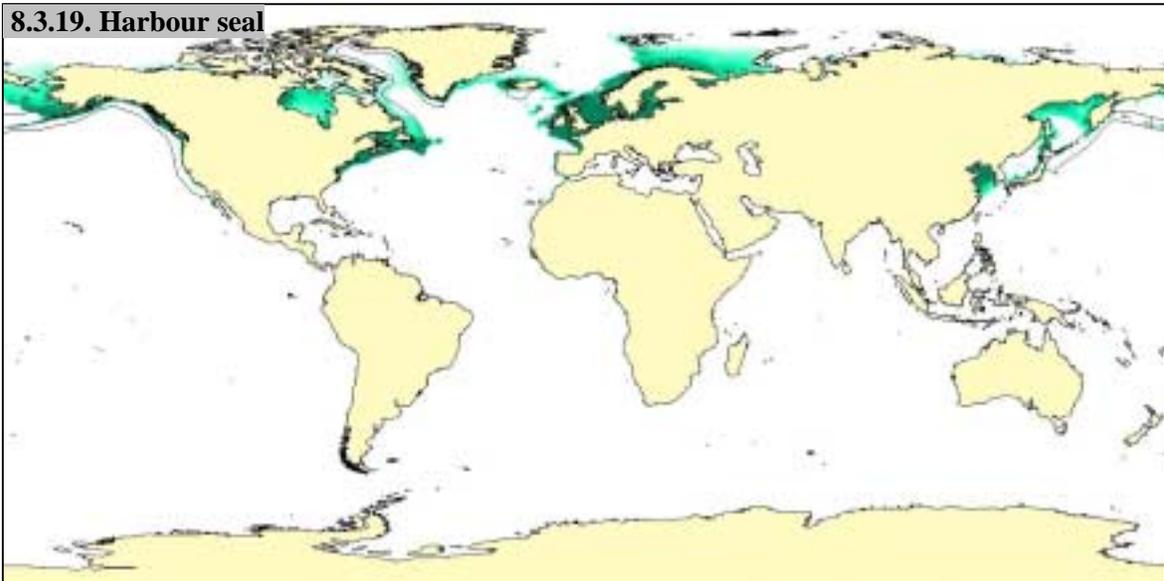
8.3.17. Hooded seal



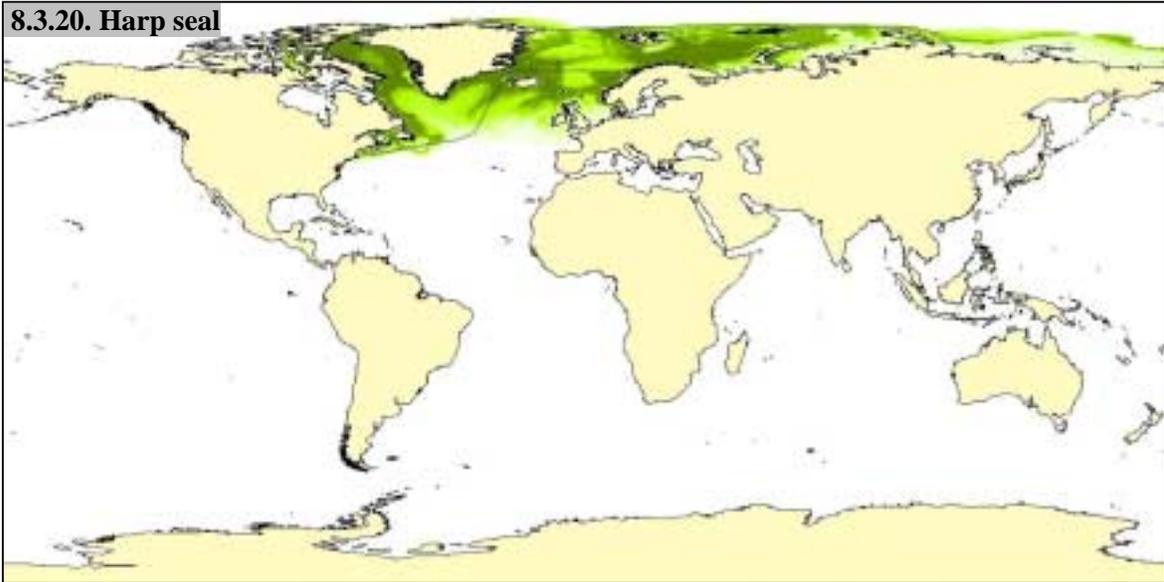
8.3.18. Bearded seal



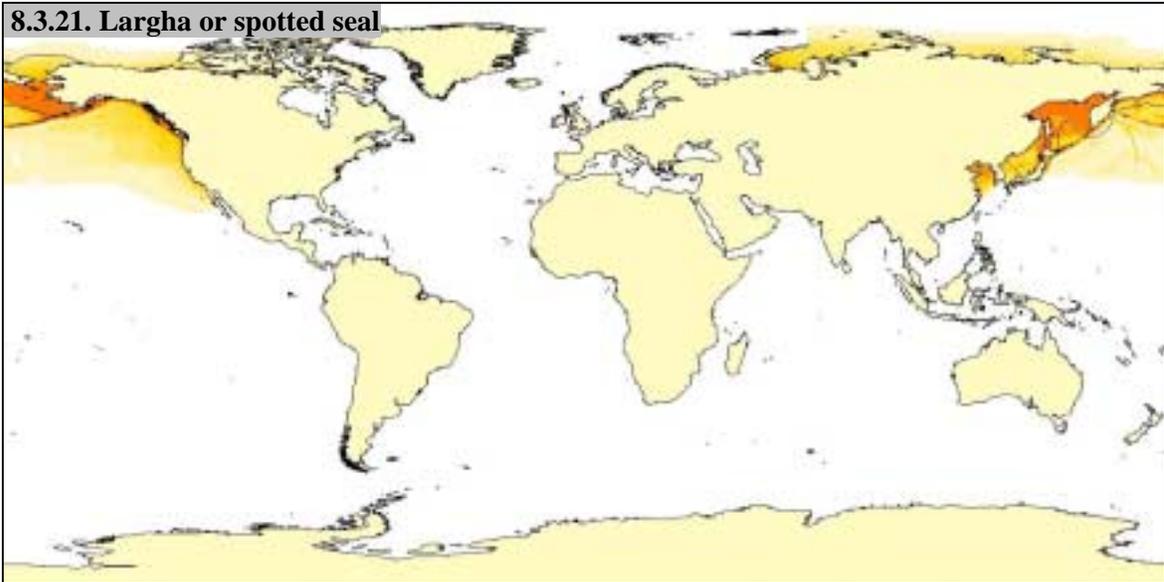
8.3.19. Harbour seal



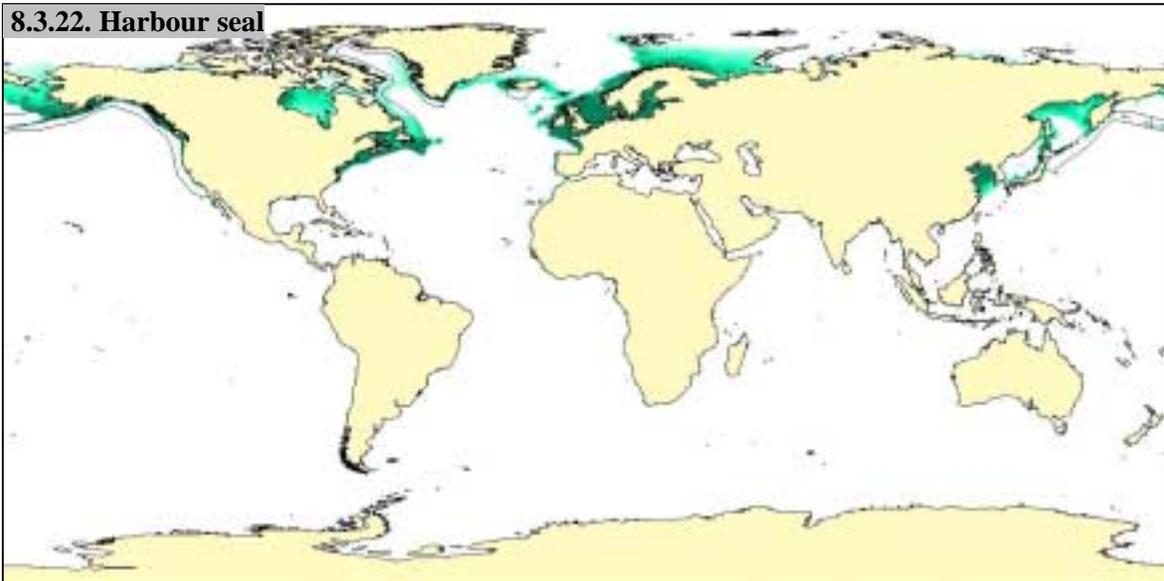
8.3.20. Harp seal



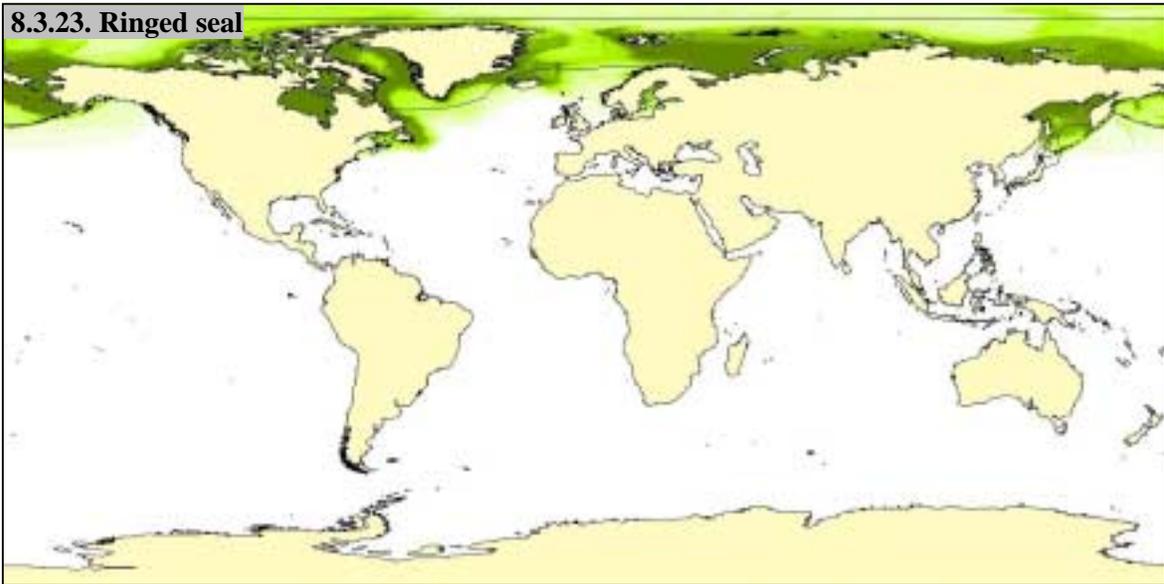
8.3.21. Larga or spotted seal



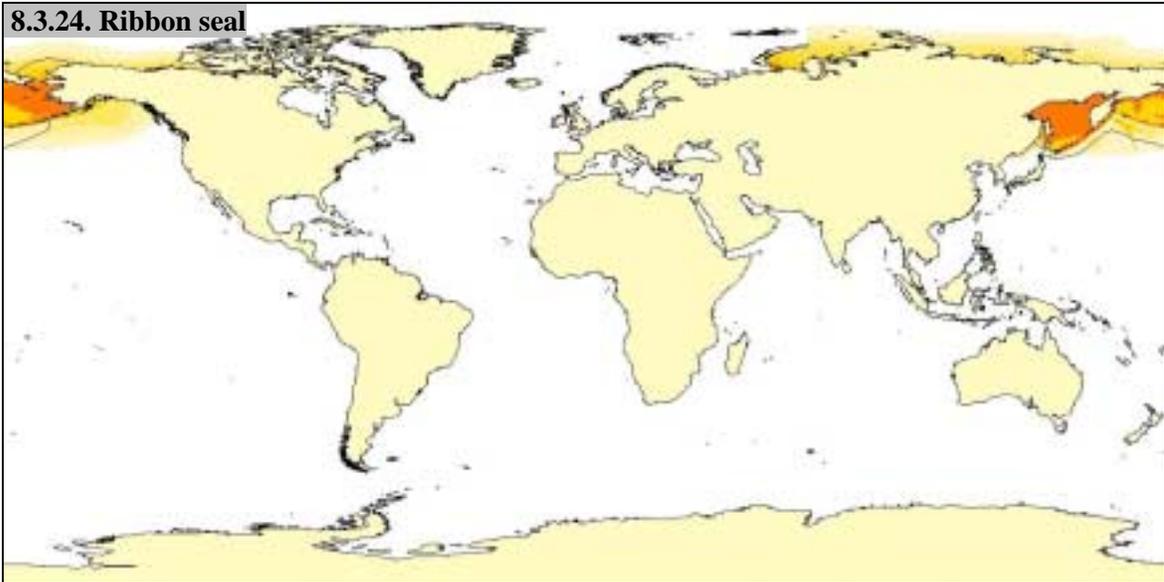
8.3.22. Harbour seal



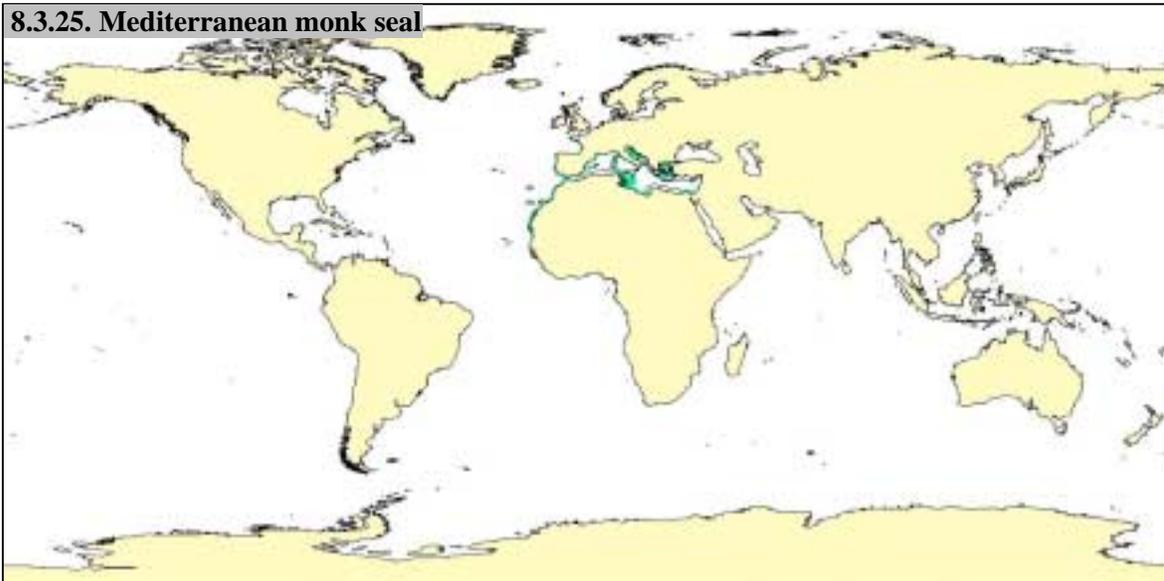
8.3.23. Ringed seal



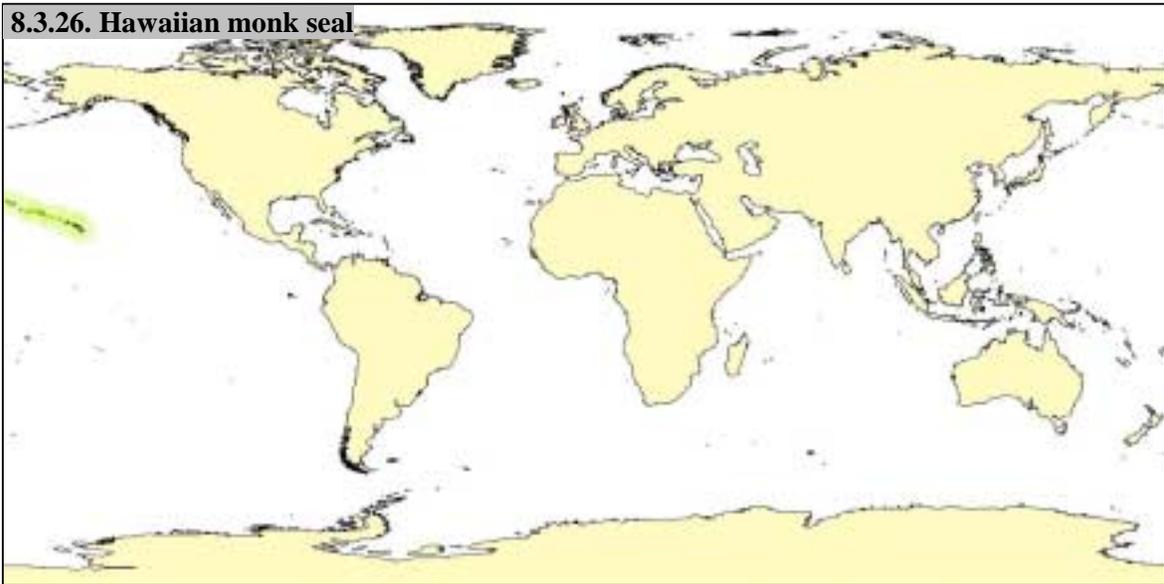
8.3.24. Ribbon seal



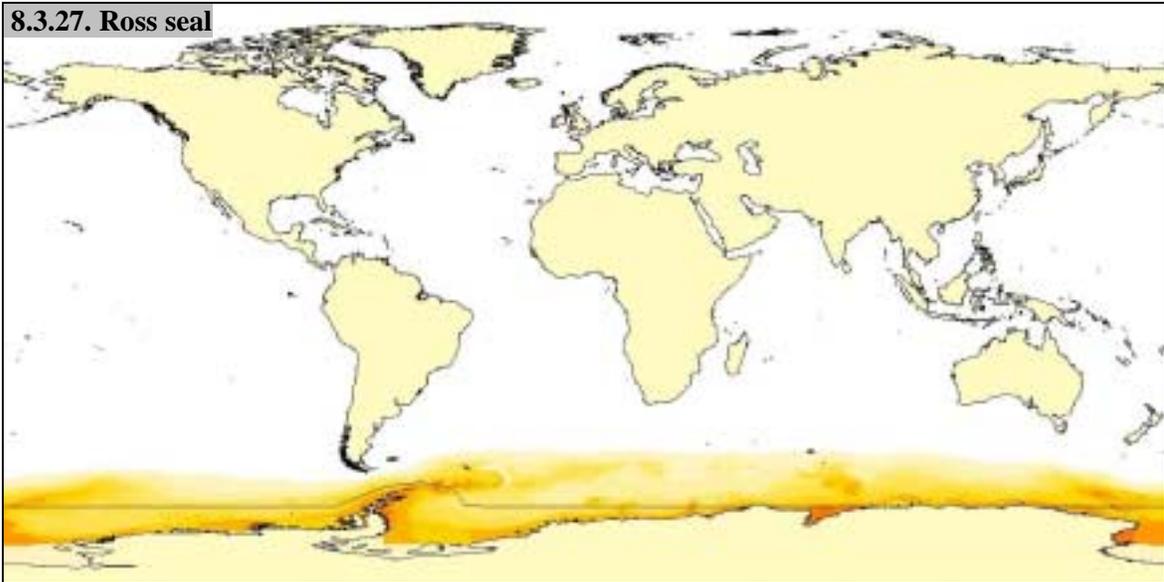
8.3.25. Mediterranean monk seal



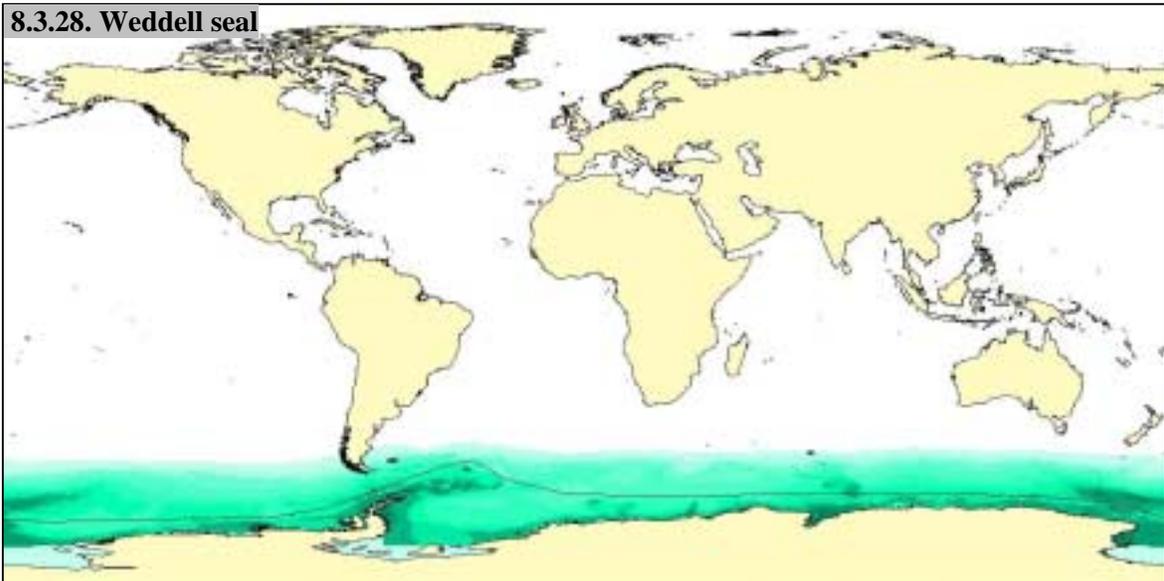
8.3.26. Hawaiian monk seal



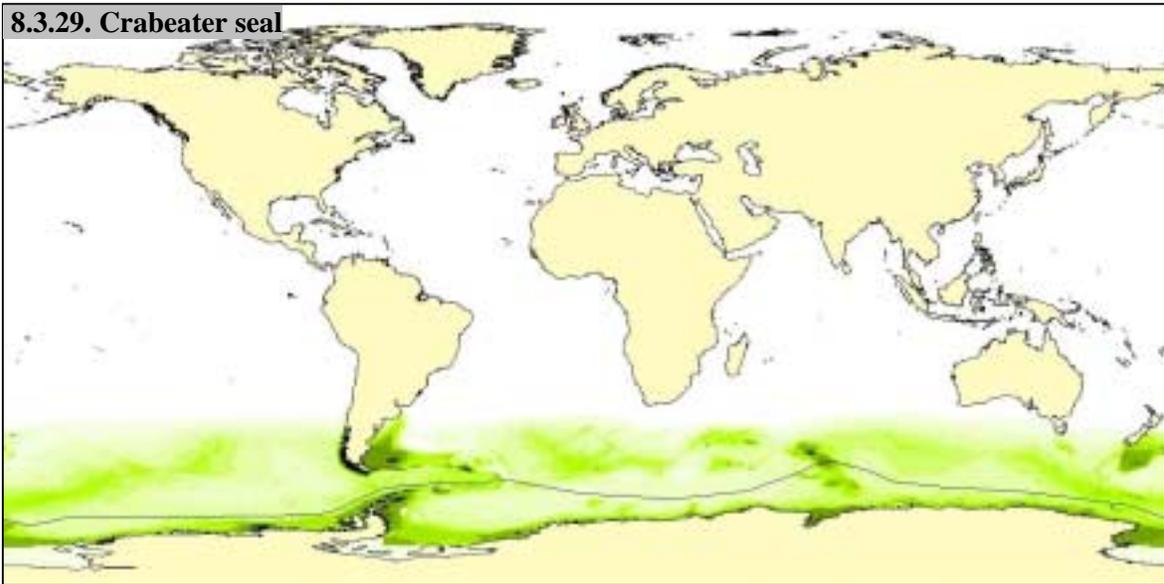
8.3.27. Ross seal



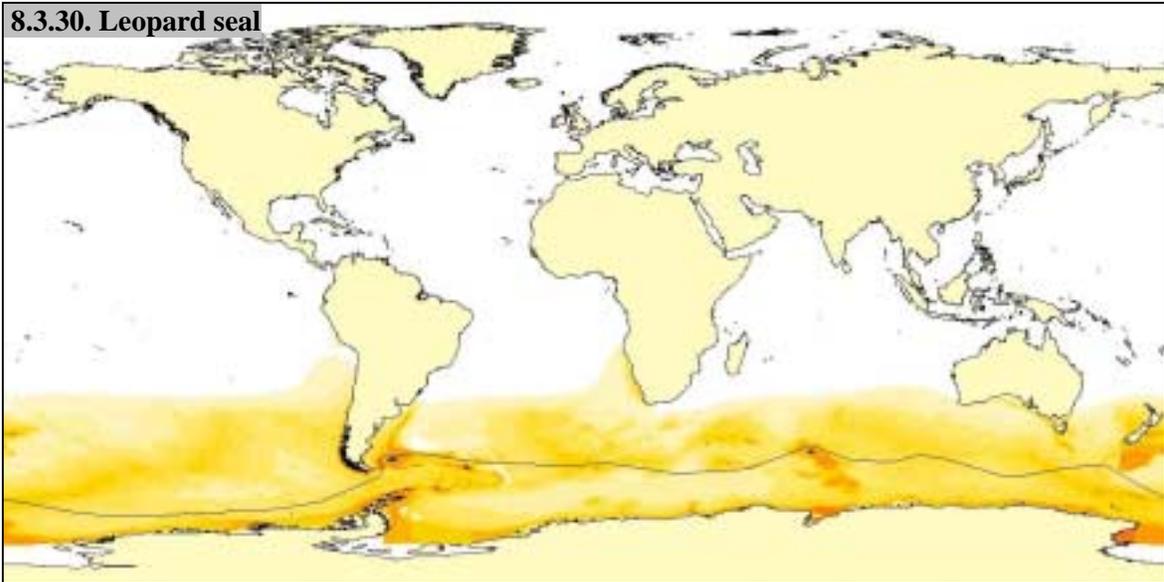
8.3.28. Weddell seal



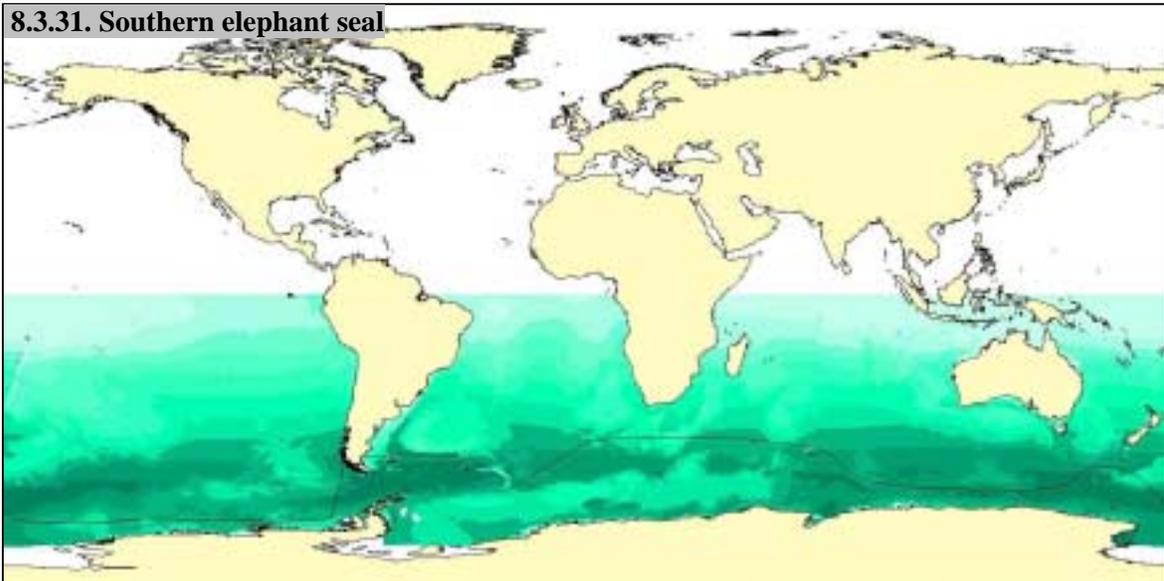
8.3.29. Crabeater seal



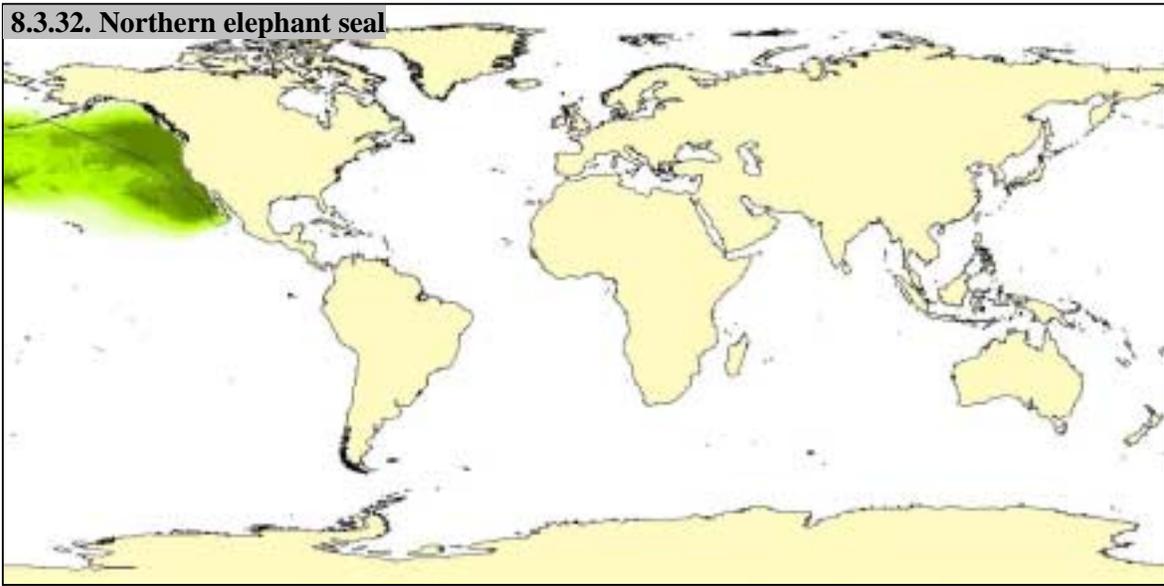
8.3.30. Leopard seal



8.3.31. Southern elephant seal



8.3.32. Northern elephant seal



9. Appendix 4: Abundance Estimates

