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## **Modeling and mapping resource overlap between marine mammals and fisheries on a global scale**

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### ABSTRACT

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. We 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, we 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 oceanographic 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 2000 publications. By linking species-specific probabilities of occurrences with estimated consumption, we obtained spatially-explicit food consumption estimates (expressed as food intake per km<sup>2</sup> 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 the food types consumed/taken and areas where food/catches were taken. Our 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 proposed. We 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.

KEYWORDS: MODELING, FOOD/PREY, FISHERIES, COMPETITION

### INTRODUCTION

Marine mammals are generally located near or at the top of marine food webs (Pauly *et al.*, 1998b) and 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 (Caddy & Rodhouse, 1998; Parsons, 1992; Pauly *et al.*, 1998a; Springer *et al.*, 2003). On the other hand, as the crisis of

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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 which 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. Beddington *et al.*, 1985; Bowen, 1997; DeMaster *et al.*, 2001; NAFO, 1997; Northridge, 1984, 1991). 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 foodwebs 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 focussed 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.

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., Bax, 1991; Bjørge *et al.*, 2002; Butterworth & Thompson, 1995; Furness, 2002; Harwood & Croxall, 1988; Punt & Butterworth, 1995). These small-scale models are generally relatively complex in structure, but – with a few exceptions (Bjørge *et al.*, 2002; Potelov *et al.*, 2000; Shelton *et al.*, 1997)- 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) as 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., Baumgartner *et al.*, 2003; Gregr & Trites, 2001; 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 e.g., 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. Our 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 modeling techniques. To achieve this, we derive spatially-explicit estimates of food intake by marine mammal species groups and disaggregated fisheries catches using new rule-based approaches within a GIS modeling framework (Kaschner *et al.*, in review; Watson *et al.*, 2004). Combining spatial predictions with information about diet and catch composition then allowed us to map hotspots of resource overlap that may indicate potential conflict between marine mammals and fisheries. We discuss the predicted large-scale patterns with respect to potential management and research implications for the investigation of competition between marine mammal and fisheries.

## METHODS

### Marine mammal species

Our model encompassed 115 species of marine mammals that live predominantly in the marine environment (Appendix 1), but did not include sirenians, sea otters and the polar bear or any of the exclusively freshwater cetacean or pinniped species. We largely followed Rice (1998) taxonomically, but recognized three separate species of right whales as supported by most recent findings (Bannister *et al.*, 2001). In addition, we incorporated a recently described additional species, Perrin's beaked whale (*Mesoplodon perrini*; Dalebout *et al.*, (2002).

### 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, and population biomass of all marine mammal species:

$$Q_i = 365 * \sum_s N_{is} W_{is} R_{is} \quad \dots 1)$$

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.

#### *Abundance estimates and sex ratios*

To obtain an estimate of the worldwide abundance of marine mammal species during the 1990s, we extracted available regional abundance estimates and information about associated uncertainties from more than 1000 published primary (e.g., Bester *et al.*, 2003; Branch & Butterworth, 2001; Mullin & Fulling, 2003; Small *et al.*, 2003; Stevick *et al.*, 2003; Whitehead, 2002) and secondary sources (e.g., Perrin *et al.*, 2002; Reijnders *et al.*, 1993; Ridgway & Harrison, 1999). 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. We 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 (see e.g. abundance estimates compiled for different species in Waring *et al.*, 2002), we 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 of the most reliable mean regional estimates available. These are presented in Appendix 1 together with an assigned level of confidence that reflects the associated uncertainties as judged by the first author. Mean estimates were used in subsequent analysis. However, to further convey the extent of uncertainty, we estimated the proportion of the total distributional area covered by reliable surveys within the 1990s (Appendix 1). In addition, we generated extreme minimum and maximum estimates of global abundance for each species. Minimum estimates were obtained by summing all reliable conservative regional estimates, although we recognize 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.

We 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.

#### *Mean body mass*

We 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:

$$W_{is} = a_{is} * L_{max_{is}}^{b_{is}} \quad \dots 2)$$

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

*Feeding rates, daily rations*

We 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. We 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:

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

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 kg.

**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:

$$R_{is} = 0.42 * W_{is}^{0.67} \dots\dots\dots 4)$$

**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

$$R_{is} = 0.035 * W_{is} \dots\dots\dots 5)$$

**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:

$$R_{is} = 0.482 * W_{is}^{0.524} \dots\dots\dots 6)$$

*Diet composition*

We 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.*, 1998b) (Table 1). We again assumed that species included in our model, but not covered by (Pauly *et al.*, 1998b) due to differences in the taxonomic approach, had the same diet composition as closely related sister species. Food type categories and criteria used to allocate taxa to different categories are briefly described in Table 1. Total consumption by food type was estimated by substituting  $R_{is}$  in the basic food consumption equation with:

$$R_{is} = \sum_{k=1}^9 pDC_{ik} * R_{is} \dots\dots\dots 7)$$

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  $i$ .

**Marine mammal distribution**

To incorporate spatial differences in species occurrence and food consumption, we predicted global distributions of all 115 species of marine mammals using a large-scale Relative Environmental Suitability (RES) model (Kaschner *et al.*, in review). This rule-based, environmental envelope modelling approach relied on published qualitative and quantitative information about species-specific habitat preferences with respect to three basic oceanographic 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 oceanographic 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 online at [www.seaaroundus.org/distribution/search.aspx](http://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 (Kaschner *et al.*, in prep; Kaschner *et al.*, in review). For the purpose of this study, we therefore assumed that RES values in 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).

**Fisheries distribution**

Annual fisheries landings from FAO and other sources from 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, we 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. An additional food type, called ‘non-marine mammal food’, was added. This food type category contained all catches of prey types unlikely to ever be taken by marine mammals, such as large sharks and was consequently set to 0 for all marine mammal species.

