

## MODELING AND MAPPING TROPHIC OVERLAP BETWEEN MARINE MAMMALS AND COMMERCIAL FISHERIES IN THE NORTH ATLANTIC

*Kristin Kaschner, Reg Watson, Villy Christensen, Andrew W. Trites and Daniel Pauly*

*Fisheries Centre, University of British Columbia  
2204 Main Mall, Vancouver, B.C., Canada V6T 1Z4*

### ABSTRACT

The impact that fishing operations may have on marine mammals and other components of marine ecosystems is a major concern today. Fisheries, in addition to causing by-catch mortalities, affect marine mammals through direct and indirect competition for the same food sources. Our goal was to assess the potential trophic impact of fisheries on mammal populations in the North Atlantic by quantifying the overlap in resource exploitation in space and time using high-resolution modeling and mapping.

We developed a relatively simple model to estimate feeding requirements (specified by food type) and population biomass of all North Atlantic marine mammal species. Main model input parameters were population abundance, sex-specific mean body mass, standardized diet compositions, and weight-specific feeding rates. A spatial model was constructed using a geographic information system to link annual food consumption estimates to the corresponding species-specific, rasterized distributional ranges. Spatially explicit food intake (expressed as proportions of total food intake per 1/2 degree latitude/longitude square) was further refined by incorporating information about habitat preferences and feeding patterns. Superimposing the geographically matching fisheries catches (generated by a similar rule-based model) allowed the calculation of overlap between fisheries catches and marine mammal consumption. The model indicates that, in the North Atlantic, total food consumption of marine mammals in the 1990s was three times higher than total fisheries catches. However, spatially disaggregating consumption and specifying intake by food type showed actual resource overlap to be quite low. Areas of high overlap in the North Atlantic are concentrated along the East coast of North America (35° - 53° N) and in European shelf waters.

This visualization of geographical 'hotspots' of marine mammal-fisheries interactions may help to identify areas of conflict, realized or potential. Hence the meta-analysis approach taken here may serve as a useful management tool in the context of defining marine mammal critical habitat and efficient MPAs design.

### INTRODUCTION

Marine mammals are generally located near or at the top of marine food webs (Pauly *et al.*, 1998) and it has been suggested that, being apex predators, some species may have or have had considerable impact on the structuring of pelagic ecosystems (Merrick, 1997). Hence, the status of marine mammal populations may reflect the state of an ecosystem (Timoshenko, 1995) and may serve as an indicator of the sustainability with which it is being managed. As a result, many studies have attempted to qualitatively and quantitatively assess the ecological role of marine mammals (e.g., NAFO, 1997; Trites *et al.*, 1997). The influence of marine mammals on the ecosystem, however, is difficult to describe by any single feature, or indeed even several features. Nonetheless, modeling some aspects of marine mammal ecology may help delineate ranges, test hypotheses, and describe patterns qualitatively (Bogstad *et al.* 1997; Stenson *et al.* 1997).

In the past fifty years the majority of marine mammal populations have been reduced to very low levels and, despite extensive management efforts, have failed to recover in many cases. It has been speculated that human fishing activities may be one of the major factors affecting recovery rates (Bowen, 1985; Crespo *et al.*, 1997). Mortality may occur through incidental entanglement of marine mammals in fishing gear (Northridge, 1984, 1991) or through competition for food resources (Bowen, 1985; Trites *et al.*, 1997). Understanding the mechanisms and the extent to which fisheries are competing with marine mammals would greatly facilitate management decision regarding conservation measures to protect endangered marine mammal populations.

To quantify the degree of overlap between two of the top predators in marine food webs (marine mammals and humans), estimates of food resource utilization for both predators are required. Available fisheries catch data have numerous shortcomings, lack of spatial resolution and reliable quantification of discards first amongst them. Nonetheless, quantification of global fisheries catches is, for obvious reasons, more reliable than any direct attempts to

determine the total intake of a very large and diverse group of free-ranging animals. Modeling feeding requirement has therefore been recognized as the only avenue to estimate marine mammal consumption (Bogstad *et al.*, 1997).

A multitude of approaches, varying greatly in complexity and detail, have been applied to the problem of modeling food consumption. Approaches differ in three main respects: geographic scale, number of species included and model complexity, i.e., the number of parameters taken into account. However, until now, most studies have focused on small numbers of species in limited geographic areas (e.g., Doidge and Croxall, 1985; Stenson *et al.*, 1997; Nilssen *et al.*, 2000) and included sex- and age-specific information for each input parameter as well as specifying seasonal changes (Bogstad *et al.*, 1997). Some of these have also integrated explicit spatial and temporal changes in food requirements (Sigurjonsson and Vikingsson, 1997; Potelov *et al.*, 2000).