Appendix 4. Minimum, mean and maximum global abundance estimates of 115 marine mammals together with the estimated proportion of distributional range covered by reliable surveys in the 1990s and assigned levels of confidence (ranging from 1 = highest to 6 = lowest) in abundance estimate considering uncertainties of estimation technique, date of most recent estimate and proportion of distribution covered.

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
Bowhead whale	<i>Balaena mysticetus</i>	8,100	9,200	10,500	2	0.75	Belikov et al, 1989; Cosens et al, 1997; Vladimirov, 1994; Zeh et al, 1993; Zeh et al, 1995
North Pacific right whale	<i>Eubalaena japonicus</i>	500	1,250	2,600	3	0.5	IWC, 1998; Perry et al, 1999
Southern right whale	<i>Eubalaena australis</i>	6,000	7,000	8,000	3	0.5	IWC, 1998
North Atlantic right whale	<i>Eubalaena glacialis</i>	263	291	300	1	1	Bannister et al, 2001; Kraus et al, 2001; Perry et al, 1999
Sei whale	<i>Balaenoptera borealis</i>	20,000	24,000	60,000	4	0.25	Caretta et al, 2002; COSEWIC, 2003; Horwood, 2002; IWC, 1996; Mitchell, 1974; Mitchell & Chapman, 1977; Perry et al, 1999; Tillman, 1977
