I - Executive Summary

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1. INTRODUCTION

Long-lived, slow-reproducing marine species such as cetaceans are becoming increasingly endangered due to growing human impacts on the marine environment (Reeves *et al.*, 2003). The interaction between cetaceans and other high predators (notably fisheries) has proved particularly hard to track and understand. Yet, gaining a better insight of the roles played by cetaceans in the dynamics and functioning of the marine ecosystem is a key to propose management policies and measures that would ensure that possible competition for prey resources between cetaceans and fisheries is managed in an optimal fashion. The problem goes in both directions. First, are cetaceans posing significant threats to fishery activities? Second do fisheries leave sufficient resources for the long term survival of these mammals?

In the past, the issue of the role of marine mammals in the ecosystem has been touched upon only sporadically, mostly emphasising the negative effects of marine mammals on fisheries, while the effects of fisheries on marine mammals were downplayed (e.g., ICES 1995). Katona and Whitehead (1988) were the first to argue that cetaceans are ecologically important, urging the implementation of long-term investigations on the ecological role of cetaceans in the various sectors of the world ocean.

The Workshop was held in Venice from 28 to 31 January 2004 to address such issues. The meeting was generously hosted by Thetis S.p.A., in the historic “Arsenale”. Sixteen scientists from eight countries participated in the meeting at the invitation of CIESM.

In welcoming the participants, Frédéric Briand highlighted the exploratory nature of CIESM workshops and recalled the objectives of this meeting which would attempt to capture (at least some of) the multiple facets and dimensions of the problem, from a strict, rigorous scientific perspective. Giuseppe Notarbartolo di Sciara, coordinator of CIESM Task Force on Marine Mammals, followed, introducing the various threads, from physical oceanography, cetacean feeding ecology, conservation biology, to modelling which would be discussed at length in the next days. It was intended that participants would mostly focus on the scientific and methodological aspects of the problem, while naturally keeping important management implications in mind. The Mediterranean was considered a realistic test bed for this issue, as a semi-enclosed sea where sizable numbers of cetacean populations are confronted with intense levels of human activities, particularly fisheries.

1.1 Terminology

Some explanations appear in order for the choice of words. In the workshop title, “role” is a metaphor of course, a human concept (as is “ecosystem”), and its identification depends on the context and purpose of the analysis. Here it was seen as a useful working concept.

Next, why choose “cetaceans” as a whole taxonomic group? What do cetaceans have in common as role players? Obviously they are mostly large (compared to humans), conspicuous animals, especially by virtue of their frequent appearance at the surface as air-breathers. This constant link to the surface, imposed by the cetaceans’ respiratory physiology, enables the adoption of scientific methods for the study of their distribution and abundance, making cetaceans among the best studied marine top predators. As they are naturally rather long lived, cetaceans can accumulate contaminants in their tissues, and thus may act as broad indicators of the state of the oceans.

Cetaceans also draw our attention by their behaviour, their striking form and movement. For millennia they received special status in storytelling, myths and art, particularly in human cultures that have understood that cetaceans are - very unlike fishes - warm-blooded mammals and, like us, have prolonged relationships with their young. Human perception of cetaceans has been sharpened in recent decades by the discovery of complex acoustic communication among them and by observations of their mutual assistance at critical times, for instance during parturition or when under attack.

At one place and time or another, most cetacean species have been targets of fisheries. At other places and times cetaceans have had a “mutualistic” relationship with humans, “assisting” in fishing operations and “sharing” the catches. As a result of growing awareness in human societies, through “whale watching” or other cultural activities, cetaceans are now increasingly seen as symbols of the fragile state of ocean life as a whole.

Cetaceans demand our special attention as particularly vulnerable elements of the ecosystem: they have slow reproductive rates and they are easy targets of modern technologies for locating and killing them. Those cetacean species that move through vast expanses of ocean are especially vulnerable because of the gaps in international law pertaining to the high seas. Another emerging concern is the enormous increase in “industrial” fishing activities aimed at species that are usually part of the cetaceans’ diet.