The few models encompassing larger areas and higher taxonomic groupings generally assume homogenous geographic distribution and feeding patterns, which positions them at the other end of the scale with respect to model complexity (Hinga, 1979; Trites *et al.*, 1997; Tamura and Ohsumi, 1999, 2000; Young, 1999). Furthermore, these highly simplified models assume uniform feeding rates across all age classes within a given species, ignoring the effect of individual size or sex on food requirements as well as spatial and seasonal differences (e.g., Tamura and Ohsumi, 1999).

While the danger of simplistic models is well known, it must also be realized that over-parameterization may also reduce model precision due to the accumulation of uncertainties (Stenson *et al.*, 1997). Problems related to the estimation of detailed input parameter values are certainly likely for a large proportion of marine mammal species, considering the dearth of reliable information about life history, growth curves and feeding ecology.

The importance of choosing the appropriate analytical scale when modeling ecological systems has been stressed by numerous researchers (Legendre and Fortin, 1989; Levin, 1992; Jaquet, 1996; Jaquet and Whitehead, 1996; Logerwell *et al.*, 1998; Pauly and Pitcher, 2000). When temporal and spatial scales are too small relative to the processes of interest, high parameter variation will overwhelm the model's ability to

detect patterns (Jaquet, 1996). Although comparatively small geographic scales will suffice when studying certain marine mammal species, a large number of species is highly migratory, and range globally or hemispherically. Similarly, modern fishing fleets cover long distances, roaming the world's oceans. Due to feeding patterns, availability of prey species or management decisions, exploitation of the resources sustaining both groups may be highly irregular over the course of a year. A model should, therefore, be global in scale and cover time spans of, at least, a year to capture the interactions between the two groups. Adding more species is also desirable, as it will increase the model's scope.

Resolution is another critical consideration (Jaquet, 1996). Investigators have suggested that a consistent ratio between marine mammal biomass and primary production may exist, indicating these top predators may be very efficient in the utilization of available food web energy (Trites *et al.*, 1997). Such basin-scale patterns may only be detectable at very large scales through cross-ecosystem comparisons. However, if the resolution of data is too coarse, details are averaged and patterns are masked. Storing input parameters at a high resolution allows for studying broad scales, while preserving detail, thus allowing for analysis on multiple scales (Jaquet, 1996)

## METHODS

### Marine mammal 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 47 North Atlantic marine mammal species (excluding West Indian manatee and polar bear):

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

where  $N_{is}$  is the number of individuals by sex  $s$  of species  $i$ ,  $W_{is}$  is the mean individual weight by sex and species; and  $R_{is}$  is the daily ration (by sex and species) for an individual of weight  $W_{is}$ .

The main advantage of this model is that it can be applied to the numerous species of marine mammals about which very little is known. Unknown parameter values can be inferred through empirical relationships, e.g., those of Innes *et al.* (1987), or Trites and Pauly (1998),

wherein required parameters are estimated based on other, often more readily available data.

Main model input parameters were species-specific abundance estimates, mean body mass (specified by sex), standardized diet compositions and weight-specific feeding rates, which have been compiled in a global marine mammal database. Below is a brief description of the approach taken for each input parameter.

### **Species abundance and sex ratio**

As the areas covered by surveys are usually limited, abundances are generally estimated only for a fraction of the total population, such as subspecies or sub-populations, or for a limited geographical stratum. To obtain an estimate of the total North Atlantic abundance of a species, the following approach was taken. Abundance estimates were taken from primary data sources, wherever possible (e.g., Oeien and Oeritsland, 1993; Jefferson, 1996; IWC, 1997; Jefferson and Schiro, 1997; Waring *et al.*, 2000) supplemented by secondary sources (e.g., Riedman, 1990; Reijnders *et al.*, 1993; Ridgway, 1994, 1999) when necessary. All available regional estimates were compiled in a database, jointly with information about the time period and geographical area covered by the estimate, the method used to obtain it, and the associated uncertainties. Estimates were then assigned to specific standardized areas and time periods and ranked based on the reliability of the surveying technique and the estimate itself, as judged by the first author. (Surveys explicitly devoted to population/abundance estimation are relatively rare and, in many cases are conducted with a frequency of over a decade. Consequently, the most recent abundance estimate available was classified as a 1990s estimate and all historic estimates predating the 1970s were classified as 1950s (including so-called 'pre-exploitation' estimates). In cases where no historic estimate could be found, a conservative approach was taken, assuming no change in population abundance during the past 50 years).

Default model input parameter values, i.e., the total North Atlantic abundance estimates for each species, were then derived through summation of the most reliable regional abundance estimates available or via extrapolation to the total distributional range of a species.

Population sex ratios were assumed to be balanced, except in cases where explicit information on other population ratios was available (including closely related species with similar life histories).