Blue whale	<i>Balaenoptera musculus</i>	9,000	11,000	12,000	3	0.75	Barlow, 1997; Gambell, 1976; Gunnlaugsson, 1990; Sears et al, 1987; Wade & Gerrodette, 1993
Eden/Bryde's whale	<i>Balaenoptera edeni</i>	34,600	39,000	48,300	4	0.25	Barlow, 1997; Carretta et al, 2002; Hansen et al, 1995; IWC, 1997; Kato, 2002; Ohsumi, 1981; Ohsumi & Tamura, 2000; Tershy et al, 1990; Wade & Gerrodette, 1993; Waring et al, 2002
Bryde's whale	<i>Balaenoptera brydei</i>	67,000	80,000	97,600	4	0.25	Barlow, 1997; Carretta et al, 2002; Hansen et al, 1995; IWC, 1997; Kato, 2002; Ohsumi, 1981; Ohsumi & Tamura, 2000; Tershy et al, 1990; Wade & Gerrodette, 1993; Waring et al, 2002
Fin whale	<i>Balaenoptera physalus</i>	42,000	80,000	150,000	4	0.25	Aguilar, 2002; Branch & Butterworth, 2001a; Carretta et al, 2002; IWC, 1992; IWC, 1996; IWC, 2004; Moore et al, 2000; Perry et al, 1999
Antarctic minke whale	<i>Balaenoptera bonaerensis</i>	219,000	761,000	1,300,000	2	0.75	Branch & Butterworth, 2001b; IWC, 1991b
Dwarf minke whale	<i>Balaenoptera acutorostrata</i>	134,000	181,600	244,000	2	0.75	Borchers et al, 1997; Buckland et al, 1992; IWC, 1984; IWC, 1991a; IWC, 2004; Palka et al, in review; Kingsley & Reeves, 1998; Schweder et al, 1990; Schweder, 1997; Waring et al, 2001;