### **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, we obtained spatially-explicit estimates of annual food consumption rates for each species, expressed as food intake per km<sup>2</sup> per year for each cell in our global grid. We 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, we ignored all spatial effects of feeding patterns.

For the assessment of resource overlap between marine mammals and fisheries, we 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 Horn (1966) and Morisita (1959). 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. We 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 overall quantity of catch or food taken by either player in this cell, leading to:

$$\alpha_{jl} = \left( \frac{2 \sum_k p_{lk} p_{jk}}{\sum_k p_{lk}^2 + p_{jk}^2} \right) * (pQ_l * pC_j) \quad \dots 8)$$

where  $\alpha_{jl}$  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 that each of the 9 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.

## RESULTS

Although we estimated that food intake of all marine mammal species combined was several times as high as global fisheries catches in the 1990s, our model predicted low overlap in resource exploitation between all marine mammal groups and fisheries if spatial and dietary aspects were taken into account (Fig. 6 A - D).

### 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 4 feeding rate models, with baleen whales, though comparatively low in numbers, taking the bulk of the food due to their large size (Table 2). 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. 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 group 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 1 & Fig. 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 1). 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 1). 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 1 & Fig. 1). Note that error bars in Fig. 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 red in Fig. 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. Marine mammal consumption of food types targeted by fisheries was at the most about the same amount than that taken by fisheries if intake was calculated using any other feeding rate (e.g., Method 3 for baleen whales or Method 2 for pinnipeds; see Table 2).

More than 90% of all fisheries catches fell into 3 food type categories (shown in hues of red and yellow in Fig. 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’.

#### **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. 3). Fisheries were concentrated in relatively small areas and fishing rates can be extremely high, amounting to more than 1000 tonnes per km<sup>2</sup> per year in many of the dark red areas shown in Fig. 3. Highest catches occurred in areas where continental shelves are wide, such as the Bering, East China or North Sea, 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 Indian subcontinent, although catch rates were also relatively high along the coasts of Northwest Africa and the west coast of the Indian subcontinent.

We predicted most of the food that marine mammals consume to be taken further offshore and/or in polar waters (Fig. 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 km<sup>2</sup>) for these groups were comparatively low in most regions and fairly homogenous across large areas (Fig. 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 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 B). However, predicted maximum food consumption densities did not exceed 10 tonnes per km<sup>2</sup> per year for any species group anywhere in the world. Note that predictions of high overlap in some areas, such as the northwestern 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 our 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 estimates, regional differences in stock size are ignored and areas of highly depleted populations, such as e.g. 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 Discussion for more details).

#### **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. 5). 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.

### **Spatially-explicit resource overlap between marine mammals and fisheries**

Overall, our model predicted low overlap in resource exploitation between all marine mammal groups and fisheries in the 1990s (Fig. 6 A - D). High overlap appeared to be restricted to small geographical regions and is mostly concentrated in temperate continental shelf areas of the Northern Hemisphere and the highly productive upwelling systems in the Southern Hemisphere. We predicted highest overlap to occur between pinnipeds and fisheries, with particularly high concentrations in the North Atlantic, Bering Sea and Sea of Okhotsk (Fig. 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. 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. 6 C).

We 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. 7 A – D). Similarly the majority of all fisheries catches ( i.e., > 85 %) stemmed from areas of low overlap.

## **DISCUSSION**

Few studies have attempted to incorporate spatial aspects into marine mammal food consumption and fisheries interaction model and most of these have focussed on smaller geographic scales (Bjørge *et al.*, 2002; García-Tiscar *et al.*, 2003; Shelton, Warren & Stenson, 1997). Our 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 (Kaschner *et al.*, in prep; Kaschner *et al.*, in review), providing support for the approach taken here. The worldwide consumption by major marine mammal groups we estimated is similar to previously published global estimates (Tamura, 2003; Trites, Christensen & Pauly, 1997; Young, 2000). However, our 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 (Furness, 2002; Hammill & Stenson, 2000; 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 (Bax, 1991; Bjørge *et al.*, 2002; Butterworth & Thompson, 1995; Furness, 2002; Harwood & Croxall, 1988; Punt & Butterworth, 1995). 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 (Boyd, 2002b; Schweder *et al.*, 2000; Sigurjónsson & Víkingsson, 1997). 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 (review in Kaschner & Pauly, 2004).

The generated maps of resource overlap presented here add new perspectives to the issue of potential competition. Our 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. Our 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 foodweb dynamics (e.g. Trites, 2002), we 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., Harwood & McLaren, 2002; IWC, 2003; UNEP, 1999) 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., Harwood & McLaren, 2002; IWC, 2003;

UNEP, 1999). 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, we suggest that it is unlikely for direct competition to pose a severe threat to marine mammal species with large foraging ranges. In contrast, our 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 our 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 our 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. 5 include the Bering Sea where the potential negative impacts of the US groundfish fisheries on the endangered western population of Steller sea lions has been of much 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 e.g. Yodzis, 2001). In addition, the model identifies 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 (Punt & Butterworth, 1995; Wickens *et al.*, 1992) or in the waters surrounding Japan where the perception of marine mammals as competitors appears to be particularly prevalent (Anonymous, 2001a, b). Looking at our 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.

## **Biases and limitations**

### *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, we arrive 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 (Tamura, 2003; Trites, Christensen & Pauly, 1997; Young, 2000), with the notable exception of our global estimate for sperm whale population, which was a substantially adjusted downward estimate based on Whitehead (2002). Given the large body weight of this species, our much lower abundance estimate by itself accounts for most of the observed differences between our results and previously estimated large-scale marine mammal food consumption (Tamura, 2003; Trites, Christensen & Pauly, 1997; Young, 2000).