### **Mean body mass**

The estimation of mean individual body mass, required to calculate total population biomass, is comparatively simple if life tables and growth curves are available. Unfortunately, this information is unobtainable for many species. Based on the strong correlations between growth rate, survival, longevity and maximum length, Trites and Pauly (1998) developed a method allowing the estimation of mean body masses of marine mammals from maximum body length. The functional relationship between the two parameters can be expressed as:

$$W_{is} = a_{is} L_{\max, is}^{b_{is}} \quad \dots 2)$$

where  $W_{is}$  is the mean body mass of an individual of the species  $i$  and the sex  $s$ ,  $L_{\max, is}$  is the corresponding maximum length reported for such an individual. Variables  $a_{is}$  and  $b_{is}$  are sex-specific regression coefficients varying for different high-order taxonomic groups, established by regressing (log) maximum length against (log) mean body mass in 30 marine mammal species with known growth curves and life tables (see Trites and Pauly (1998) for details and for the species-specific body mass estimates for North Atlantic marine mammal species thus obtained).

### **Daily rations and diet composition**

Food consumption of marine mammals have been studied extensively using direct observations of consumption and scat analysis as well as using indirect approaches, such as isotope ratios (Todd *et al.*, 1997). Feeding rates have been estimated based on direct measurements of food intake or maximum stomach contents (Innes *et al.*, 1987; Lockyer, 1987). Alternatively, feeding rates can be derived from calculated energy budgets using bioenergetic models (Lockyer, 1981). These models are based on certain assumptions about physiological parameters, the feeding requirements of a specific individual (e.g., Klumov, 1963; Innes *et al.*, 1986) or standard metabolic rates of the species (Sigurjonsson and Vikingsson, 1997). Here, daily food rations were estimated from the empirical model of Innes *et al.* (1987), as modified by Trites *et al.* (1997; see below).

Diet composition of marine mammals is difficult to obtain, and most dietary information is only available in the form of qualitative summaries (e.g., Riedman, 1990), thus precluding its direct use in trophic modeling studies. However, by combining scattered quantitative studies with qualitative summaries mentioned in the literature, Pauly *et al.* (1998) were able to obtain

standardized diet compositions for the overwhelming majority of marine mammal species, consisting of the proportion of eight prey types (see Table 1). Thus, total food consumption by food type can here be estimated by substituting  $R_{is}$  in the basic food consumption equation with:

$$R_{is} = \sum_{j=1}^8 pDC_{ijs} * (0.1 * W_{is}^{0.8}) \quad \dots 3)$$

where  $pDC_{ijs}$  is the proportion of food type  $j$  in the diet of species  $i$  and the sex  $s$  and the second part of the product describes the weight specific energy requirements or feeding rate of an individual with  $W_{is}$  as the mean body weight of an individual in kg. The exponent of this equation was derived by Innes *et al.* (1987), whereas the multiplicative term was adjusted by Trites *et al.* (1997) to account for the difference between consumption for growth and for maintenance.

**Table 1.** Correspondence between the eight marine mammals food groups used here (left column) and groups reported in the fisheries catch databases.

Food group <sup>a)</sup>	Taxa included	ISSCAAP Group <sup>b)</sup>
<b>Benthic invertebrates</b>	All crustaceans (except krill), seasquirts, bivalves, gastropods, octopus	42 -45, 47, 52-56, 58, 75-77
<b>Large zooplankton</b>	Krill (especially <i>Euphausia superba</i> )	46, 74
<b>Small squid</b>	Mantle length < 50 cm; e.g., Gonatidae	Part of 57
<b>Large squid</b>	Mantle length ≥ 50 cm; e.g., Onychoteuthida	Part of 57
<b>Miscellaneous fishes</b>	<i>FishBase</i> <sup>c)</sup> habitat attributes: demersal; benthic; benthopelagic; bathydemersal; reef-associated (max. size so far: all); pelagic (max. size: ≥ 80 cm)	21-25, 32-34, 36-39
<b>Mesopelagic fishes</b>	<i>FishBase</i> <sup>c)</sup> habitat attributes: bathypelagic (max. size: all)	Not covered
<b>Small pelagic fishes</b>	<i>FishBase</i> <sup>c)</sup> habitat attributes: pelagic (max. size < 80 cm)	Part of 35

<sup>a)</sup> From Pauly *et al.* (1998);

<sup>b)</sup> From FAO's International Standard Statistical Classification of Aquatic Animals and Plants;

<sup>c)</sup> See Froese and Pauly (2000).

## Spatially explicit food consumption model

### **Distributional ranges of species**

As a next step, the species-specific estimates of food consumption generated by the model were linked to the corresponding distributional ranges of each species.

Delineation of geographical ranges of marine mammals is greatly hampered by difficulties in defining the limits of the distribution of these elusive and often highly mobile animals. Due to the vastness of the marine environment, surveys designed for estimating population sizes usually cover only a small fraction of the distributional ranges of most species (e.g., Waring *et al.*, 2000). Also, a substantial proportion of marine mammal species were described based only on a few stranded specimens or sightings (e.g., some of the beaked whales). For these, determining distributional ranges other than 'ocean-wide' is presently not possible. (Note that the low population numbers assigned to these rare species preclude their biasing the results presented below.)