Appendix 4. (cont.)

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
Humpback whale	<i>Megaptera novaeangliae</i>	22,290	28,000	40,000	3	0.5	Branch & Butterworth, 2001a; Calambokidis et al, 1997b; Calambokidis et al, 2001; Carretta et al, 2002; IWC, 2000b; IWC, 2004; Stevick et al,
Gray whale	<i>Eschrichtius robustus</i>	17,500	26,500	32,500	1	1	Angliss & Lodge, 2002; Buckland & Breiwick, 2002; Deecke, 2004; Hobbs & Rugh, 1999; IWC, 2003; Weller et al, 1991; Weller et al 2002;
Pygmy right whale	<i>Caperea marginata</i>	1,000	3,000	10,000	6	0	Baker, 1985; Kemper, 2002; Klinowska, 1993; Trites et al, 1997
Heaviside's dolphin	<i>Cephalorhynchus heavisidii</i>	1,000	3,000	5,000	5	0	Best & Abernethy, 1994; Culik,2002; Dawson, 2002
Hector's dolphin	<i>Cephalorhynchus hectori</i>	5,300	7,300	10,000	1	1	Dawson, 2002; Slooten et al, 2002
Commerson's dolphin	<i>Cephalorhynchus commersonii</i>	800	1,300	5,000	3	0.5	Dawson, 2002; Goodall, 1994b; Leatherwood et al, 1988; Lescrauwaet et al, 2000; Venegas, 1987