#### **FEEDING RATES**

As apparent from the range of results presented in Table 2 and Fig. 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, 1981a, b; Winship *et al.*, 2002). All models are based on certain assumptions about physiological parameters about the feeding requirements of a specific individual (e.g., Innes *et al.*, 1986; Klumov, 1963) 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 (IWC, 2003; Leaper & Lavigne, 2002) 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 our 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. We 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, our 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 & Schell, 1996; Best *et al.*, 1995). 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, we therefore likely overestimated total marine mammal consumption. Unfortunately, evaluating the impact of the lack of seasonal feeding patterns on our estimates is difficult as direct comparisons with other studies that have considered such seasonal variation (Boyd, 2002b; Kenney *et al.*, 1997; Shelton, Warren & Stenson, 1997; Sigurjónsson & Víkingsson, 1997) is hampered by the differences in modelling approaches and parameterisation.

#### **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; Das *et al.*, 2003; Hooker *et al.*, 2001) and fatty acid (Grahl-Nielsen *et al.*, 2003; Hooker *et al.*, 2001; Iverson, 1993; Lea *et al.*, 2002) analyses allow the investigation of diets over longer time period, but results are often difficult to interpret and come with their own sets of uncertainties (Smith *et al.*, 1997).

The standardized diet composition used here may be fairly robust to these sources of biases, as our 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, 1997, 16] – 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 our 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. 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.

#### *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 and the currently documented occurrence of a species. This is not surprisingly given the broad approach we took.

By their nature, RES predictions are often closer to likely historical distributions of species than their currently utilized range extent (Kaschner *et al.*, in review). In combination with a current feature of our 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 grey whale population, part of whose biomass is falsely allocated to this area, since it is predicted to be ‘suitable’ by the RES model.

Similarly, our 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, we ignored large differences in food intake in feeding versus breeding grounds. Food consumption is likely much more concentrated in polar areas than we 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; Murase *et al.*, 2002; Ribic *et al.*, 1991), but migrate to subantarctic (pinnipeds) or even tropical breeding grounds (baleen whales).

#### *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 (Chase & Leibold, 2003; Hanski, 1978; Hurlbert, 1978). The index developed by Horn (1966) and Morisita (1959) that formed the basis for our resource overlap index (Equation 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, we 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 our 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 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.

Our 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 our 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.

#### **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 our 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 our model, can furthermore help to determine research priorities and select appropriate scales for the development of management approaches that deal with issues of marine mammal-fisheries interactions.

#### **CONCLUSIONS**

We 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, we 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 our 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.

Our analysis, in conjunction with others that have focused on fisheries-related issues at the same global scale (Myers & Worm, 2003; Pauly *et al.*, 2003; Pauly *et al.*, 2002; Watson *et al.*, 2004; Watson & Pauly, 2001; Worm *et al.*, 2003), 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.

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Table 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 <sup>a</sup>
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;

Table 2. Global annual food consumption estimates for 4 major marine mammal groups during an average year of the 1990s generated using 4 different feeding rate models. Global mean fisheries catches for the same time period are included for comparison

	Abundance	Food consumption			Catches
		[million tonnes * year <sup>-1</sup> ]			
		Feeding rate method			
		1	2	3	4
Mysticetes	1,249,841	81.82	98.48	202.01	28.26
Pinnipeds	35,710,705	61.85	135.44	59.88	75.55
Large odontocetes	15,647,267	40.20	50.23	94.80	34.72
Small odontocetes	1,043,000	29.90	63.48	31.27	15.25
Fisheries					80.92



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Figure 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 red (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 2. 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.*, 1998b). 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.

Figure 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 Figure 4, except for the lowest category, which combines 3 of the marine mammal categories. Highest concentrations of fisheries catches are taken from northern hemisphere shelf areas and from the highly productive 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 to more than 1000 tonnes per km<sup>2</sup> per year – more than 100 times the top marine mammal food consumption rates predicted anywhere in the world (Kaschner, 2004).

Figure 4. 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. Maps were produced by linking species-specific food consumption estimates to predicted species distributions and then summing rates across all species within a taxonomic group. Non-regular colour-coded scale, described in the legend, is the same as in Figure 3, except for 3 added low-density categories needed to make patterns visible for all species groups. Food consumption is more homogeneously distributed than fisheries catches (Compare Figure 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 km<sup>2</sup> per year anywhere in the oceans – 100 times less than top fisheries extraction rates. Also note that some areas of apparent high consumption, such as the northwestern 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 our model..

Figure 5. 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.

Figure 6. 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. The overlap index is based on a comparison of similarity in the composition of diets of marine mammal species and catches of global fisheries in a particular cell, as represented by the proportions of different food types taken by each player in this cell and then weighted by the proportion of total global catch and food consumption taken in the cell. Overall 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. Specifically, overlap between pinnipeds and dolphins is predicted to be higher in the northern hemisphere, while overlap between baleen whales and the larger toothed whales appears to be more concentrated in the southern hemisphere. 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. Predictions of high overlap in some areas, such as the northwestern Pacific for the baleen whales, are misleading as these are based on overestimates of food consumption in these areas. Overestimates are due to a specific feature of our 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.

Figure 7. 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 more than 99 % of all marine mammal food consumption stems from areas of very low overlap. Similarly, more than 85 % of all fisheries catches are taken in areas of very low overlap.