In consequence, delineation of a species range is mostly based on the professional judgment of experts rather than actual quantitative analysis (e.g., Riedman, 1990; Reijnders *et al.* 1993), except in a few cases where unusually large and regionally stratified sighting data are available (e.g. Townsend, 1935).

We used the distributional ranges of pinniped species as compiled in Reijnders *et al.* (1993), who based their delineations on direct consultation with experts for the individual species. Geographic ranges of the other taxonomic groups of marine mammals (cetaceans, sirenians, marine otters and polar bear) were plotted based on the distribution maps in Jefferson *et al.* (1993). All ranges describe the maximum limits of the geographical distribution of a species over the course of a whole year, i.e., including all areas covered during the annual migrations. Levels of confidence in the distributional range, ranked by the authors based on information provided by Jefferson *et al.* (1993) and Reijnders (1993) have been included in the

model to reflect the origin and reliability of the information and only the most reliable distributions were used.

Species geographic ranges were manually digitized as shapefile polygons using the ArcView GIS tools. Ranges were subsequently re-expressed as presence/absence grid cells in the raster database of 1/2 degree longitude/latitude squares used by the *Sea Around Us* project (see Watson *et al.*, this volume). The total area of the geographic extension  $A_i$  of a species  $i$  was calculated using:

$$A_i = \sum_{c_i} a_{c_i} \quad \dots 4)$$

where  $a_{c_i}$  is the area of a grid cell  $c_i$  in which a species  $i$  is present. Assuming a homogenous distribution of the animals, food consumption densities  $qD_i$  in each cell for individual species can be estimated from:

$$qD_i = Q_i/A_i \quad \dots 5)$$

where  $Q_i$  is the total food consumption of a species  $i$  divided by its distributional range  $A_i$ .

Specific fractions of total species abundances, biomass and food consumption can then be assigned to individual grid cells.

#### *Incorporation of habitat preferences*

Obviously the assumption of a homogenous distribution does not reflect well the real distribution of population, biomass and food consumption. Studies have shown that distributions of some species of marine mammals are closely correlated with certain biological and physical environmental parameters, such as depth, slope, sea surface temperature, ice cover and zooplankton distributions (Jaquet and Whitehead, 1996; Griffin, 1997; Moore and DeMaster, 1997). These factors can thus be used as indicators to predict the preferred habitats of a species within its total range of occurrence and some of them were therefore integrated into the model to spatially refine biomass distribution for those species for which the information is available.

Here, specific depth ranges and association with ice edges were encoded for each of the marine mammal species considered in this model, to allow use of the depth information and ice coverage index that are attributes of the 1/2 degree spatial cells in the SAUP database (see Watson *et al.*, this volume). An algorithm was then developed, using a trapezoid probability

distribution, which converted these parameters into 'weighting factors', describing the probability of occurrence of a member of a given species in a particular cell, which would be highest within its preferred range of habitat parameters and lower if the depth and ice attributes of a cell diverge from this optimum. Multiplication of the initial portions of biomass and food consumption densities with the weighting factors of a each spatial cell and a subsequent normalization procedure resulted in realistic spatial distribution of the marine mammal species in question.

#### **Fisheries catches**

Annual fisheries landings from FAO and other sources were adjusted for misreporting, underreporting, etc. following the procedures in Pitcher and Watson (2000), then taxonomically disaggregated and re-assigned into spatial cells of 1/2 degree of longitude by 1/2 degree of latitude using the rule-based procedure described in Watson *et al.* (this volume). The catches were then regrouped into the eight marine mammal food categories mentioned above (Table 1).

This led to maps of fisheries catches, expressed in  $t \cdot km^{-2} \cdot year^{-1}$ , with a resolution of 1/2 degree latitude/longitude, in which the fisheries catches were expressed in the same eight categories also used to describe the food composition of marine mammals, thus allowing computation of an overlap index.

#### **Resource overlap/fisheries impact index**

As the assessment of overlap with fisheries is more sensible at higher taxonomic levels, marine mammal species were grouped into suborders (pinnipeds, odontocetes, mysticetes), with the exception of the beaked whales, here defined as a group distinct from the other odontocetes due to their life history, oceanic distribution, and specialized diet composition. Food intake and diet composition of all marine mammals belonging to the same taxonomic group were averaged within each cell, to obtain an average diet composition and food consumption representative of a given group within each cell.