Black dolphin	<i>Cephalorhynchus eutropia</i>	1,000	1,500	3,000	6	0	Culik,2002; Dawson, 2002; Goodall, 1994a
Long-beaked common dolphin	<i>Delphinus capensis</i>	20,000	32,000	87,000	4	0.25	Barlow, 1997
Arabian common dolphin	<i>Delphinus tropicalis</i>	5,000	10,000	15,000	6	0	Guesstimate
Short-beaked common dolphin	<i>Delphinus delphis</i>	2,300,000	3,700,000	12,000,000	3	0.5	Barlow, 1997; Carretta et al, 2002; Goujon, 1996; Hammond et al, 2003; Palka et al, in review; Wade & Gerrodette, 1993; Waring et al, 2002; Yukov, 1986
Pygmy killer whale	<i>Feresa attenuata</i>	20,000	40,000	100,000	5	0.25	Donohue, 2002; Wade & Gerrodette, 1993; Waring et al, 2002
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	150,000	224,000	600,000	4	0.25	Barlow, 1997; Carretta et al, 2002; Hansen et al, 1995; Miyashita, 1993c; Mobley et al, 2000; Mullin et al, 2003; Palka in review; Wade & Gerrodette, 1993; Waring et al, 2002
Long-finned pilot whale	<i>Globicephala melas</i>	473,000	998,000	1,743,000	2	0.75	Buckland et al, 1993a; Hay, 1982; Kasamatsu & Joyce, 1995; Kingsley & Reeves, 1998; Mullin et al, 2003; Palka et al, in review; Waring et al, 2002

Appendix 4. (cont.)