Fig. 1

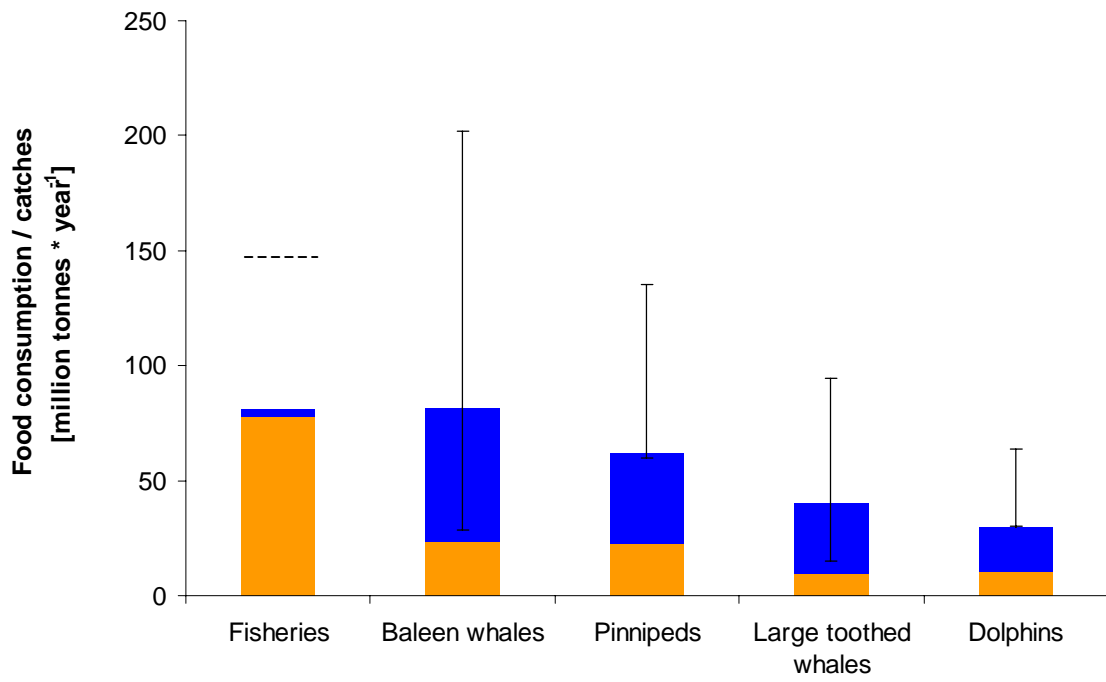
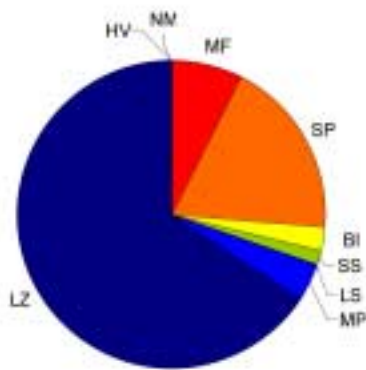
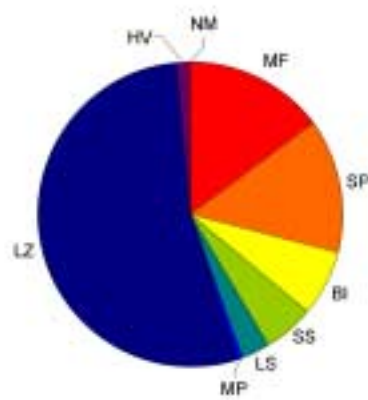