The estimation of overlap between marine mammal food consumption and fisheries catches by 1/2 degree cell was initially performed using a modified version of an ecological niche overlap index, based on an equation derived by MacArthur and Levins (1967). However, this index, which only considered the qualitative overlap of marine mammal diet vs. catch composition, produced misleading results, as it did not account for the quantities involved. To

incorporate the quantitative aspect, the original index was modified, leading to:

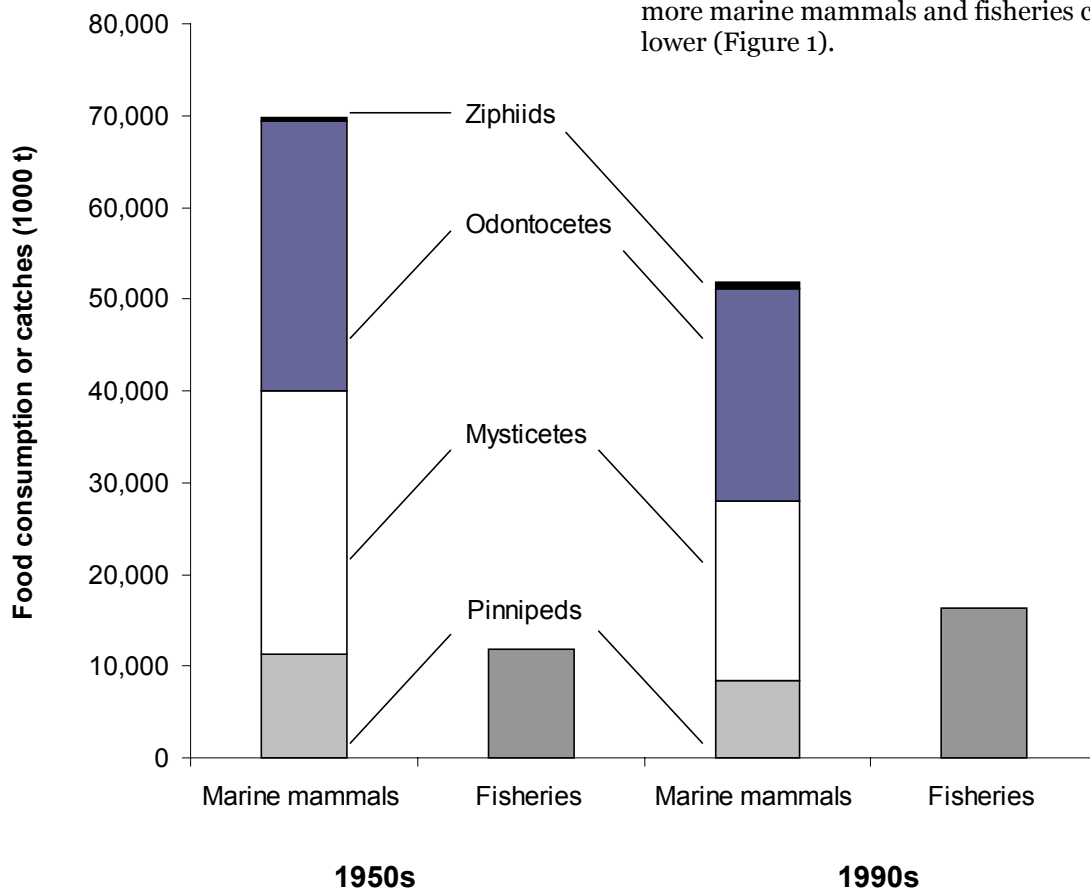
$$a_{jl} = \left( \left( \frac{2 \sum_k p_{lk} p_{jk}}{\sum_k p_{lk}^2 + p_{jk}^2} \right) * (Q_l * C_j) \right) / (NF) \quad \dots 6)$$

where  $a_{jl}$  describes the quantitative overlap between a fishery  $j$  and a marine mammal group  $l$  in each cell, and the first term of the numerator expresses the overlap in diet/catch composition between a marine mammal group  $l$  and fisheries sharing the resource  $k$ , with  $p_{lk}$  and  $p_{jk}$  representing the proportions that each of the  $k$  resources contributes to the average diet of this mammal group  $l$  or the catch composition of the fisheries  $j$ . This term is multiplied with the product of the total average food consumption of

the mammal group  $l$  and the total fisheries' catches within each cell and subsequently normalized using a normalization factor  $NF$ , which is defined as the product of the total food consumption of the marine mammal group and total catches (summed over all cells), adjusted by division by a scaling factor of  $10^9$ .

**RESULTS AND DISCUSSION**

Figure 1 presents, for the North Atlantic, our estimate of food consumption, by marine mammal group in 1950s and the 1990s, compared with the corresponding fisheries catches. In bulk, marine mammals presently consume about three times as much as the fisheries catches, a figure similar to that estimated for the Pacific Ocean (Trites *et al.*, 1997) and for the world ocean as a whole (Tamura and Oshumi, 1999, 2000). This value was higher in the 1950s, when there were more marine mammals and fisheries catches were lower (Figure 1).