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
Risso's dolphin	<i>Grampus griseus</i>	170,000	308,000	1,000,000	4	0.25	Barlow, 1997; Carretta et al, 2002; Hansen et al, 1995; Miyashita, 1993a; Mobley et al, 2000; Mullin et al, 2003; Wade & Gerrodette, 1993; Waring et al, 2002
Fraser's dolphin	<i>Lagenodelphis hosei</i>	150,000	300,000	1,000,000	4	0.25	Dolar, 1999; Hansen et al, 1995; Wade & Gerrodette, 1993; Waring et al, 2002
White-beaked dolphin	<i>Lagenorhynchus albirostris</i>	16,000	26,000	60,000	3	0.5	Alling & Whitehead, 1987; CeTAP, 1982; Hammond et al, 2002; Sigurjónsson et al, 1989; Sigurjónsson et al, 1997; Waring et al, 2002
Hourglass dolphin	<i>Lagenorhynchus cruciger</i>	100,000	145,000	200,000	3	0	Boyd, 2002; Kasamatsu & Joyce, 1995; Matsuoka et al, 2003
Dusky dolphin	<i>Lagenorhynchus obscurus</i>	4,039	10,000	20,000	4	0.25	Schiavini et al, 1999; van Waerebeek, 1999; Würsig et al, 1997
Atlantic white-sided dolphin	<i>Lagenorhynchus acutus</i>	57,000	145,000	300,000	2	0.75	MacLeod, 2001; Kingsley & Reeves, 1998; O'Cadhla et al, 2001; Palka et al, 1995; Palka et al, in review; Waring et al, 2002
Pacific white-sided dolphin	<i>Lagenorhynchus obliquidens</i>	200,000	990,000	4,200,000	1	1	Angliss & Lodge, 2002; Barlow, 1997; Buckland et al, 1993b; Carretta et al, 2002
Peale's dolphin	<i>Lagenorhynchus australis</i>	1,000	3,000	10,000	6	0	Goodall et al, 1997; Goodall, 2002a; Lesclauwaet, 1997
Northern right whale dolphin	<i>Lissodelphis borealis</i>	55,000	270,000	1,350,000	2	0.75	Buckland et al, 1993b; Forney et al, 1995; Mangel, 1993; Miyashita, 1993b
Southern right whale dolphin	<i>Lissodelphis peronii</i>	50,000	270,000	1,000,000	6	0	Lipsky, 2002; Jefferson et al, 1994 & inferred from northern right whale dolphin
Irrawaddy dolphin	<i>Orcaella brevirostris</i>	1,000	1,300	2,600	6	0	Culik, 2002; Freeland & Bayliss, 1989; Marsh, 1989; Smith & Beasley, 2003; Stacey & Leatherwood, 1997
Killer whale	<i>Orcinus orca</i>	29,500	46,000	100,000	3	0.25	Angliss & Lodge, 2002; Branch & Butterworth, 2001a; Carretta et al, 2002; Christensen, 1988; Ford et al, 2000; Gunnlaugsson & Sigurjónsson, 1990; Hansen et al, 1995; Miyashita, 1993; Wade & Gerrodette, 1993; Waring et al, 2002

Appendix 4. (cont.)

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
Melon-headed whale	<i>Peponocephala electra</i>	39,000	51,000	200,000	4	0.25	Caretta et al, 2002; Dolar, 1999; Hansen et al, 1995; Mobley et al, 2000; Wade & Gerrodette, 1993; Waring et al, 2002
False killer whale	<i>Pseudorca crassidens</i>	20,000	56,500	300,000	4	0.25	Hansen et al, 1995; Miyashita, 1993; Mobley et al, 2000; Wade & Gerrodette, 1993; Waring et al, 2002
Tucuxi	<i>Sotalia fluviatilis</i>	1,000	3,000	10,000	6	0	Culik, 2002; da Silva & Best, 1994; da Silva, 1996; Geise, 1991; Geise et al, 1999;
Indian hump-backed dolphin	<i>Sousa plumbea</i>	600	1,200	2,400	4	0.25	Jefferson & Karczmarski, 2001 & refs therein; Karczmarski et al, 1999; Pilleri & Pilleri, 1979; Ross et al, 1994
Atlantic hump-backed dolphin	<i>Sousa teuszii</i>	120	500	1,000	6	0	Nortabartolo-di-Sciara et al, 1998; Ross et al, 1994; Ross, 2002; van Waerebeek et al, 2002
Pacific hump-backed dolphin	<i>Sousa chinensis</i>	1,100	1,300	2,600	4	0.25	Corkeron et al, 1997; Culik, 2002; Jefferson & Leatherwood, 1997; Jefferson, 2000; Jefferson & Karczmarski, 2001; and refs therein
Pantropical spotted dolphin	<i>Stenella attenuata</i>	1,025,000	1,835,000	7,000,000	3	0.5	Dolar et al, 1997; Gerrodette, 2000; Miyashita, 1993; Mobley et al, 2000; Mullin et al, 2003
Atlantic spotted dolphin	<i>Stenella frontalis</i>	40,000	80,000	400,000	2	0.25	Fulling et al, 2003; Mullin & Fulling, 2003; Palka et al, in review; Waring et al, 2001
Striped dolphin	<i>Stenella coeruleoalba</i>	1,960,000	2,700,000	7,000,000	4	0.25	Barlow, 1997; Carretta et al, 2002; Forcada & Hammond, 1998; Goujon, 1993; Miyashita, 1993; Mobley et al, 2000; Mullin et al, 2003; Wade & Gerrodette, 1993
Clymene dolphin	<i>Stenella clymene</i>	12,000	18,000	56,000	4	0.25	Jefferson et al, 1996; Jefferson, 2002; Jefferson & Curry, 2003; Mullin & Hoggard, 2000; Mullin & Fulling, 2003
Spinner dolphin	<i>Stenella longirostris</i>	875,000	1,420,000	4,500,000	4	0.25	Dolar et al, 1999; Gerrodette, 1999; Mobley et al, 2000; Wade & Gerrodette, 1993
Rough-toothed dolphin	<i>Steno bredanensis</i>	90,000	150,000	500,000	4	0.25	Caretta et al, 2002; Fulling et al, 2003; Jefferson, 2002; Mobley et al, 2000; Wade & Gerrodette, 1993

Appendix 4. (cont.)