Fig. 2

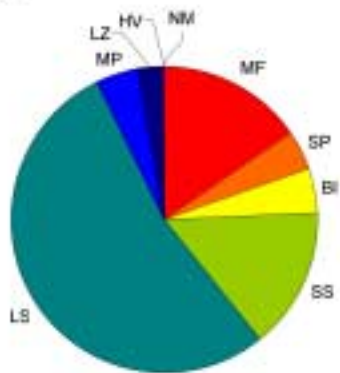
Baleen whales



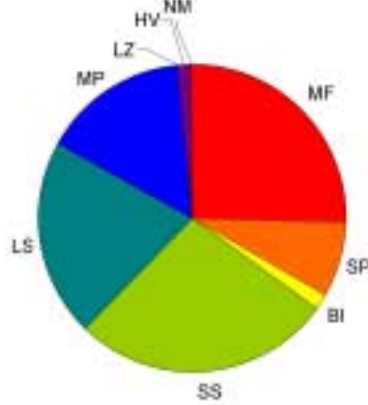
Pinnipeds



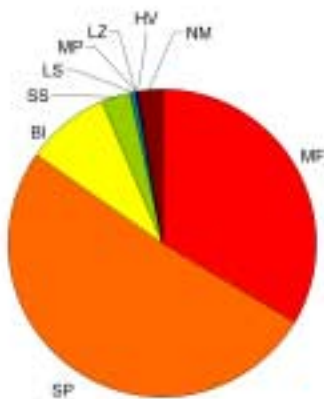
Large toothed whales



Dolphins



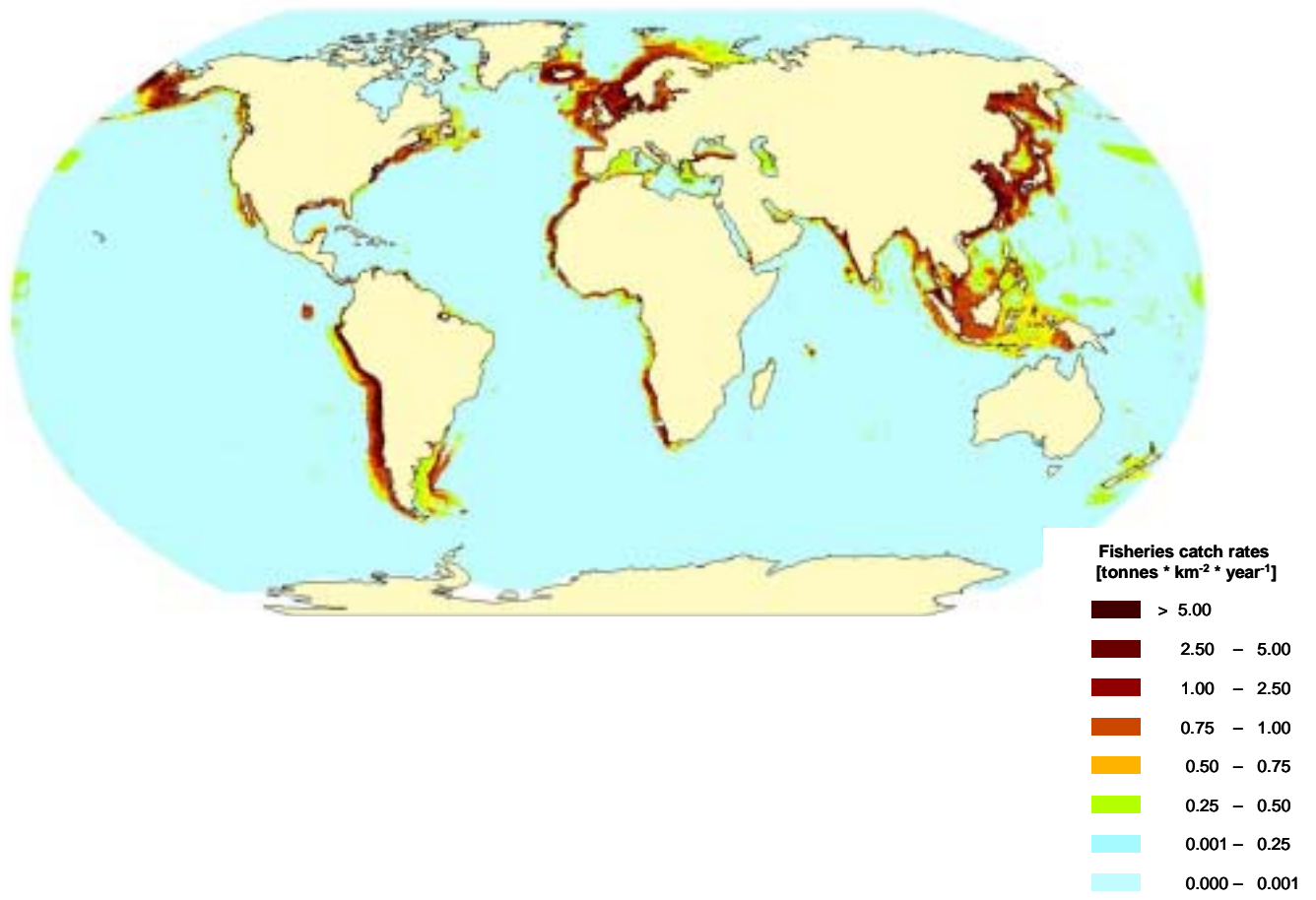
Fisheries



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)