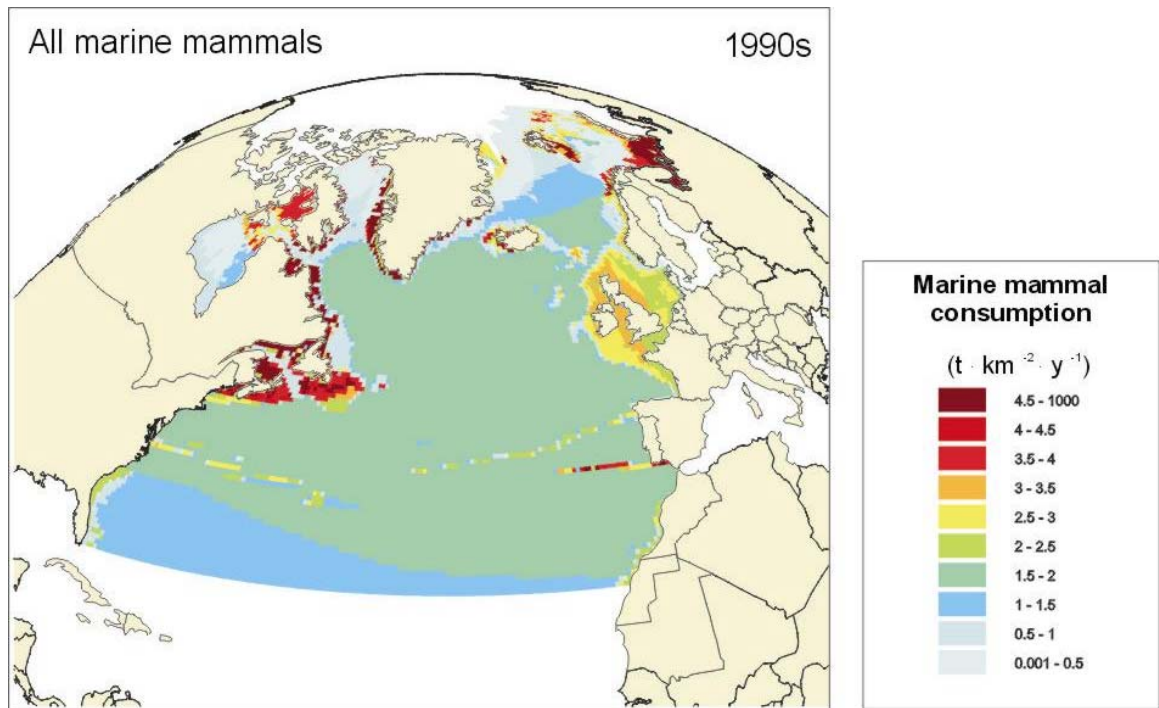


**Figure 1.** Overall marine mammal food consumption specified by marine mammal groups in the 1950s and 1990s, compared with total fisheries catches during the same decades.

This overall figure, however, masks important differences between mammal groups, of which several, with high consumptions (notably the toothed whales), consume preys not exploited by fisheries. Our new maps make this abundantly clear.

Figure 2 shows the spatial distribution of marine mammal food consumption in the 1990s. The

highest consumptions ( $t \cdot km^{-2} \cdot year^{-1}$ ) occur along the shelves, particularly so in Arctic waters, and along the East coast of North America. However, it is the large area of oceanic waters, inhabited by toothed whales (sperm and beaked whales, porpoises and dolphins) that lead, in the aggregate, to large overall consumption figures by marine mammals.



**Figure 2.** Distribution of marine mammals food consumption rates in the North Atlantic (1990s). The online version of this graph is in color (see [www.fisheries.ubc.ca/Projects/SAUP](http://www.fisheries.ubc.ca/Projects/SAUP)).