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
Indian Ocean bottlenose dolphin	<i>Tursiops aduncus</i>	1,500	5,000	7,500	6	0	Guesstimate based on bottlenose dolphin estimates
Bottlenose dolphin	<i>Tursiops truncatus</i>	350,000	510,000	1,000,000	3	0.5	Barlow, 1997; Caretta et al, 2002; Dolar et al, 1997; Fulling et al, 2003; Kaschner, 2003; Klinowska, 1991; Miyashita, 1993; Mullin et al, 2003; Sokolov, 1997; Wade & Gerrodette, 1993; Waring et al, 2002;
Pygmy sperm whale	<i>Kogia breviceps</i>	3,200	5,300	15,000	5	0.25	Barlow, 1997; Caretta et al, 2002; Mullin et al, 2003; Palka et al, in review; Waring et al, 2002
Dwarf sperm whale	<i>Kogia simus</i>	8,000	12,500	36,000	5	0.25	Barlow, 1997; Caretta et al, 2002; Mullin et al, 2003; Palka et al, in review; Wade & Gerrodette, 1993; Waring et al, 2002
Beluga or white whale	<i>Delphinapterus leucas</i>	92,500	144,265	210,000	3	0.5	Angliss & Lodge, 2002; Frost et al, 1993; Harwood et al, 1996; Hobbs, 2000; Hobbs et al, 2000; IWC, 2000a
Narwhal	<i>Monodon monoceros</i>	36,500	53,000	80,000	6	0	IWC, 2000a; Koski & Davis, 1994; Larsen et al, 1994; Richard et al, 1994
Finless porpoise	<i>Neophocoena phocaenoides</i>	10,000	20,000	40,000	3	0.5	Culik, 2002; Kasuya, 1994; Kumaran, 2002; Miyashita et al, 1994; Yoshida et al, 1997; Zhang et al, 1993
Burmeister's porpoise	<i>Phocoena spinipinnis</i>	5,000	10,000	50,000	6	0	Brownell & Praderi, 1982; Brownell & Praderi, 1994; Brownell & Clapham, 1999
Harbour porpoise	<i>Phocoena phocoena</i>	375,000	575,000	817,800	2	0.75	Angliss & Lodge, 2002; Calambokidis et al, 1997a; Caretta et al, 2002; Hammond et al, 2002; Kingsley & Reeves, 1998; Laake et al, 1997; Palka, 2000; Sokolov et al, 1997; Waring et al, 2002
Vaquita	<i>Phocoena sinus</i>	77	567	1,073	1	1	Jaramillo-Legorreta et al, 1999
Spectacled porpoise	<i>Phocoena dioptrica</i>	1,000	3,000	10,000	6	0	Goodall, 2002b
Dall's porpoise	<i>Phocoenoides dalli</i>	700,000	1,186,000	1,400,000	4	0	Angliss & Lodge, 2002; Barlow, 1997; Buckland et al, 1993b; Caretta et al, 2002; Miyashita & Kasuya, 1988; Miyashita, 1991; Turnock et al, 1995; Turnock et al, 1995

Appendix 4. (cont.)

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
Sperm whale	<i>Physeter macrocephalus</i>	106,000	360,000	616,000	1	0.25	Barlow & Taylor, 1998; Baylock et al, 1995; Christensen et al, 1992; Gunnlaugson & Sigurjónsson, 1990 IWC, 2001; Kato & Miyashita, 2000; Mobley et al, 2000; Wade & Gerrodette, 1993; Waring et al, 2000; Whitehead, 2002
Franciscana	<i>Pontoporia blainvillei</i>	4,000	20,000	60,000	4	0.25	Crespo, 2002; Culik, 2002; Secchi et al, 2001
Arnoux's beaked whale	<i>Berardius arnuxii</i>	1,000	1,500	3,000	6	0	Balcomb, 1989; Ponganis et al, 1995; Rogers & Brown, 1999; Trites et al, 1997
Baird's beaked whale	<i>Berardius bairdii</i>	3,500	7,000	10,500	4	0.25	Angliss & Lodge, 2002; Kasuya, 1997
Northern bottlenose whale	<i>Hyperoodon ampullatus</i>	10,000	44,500	60,000	4	0.25	Gowans et al, 2000; NAMMCO, 1995; Sigurjónsson et al, 1991; Sigurjónsson & Vikingsson, 1997
Southern bottlenose whale	<i>Hyperoodon planifrons</i>	450,000	560,000	700,000	3	0.75	Kasamatsu et al, 1988; Kasamatsu & Joyce, 1995; Kasamatsu et al, 2000; Matsuoka et al, 2003
Longman's beaked whale	<i>Indopacetus pacificus</i>	1,000	5,000	10,000	6	0	Pitman, 2002; Pitman et al, 1999; Wade & Gerrodette, 1993
Gray's beaked whale	<i>Mesoplodon grayi</i>	1,000	1,500	3,000	6	0	Pitman, 2002
True's beaked whale	<i>Mesoplodon mirus</i>	1,000	1,500	3,000	6	0	Pitman, 2002
Andrews' beaked whale	<i>Mesoplodon bowdoini</i>	1,000	1,500	3,000	6	0	Pitman, 2002
Gervais' beaked whale	<i>Mesoplodon europaeus</i>	1,000	1,500	3,000	6	0	Pitman, 2002
Ginkgo-toothed beaked whale	<i>Mesoplodon ginkgodens</i>	1,000	1,500	3,000	6	0	Pitman, 2002
Stejneger's beaked whale	<i>Mesoplodon stejnegeri</i>	1,000	1,500	3,000	6	0	Pitman, 2002
Hector's beaked whale	<i>Mesoplodon hectori</i>	1,000	1,500	3,000	6	0	Pitman, 2002
Spade-toothed beaked whale	<i>Mesoplodon traversii</i>	1,000	1,500	3,000	6	0	Pitman, 2002
Pygmy beaked whale	<i>Mesoplodon peruvianus</i>	1,000	2,500	5,000	6	0	Pitman, 2002; Wade & Gerrodette, 1993
Sowerby's beaked whale	<i>Mesoplodon bidens</i>	1,000	1,500	3,000	6	0	Pitman, 2002

Appendix 4. (cont.)