Fig. 3



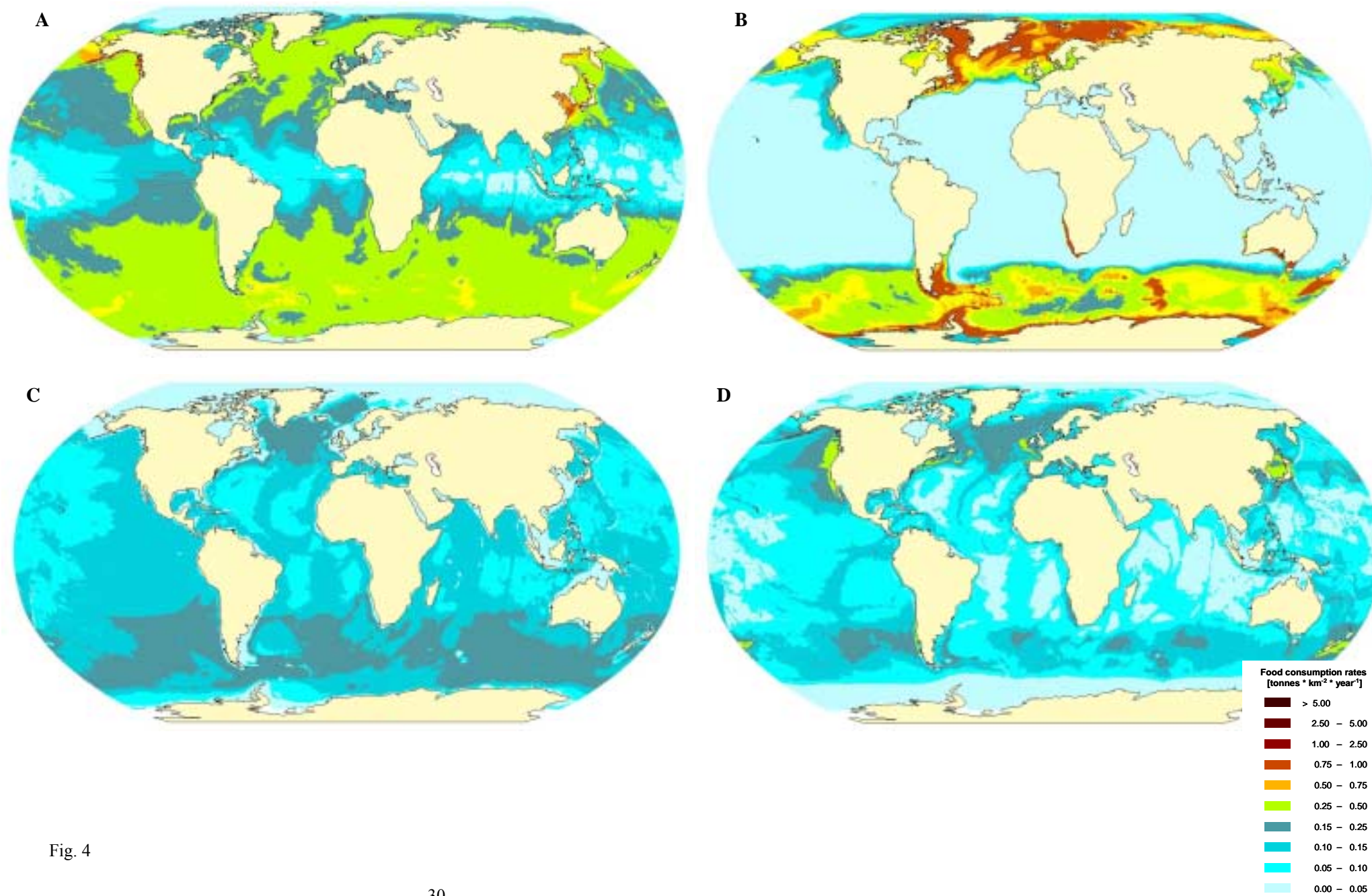


Fig. 4

Fig. 5

Food consumption / fisheries catches  
[million tonnes \* year<sup>-1</sup>]

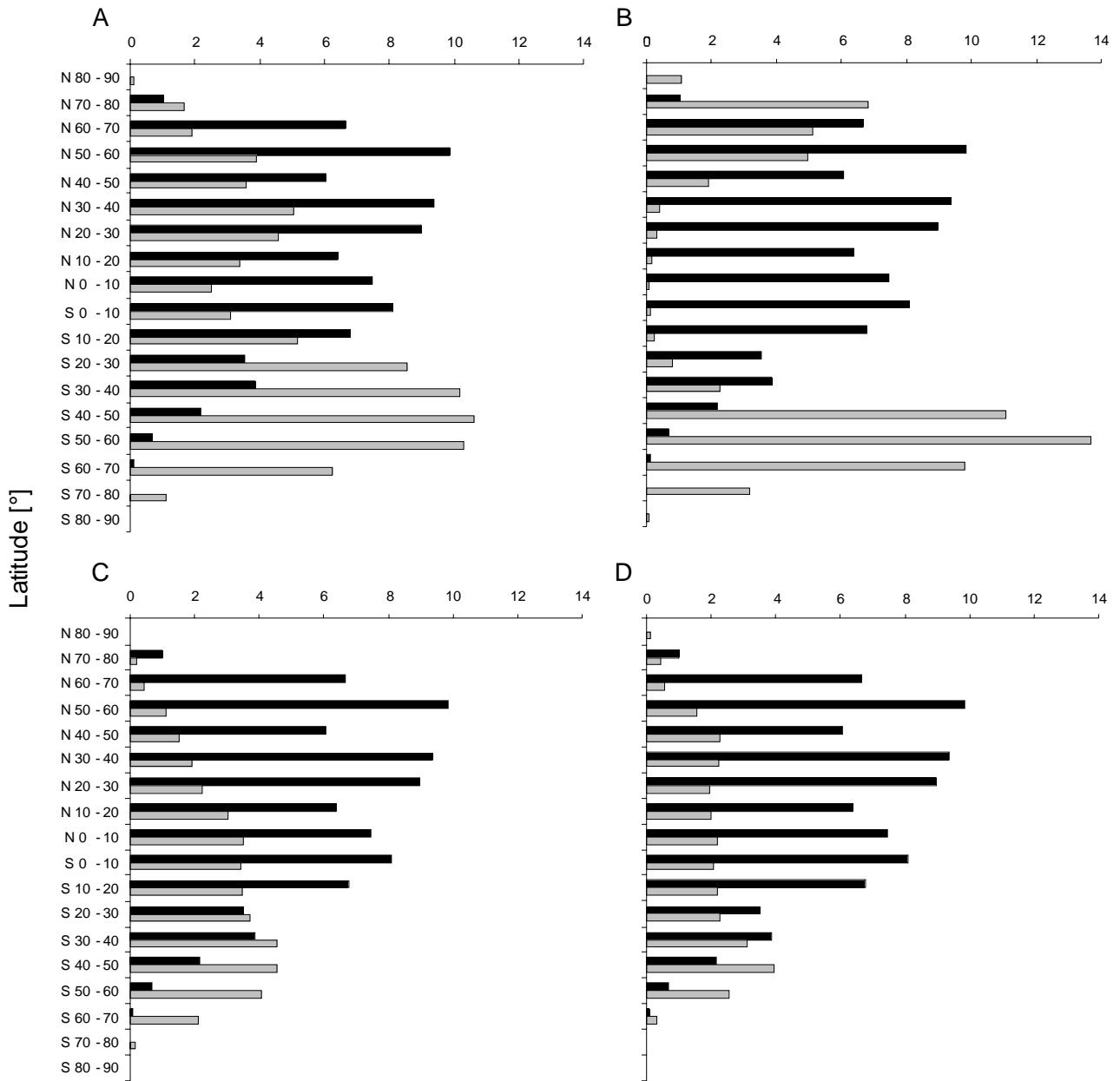
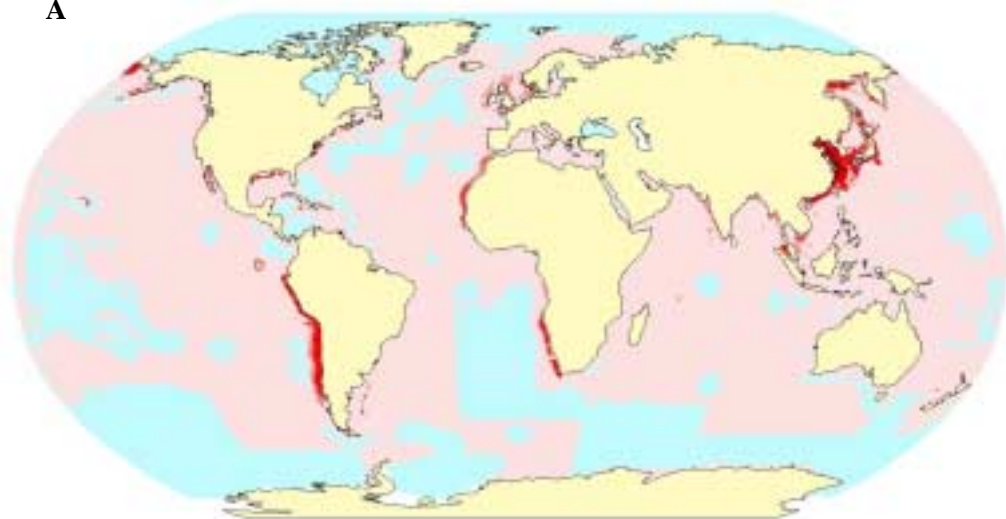