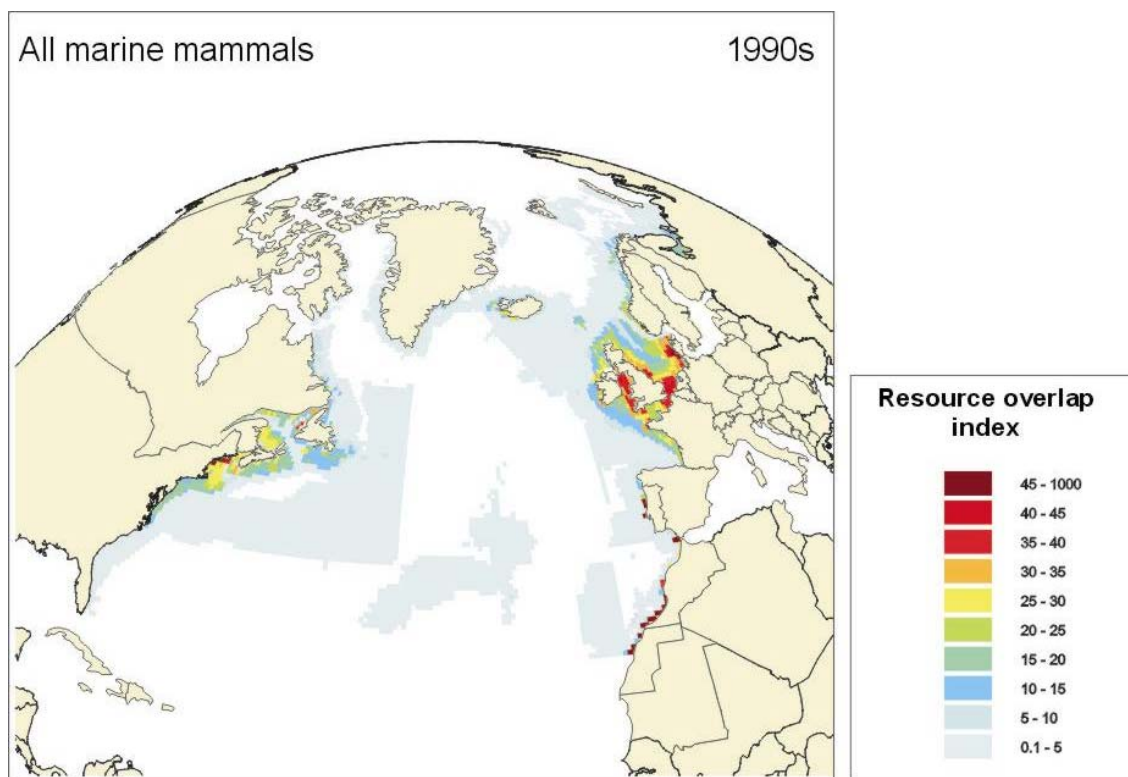
This is confirmed by Figure 3, a map of spatial diet overlap between marine mammal and fisheries. Overlap 'hot spots' occur mainly on, or along the edges of shelves, particularly along the coast of North America, from  $34^{\circ}$  -  $52^{\circ}$  North, and in the North Sea and adjacent waters. Not surprisingly, these are also the areas from which most reports of fishing-mammal interactions originate, e.g., marine mammals getting entangled in fishing nets, or fishing boats ramming whales etc.

The information in Figure 3 can be refined by presenting the data by group of marine mammal (Figure 4). This shows, that:

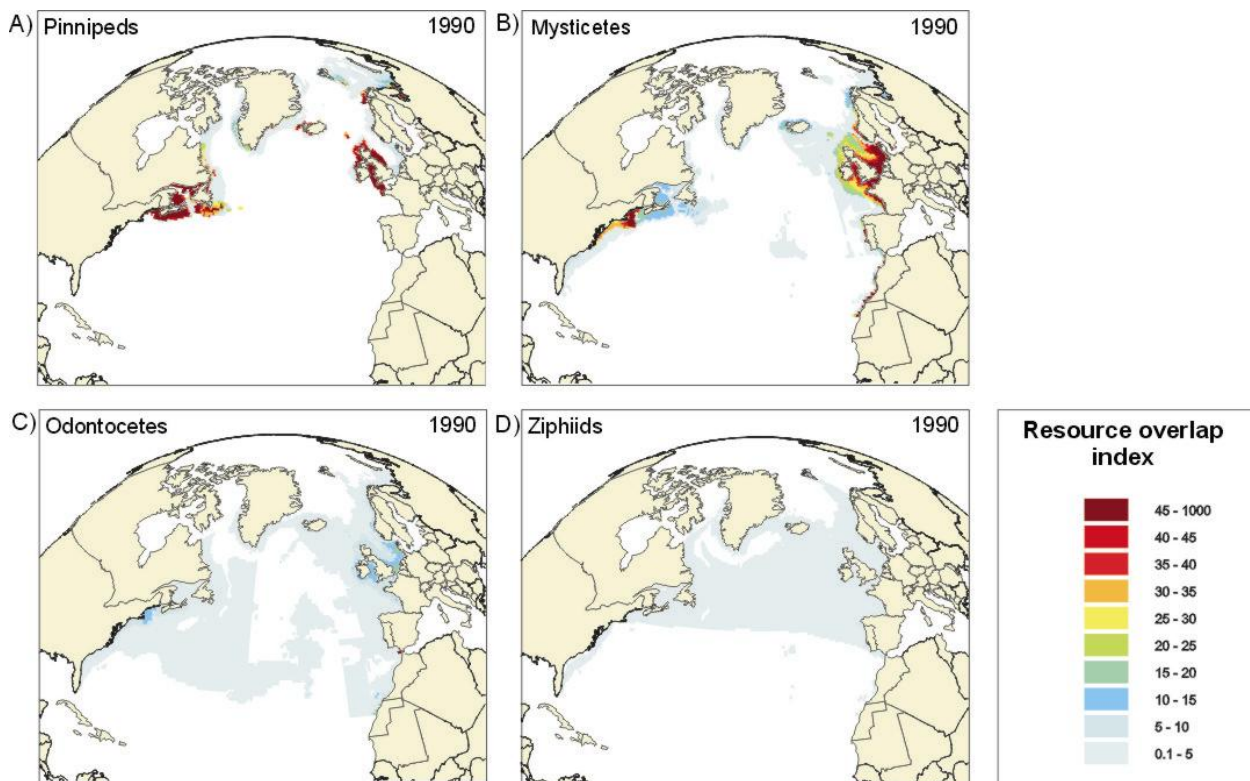
- 1) Marine mammal diet/fisheries overlap is highest for pinnipeds, notably around the British Isles, Newfoundland, the Bay of Fundy and the Gulf of Maine;

- 2) There is almost no overlap between toothed whales and fisheries;
- 3) The baleen whales show intermediate overlap.