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
Strap-toothed whale	<i>Mesoplodon layardii</i>	1,000	1,500	3,000	6	0	Pitman, 2002
Perrin's beaked whale	<i>Mesoplodon perrini</i>	1,000	1,500	3,000	6	0	Pitman, 2002
Hubb's beaked whale	<i>Mesoplodon carlhubbsi</i>	1,000	1,500	3,000	6	0	Pitman, 2002
Blainville's beaked whale	<i>Mesoplodon densirostris</i>	10,000	15,000	30,000	5	0	Barlow, 1997; Caretta et al, 2002; Mobley et al, 2000; Wade & Gerrodette, 1993; Waring et al, 2002
Tasman or Shepherd's beaked whale	<i>Tasmacetus shepherdi</i>	1,000	1,500	3,000	6	0	Pitman, 2002
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	21,700	28,000	70,000	4	0.25	Barlow, 1997; Jefferson & Schiro, 1997; Mullin et al, 2003; Palka et, in review; Wade & Gerodette, 1993; Waring et al, 2002
Walrus	<i>Odobenus rosmarus</i>	146,000	254,000	350,000	4	0	Gilbert, 1989; Gjertz & Wiig, 1995; Kastelein, 2002; Reijnders et al, 1991 & refs therein ; Udevitz et al, 2001
Guadalupe fur seal	<i>Arctocephalus townsendi</i>	3,000	7,408	10,000	1	1	Carretta et al, 2002; Gallo, 1994
South American fur seal	<i>Arctocephalus australis</i>	235,000	285,000	320,000	4	0	Reijnders et al, 1993 & Arnould, 2002
Galapagos fur seal	<i>Arctocephalus galapagoensis</i>	30,000	40,000	50,000	4	0	Trillmich & Limberger, 1985; Trillmich & Ono, 1991
South African & Australian fur seal	<i>Arctocephalus pusillus</i>	1,730,000	1,745,000	1,750,000	2	1	Arnould, 2002 & Reijnders et al, 1993
Subantarctic fur seal	<i>Arctocephalus tropicalis</i>	310,000	350,000	400,000	2	0.75	Bester et al, 2003; Croxall & Gentry, 1997; Guinet et al, 1994; Hofmeyr et al, 1997
Antarctic fur seal	<i>Arctocephalus gazella</i>	1,300,000	1,600,000	1,700,000	2	0.75	Reijnders et al, 1993 & Arnould, 2002
Juan Fernandez fur seal	<i>Arctocephalus philippii</i>	15,000	18,000	30,000	1	1	Arnould, 2002; Torres, 1987; J. Francis (pers. comm. In Wickens & York, 1997)
New Zealand fur seal	<i>Arctocephalus forsteri</i>	135,000	150,000	200,000	1	1	Arnould, 2002; Gales et al, 2000; Shaughnessy et al, 1995; Shaughnessy et al, 1996; Shaughnessy & McKeown, 2002; Wickens & York, 1997

Appendix 4. (cont.)

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
Northern fur seal	<i>Callorhinus ursinus</i>	800,000	950,000	1,150,000	1	0.75	Angliss & Lodge, 2002; Carretta et al, 2002; Gentry, 2002
Steller's sea lion	<i>Eumetopias jubatus</i>	75,000	95,000	110,000	1	0.75	Angliss & Lodge, 2002; Loughlin et al, 1993; Trites & Larkin, 1996; Sease et al, 2001
Australian sea lion	<i>Neophoca cinerea</i>	9,300	10,500	11,700	1	1	Gales et al, 1994
South (American) sea lion	<i>Otaria flavescens</i>	160,000	200,000	270,000	6	0	Aguayo & Maturana, 1973; Mailuf & Trillmich, 1981; Reijnders et al, 1993; Torres et al, 1979; Vaz-Ferreira, 1982
Hooker's or New Zealand sea lion	<i>Phocartos hookeri</i>	11,100	12,500	14,000	1	1	Gales & Fletcher, 1999
Galapagos sea lion	<i>Zalophus wollebaeki</i>	10,000	14,000	25,000	2	1	Salazar, 1999; Trillmich, 1979
California sea lion	<i>Zalophus californianus</i>	145,000	260,000	275,000	1	1	Aurioles-Gamboa & Zavala-Gonzalez, 1994; Carretta et al, 2002; Heath, 2002;
Hooded seal	<i>Cystophora cristata</i>	600,000	625,000	700,000	3	0.5	Hamill et al, 1992; Hamill et al, 1992; ICES, 1991; Reijnders et al, 1993; Stenson et al, 1997; Waring et al, 2002
Bearded seal	<i>Erignathus barbatus</i>	220,000	330,000	700,000	5	0.25	Angliss & Lodge, 2002; Cleator, 1996; Kovacs, 2002; Lunn et al, 1997; Popov, 1982; Reijnders et al, 1993
Gray seal	<i>Halichoerus grypus</i>	206,000	256,000	315,000	2	0.75	Haug et al, 1994; Hauksson, 1987; Hiby et al, 2001; ICES, 2003; Mohn & Bowen, 1996; Reijnders et al, 1993; Stenman & Helle, 1990; Wiig, 1986
Ribbon seal	<i>Histiophoca fasciata</i>	350,000	500,000	750,000	3	0.75	Angliss & Lodge, 2002; Burns, 1981; Fedosev, 2000; Fedosev, 2002; Mizuno et al, 2002; Popov, 1982
Leopard seal	<i>Hydrurga leptonyx</i>	220,000	296,454	440,000	6	0	Bester et al, 1995; Boyd, 2002; Erickson & Hanson, 1990; Laws, 1984; Rogers, 2002
Weddell seal	<i>Leptonychotes weddellii</i>	200,000	400,000	1,000,000	6	0	Bester et al, 1995; Boyd, 2002; Erickson & Hanson, 1990; Thomas, 2002b
Crabeater seal	<i>Lobodon carcinophagus</i>	10,000,000	12,500,000	20,000,000	6	0	Bengtson, 2002; Gilbert & Erickson, 1977; Erickson & Hanson, 1990; Laws, 1984

Appendix 4. (cont.)

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
Southern elephant seal	<i>Mirounga leonina</i>	500,000	640,000	800,000	2	0.75	Boyd, 2002; Boyd et al, 1996; Hindell, 2002; Laws, 1994; Slip & Burton, 1999
Northern elephant seal	<i>Mirounga angustirostris</i>	61,000	101,000	150,000	1	1	Carretta et al, 2002; Hindell, 2002; Stewart et al, 1994
Hawaiian monk seal	<i>Monachus schauinslandi</i>	1,437	1,463	1,500	1	1	Baker & Johanos, 2003; Carretta et al, 2002; Gilmartin, 2002; Johanos & Baker, 2001;
Mediterranean monk seal	<i>Monachus monachus</i>	300	380	470	3	0.5	Aguilar, 1998; Forcada et al, 1999; Forcada, 2000; Gilmartin, 2002
Ross seal	<i>Ommatophoca rossii</i>	100,000	130,000	400,000	6	0	Bester et al, 1995; Boyd, 2002; Erickson & Hanson, 1990; Laws, 1984; Nowak, 1991; Thomas, 2002a
Harp seal	<i>Pagophilus groenlandica</i>	6,130,000	7,200,000	8,000,000	2	1	Healey & Stenson, 2000; ICES, 1994; Lavigne, 2002; Nilssen et al, 2000; Warren et al, 1997; Waring et al, 2002
Largha or spotted seal	<i>Phoca largha</i>	60,000	75,000	200,000	4	0.25	Angliss & Lodge, 2002; Burns, 2002; Dong & Shen, 1991; Lowry et al, 1998; Mizuno et al, 2002; Rugh et al, 1995; Trukin et al, 2000
Harbour seal	<i>Phoca vitulina</i>	367,000	404,000	441,000	2	0.75	Angliss & Lodge, 2002; Bjørge, 1991; Burns, 2002; Carretta et al, 2002; Gilbert & Guldager, 1998; Härkönen et al, 2002; ICES, 2003; Loughlin, 1994; Olesiuk et al, 1990; Waring et al, 2002; Withrow & Loughlin, 1996
Ringed seal	<i>Pusa hispida</i>	4,500,000	6,000,000	8,000,000	3	0.5	Belikov & Boltunov, 1998; Bengston et al, 2000; Born et al, 1998; Härkönen et al, 1998; Frost et al, 1988; Popov, 1982; Reeves, 1998

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