Fig. 6

A



B



C



D

Resource  
overlap index

High

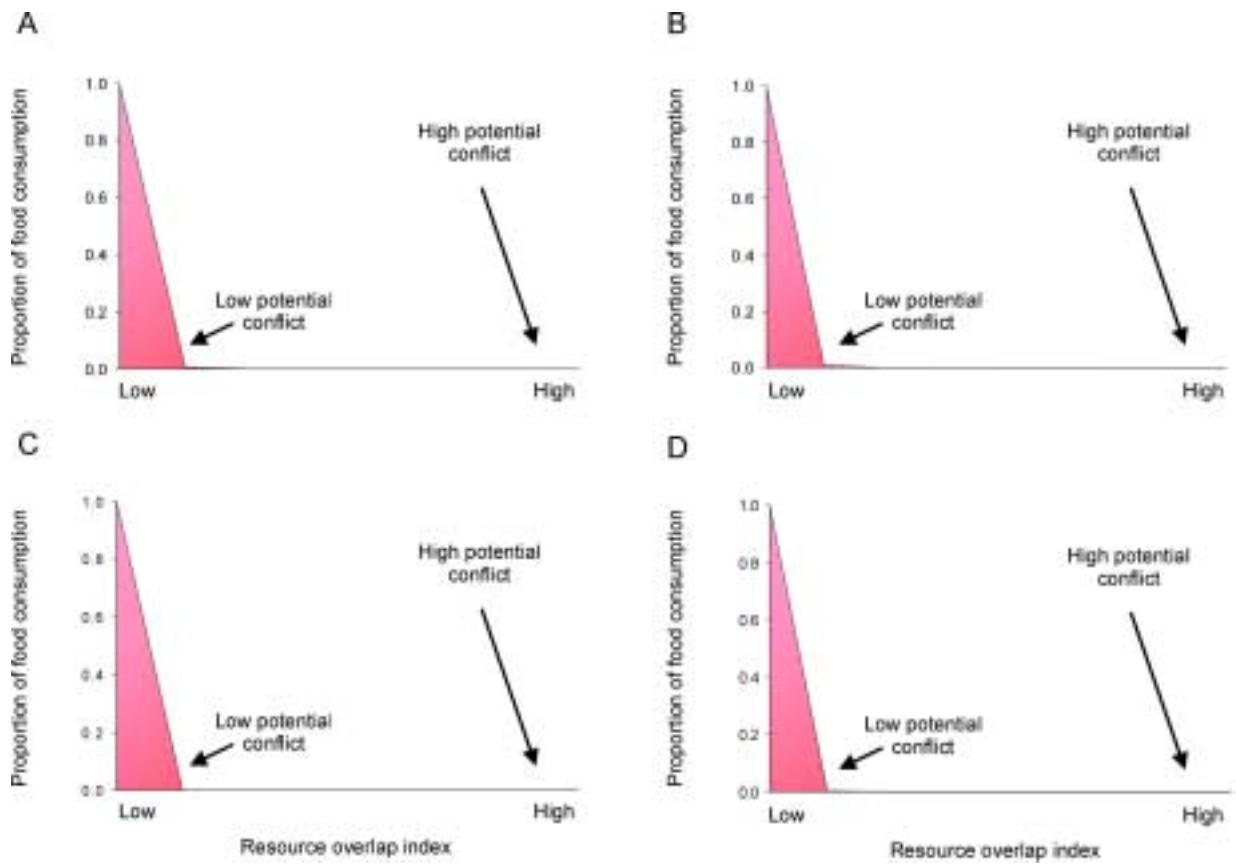


Low

0



Fig. 7



Appendix 1. 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 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
Southern right whale	<i>Eubalaena australis</i>	7,000	7,000	7,000	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
North Pacific right whale	<i>Eubalaena japonicus</i>	500	1,250	2,600	3	0.5	IWC, 1998; Perry et al, 1999
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;
Antarctic minke whale	<i>Balaenoptera bonaerensis</i>	219,000	761,000	1,300,000	2	0.75	Branch & Butterworth, 2001; IWC, 1991b
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
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
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
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
Fin whale	<i>Balaenoptera physalus</i>	42,000	80,000	150,000	4	0.25	Aguilar, 2002; Branch & Butterworth, 2001; Carretta et al, 2002; IWC, 1992; IWC, 1996; IWC, 2004; Moore et al, 2000; Perry et al, 1999
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
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;