Regarding item (3), we should perhaps add that we believe the overlap to be biased upward, because the baleen whale group is presently dominated by Minke whales, which have a higher biomass than all other species combined, and which have been here classified as a 'shelf species', an assignment which some experts will contest. This is a theme that will have to be revisited. Such reviews will also have to consider the sub-population structure of marine mammals (to the extent as they are known), and especially seasonal migration and feeding patterns, so far ignored, and which will have to be modeled explicitly.



**Figure 3.** Distribution of overlap between all marine mammal food consumption and fisheries catches in the North Atlantic (1990s). The online version of this graph is in color (see [www.fisheries.ubc.ca/Projects/SAUP](http://www.fisheries.ubc.ca/Projects/SAUP)).



**Figure 4.** Distribution of overlap between individual marine mammal groups and fisheries catches (1990s). **A:** Pinnipeds; **B:** Baleen whales; **C:** Toothed whales (excl. Beaked whales); **D:** Beaked whales. The online version of this graph is in color (see [www.fisheries.ubc.ca/Projects/SAUP](http://www.fisheries.ubc.ca/Projects/SAUP)).

However, we believe our key result to be the demonstration that our goal, the mapping of marine mammal food consumption, and its overlap with fisheries catches, could actually be reached, despite the lack of detailed data often alleged to preclude approaches of this sort. Clearly, if it is useful to publish maps of species distribution, estimated population numbers, and diet composition, then it is useful, as well, to combine such information into maps such as presented here. Indeed, there is no reason to assume that the uncertainty inherent in the components will render the synthesis useless. For example, many of these uncertainties pertain to local features of the basin-wide distributions that we emphasize here. Moreover, there is no reason to assume that, e.g., the food consumption rate, or mean diet composition of the mammal species considered here would all be biased in the same manner. Indeed, we assume the opposite to be the

case, i.e., that errors in a few species will tend to be compensated by errors in the opposite direction in other species.

We conclude this by pointing out the potential of whale watching as a non-extractive activity that may provide market incentives for encouraging the rebuilding of marine mammal populations. Table 2 provides indicators that the industry presently generates 80 million US\$ in direct expenses, and about 350 million US\$ when indirect expenses are considered. As it appears, this industry is rapidly growing, including in countries – such as Iceland - which officially maintain its option to re-initiate whaling. We consider this an interesting development, as it may contribute to mitigate some of the issues of overlap between fisheries and marine mammals discussed here.

**Table 2.** Direct and total expenses by whale watching tourists, in 1998, both boat- and land-based<sup>a)</sup>

<b>Area</b>	<b>Direct expenses (US \$ '000)<sup>b)</sup></b>	<b>Total expenses (US \$ '000)<sup>b)</sup></b>
<b>Western North Atlantic</b>		
Atlantic Canada	18,336	127,086
St Pierre & Miquelon (France)	16.4	94
New England (USA)	30,600	107,250
Eastern USA	500	1,500
Bermuda	13	20
Bahamas	2,700	2,970
<b>Eastern North Atlantic</b>		
Norway	1,632	12,043
Iceland <sup>c)</sup>	2,958	6,470
Greenland	832	2,750
United Kingdom	1,884	8,231
Ireland	1,322	7,119
France (Mainland)	41	51
Spain (Mainland)	55	192
Canary Islands (Spain)	17,770	62,195
Gibraltar (UK)	225	1,350
Portugal (Mainland)	31	87
Azores Islands (Portugal)	582	3,370
<b>Subtotal Atlantic</b>	<b>79,497.4</b>	<b>342,778</b>
<b>Global expenses</b>	<b>299,509</b>	<b>1,049,057</b>

<sup>a)</sup> All estimates adapted from Hoyt (2001).

<sup>b)</sup> Values scaled to North Atlantic by removing British Columbia from Canadian returns, and assuming the following North Atlantic % components for totals that include the Mediterranean: France: 10%; Spain 10%, Gibraltar 50%.

<sup>c)</sup> In Iceland, as of July 2001, one of eight tourists goes whale watching and total expenses range from \$ 10-13.5 millions.

**ACKNOWLEDGEMENTS**

We would like to thank the Environment Program of The Pew Charitable Trusts, Philadelphia, for funding the *Sea Around Us* project. The senior author would like to acknowledge the financial support received through a Li Tze Fong Memorial fellowship.

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