Appendix 1. (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, 2001; Calambokidis et al, 1997; Calambokidis et al, 2001; Carretta et al, 2002; IWC, 2000; IWC, 2004; Stevick et al, 2003
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
Commerson's dolphin	<i>Cephalorhynchus commersonii</i>	800	1,300	5,000	3	0.5	Dawson, 2002; Goodall, 1994; 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, 1994
Heaviside's dolphin	<i>Cephalorhynchus heavisidii</i>	1,000	3,000	5,000	6	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
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, 2000
Long-beaked common dolphin	<i>Delphinus capensis</i>	20,000	32,000	87,000	4	0.25	Barlow, 1997
Short-beaked common dolphin	<i>Delphinus delphis</i>	2,300,000	3,700,000	12,000,000	3	0.5	Hammond et al, 2003; Palka et al, in review; Sokolov et al, 1997; Wade & Gerrodette, 1993; Waring et al, 2002
Arabian common dolphin	<i>Delphinus tropicalis</i>	5,000	10,000	15,000	6	0	guestimate
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, 1993; 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, 1993; Hay, 1982; Kasamatsu & Joyce, 1995; Kingsley & Reeves, 1998; Mullin et al, 2003; Palka et al, in review; Waring et al, 2002
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, 1993; Mobley et al, 2000; Mullin et al, 2003; Wade & Gerrodette, 1993; Waring et al, 2002

Appendix 1. (cont.)

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
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 & Víkingsson, 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
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
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
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
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
Peale's dolphin	<i>Lagenorhynchus australis</i>	1,000	3,000	10,000	6	0	Goodall et al, 1997; Goodall, 2002; Lescrauwaet, 1997
Hourglass dolphin	<i>Lagenorhynchus cruciger</i>	100,000	145,000	200,000	3	0	Boyd, 2002; Kasamatsu & Joyce, 1995; Matsuoka et al, 2003
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, 1993; Carretta et al, 2002
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
Northern right whale dolphin	<i>Lissodelphis borealis</i>	55,000	270,000	1,350,000	2	0.75	Buckland & Cattanach, 1993; Forney et al, 1995; Mangel, 1993; Miyashita, 1993
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
Sowerby's beaked whale	<i>Mesoplodon bidens</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
Hubb's beaked whale	<i>Mesoplodon carlhubbsi</i>	1,000	1,500	3,000	6	0	Pitman, 2002

Appendix 1. (cont.)

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
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
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
Gray's beaked whale	<i>Mesoplodon grayi</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
Strap-toothed whale	<i>Mesoplodon layardii</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
Perrin's beaked whale	<i>Mesoplodon perrini</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
Stejneger's beaked whale	<i>Mesoplodon stejnegeri</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
Narwhal	<i>Monodon monoceros</i>	36,500	53,000	80,000	6	0	IWC, 2000; 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
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, 2001; 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
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
Spectacled porpoise	<i>Phocoena dioptrica</i>	1,000	3,000	10,000	6	0	Goodall, 2002
Harbour porpoise	<i>Phocoena phocoena</i>	375,000	575,000	817,800	2	0.75	Angliss & Lodge, 2002; Calambokidis et al, 1997; 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

Appendix 1. (cont.)

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
Burmeister's porpoise	<i>Phocoena spinipinnis</i>	5,000	10,000	50,000	6	0	Brownell & Praderi, 1982; Brownell & Praderi, 1994; Brownell & Clapham, 1999
Dall's porpoise	<i>Phocoenoides dalli</i>	700,000	1,186,000	1,400,000	4	0	Angliss & Lodge, 2002; Barlow, 1997; Buckland & Cattanach, 1993; Caretta et al, 2002; Miyashita & Kasuya, 1988; Miyashita, 1991; Turnock et al, 1995; Turnock et al, 1995
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
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;
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
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
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
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
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

Appendix 1. (cont.)

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
Atlantic spotted dolphin	<i>Stenella frontalis</i>	40,000	80,000	400,000	4	0.25	Fulling et al, 2003; Mullin & Fulling, 2003; Palka et al, in review; Waring et al, 2001
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
Tasman or Shepherd's beaked whale	<i>Tasmacetus shepherdi</i>	1,000	1,500	3,000	6	0	Pitman, 2002
Indian Ocean bottlenose dolphin	<i>Tursiops aduncus</i>	1,500	5,000	7,500	6	0	guestimate based on bottlenose dolphin
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;
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
South American fur seal	<i>Arctocephalus australis</i>	235,000	285,000	320,000	4	0	Reijnders et al, 1993 & Arnould, 2002
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
Galapagos fur seal	<i>Arctocephalus galapagoensis</i>	30,000	40,000	50,000	4	0	Trillmich & Limberger, 1985; Trillmich & Ono, 1991
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)
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
Guadalupe fur seal	<i>Arctocephalus townsendi</i>	3,000	7,408	10,000	1	1	Carretta et al, 2002; Gallo, 1994
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

Appendix 1. (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
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
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
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	2	0	Bester et al, 1995; Boyd, 2002; Erickson & Hanson, 1990; Thomas, 2002
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
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
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
Mediterranean monk seal	<i>Monachus monachus</i>	300	380	470	3	0.5	Aguilar, 1998; Forcada et al, 1999; Forcada, 2000; Gilmartin, 2002
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;
Australian sea lion	<i>Neophoca cinerea</i>	9,300	10,500	11,700	1	1	Gales et al, 1994
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



Appendix 1. (cont.)

Common name	Scientific name	Minimum abundance	Mean abundance	Maximum abundance	Level of confidence	Proportion of distribution covered by surveys	Source
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, 2002
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
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
Hooker's or New Zealand sea lion	<i>Phocarcetos hookeri</i>	11,100	12,500	14,000	1	1	Gales & Fletcher, 1999
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
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;
Galapagos sea lion	<i>Zalophus wollebaeki</i>	10,000	14,000	25,000	2	1	Salazar, 1999; Trillmich, 1979

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