Many other human activities can, sometimes unexpectedly, be detrimental to cetaceans. One example, in the Black Sea (see CIESM Monograph 14, 2001), was the introduction, from the ballast-water of ships plying from elsewhere, of a ctenophore that preys on the larvae of the anchovy, the small clupeoid fish that nourished the once-very large populations of dolphins in the Black Sea and supported the region’s largest fishery. This example carries two related lessons for us. First, the ecological role of specific cetaceans in particular places can change greatly over time as a result of human activities, as well as of natural causes. Second, the common assumption that change resulting from past exploitation is reversible is not necessarily the most plausible assumption to make.

As a first step in the discussion, consensus was reached on the definitions of the following key concepts:

Ecosystem. There are various ways to define an ecosystem (e.g., a group of interacting organisms that forms a relatively closed environmental unit, the definition that is used in much of this report), depending on the communities and spatial scales considered. Recently, much effort has been devoted to defining “Large Marine Ecosystems” of the world (Sherman and Duda, 1999; www.lme.noa.gov) which might provide a proper ecological framework for studying the roles of the cetaceans. Obviously, some cetaceans will be restricted within the boundaries of one system, as relatively narrowly defined, while others (e.g., most of the great whales) span two or more systems.

Competition. A direct or indirect ecological relationship where a change in the abundance of one of the components results in the opposite change in the abundance of the other.

Direct effect. An interaction between two components of a system which involves no intermediate components (e.g. predation).

Indirect effect. An interaction between two components of a system which occurs through an intermediate component of the system (e.g. competition).

Concerning the types of interactions between marine mammals and fisheries, Goldsworthy *et al.* (2003) provide the following useful distinction: *operational interactions* (also known as *direct* or *overt*), which occur between marine mammals and fisheries operations, and *trophic interactions* (also known as *ecological*, *indirect* or *covert*) where the consumption of resources by marine mammals may impact on the resources available to the human fisheries, or vice versa.

1.2 Trophodynamics

As large, and in many places numerous, predators, cetaceans are ecologically significant as stoers and movers of nutrients (carbon and nitrogen, especially) and energy, within and between ecosystems. Categorising cetaceans generally as large predators does tend to obscure their trophic diversity: most of the baleen whales, for example, especially in the southern hemisphere, carry biological production directly from the bottom of the animal food–chain – the small zooplankton – to the top trophic level, whereas the smaller cetaceans, as well as the sperm whales and orcas, have a diet based on much larger species and play very different roles in ecosystem dynamics.

The workshop participants were able to substantively discuss only the trophodynamics of certain marine biological systems, focusing on the cetaceans' role as accumulators and movers of largely undifferentiated biomass, on what, and how much, cetaceans eat, what humans take and how much, and the overlaps between these; what other components of the biological systems are also consuming the same prey species, and so on.

Inevitably the participants addressed the claims made in some circles that predation by cetaceans is harming, or is a danger to, fishing industries, and thus requires management measures such as "culling" or resuming commercial whaling or hunts. As this Monograph will make evident (see for instance Trites, this volume), a mere overlap of diet, either qualitative or quantitative, is no evidence of "competition" and cannot in itself justify such measures.

Before reviewing the main cetacean species found in the Mediterranean, the workshop first considered the oceanographic characteristics in the Basin which might be relevant in shaping the distribution of cetaceans.

2. SPATIAL STRUCTURING OF THE MEDITERRANEAN THROUGH OCEANOGRAPHIC PROCESSES

In oceanic systems, physical processes have a major effect in driving the primary production through ascending movements of nutrient-rich deep waters into the euphotic layer, and in structuring spatially and temporally the marine environment.

The spatial distribution and intensity of primary production in turn drives the spatial structuring of oceanic food webs, which will be reflected - to a certain degree - by the location of top predators such as cetaceans. Spatial structuring and scaling is a major issue when investigating the relationships between top marine predators and their environment. Several studies (for example Jaquet and Whitehead, 1996) have shown that at small spatial scales there is often a lack of correlation between the location of top marine predators and the areas of primary production, reflecting a complex interplay between variables such as water mass circulation and time lags in biological production between trophic levels … or simply the unability of cetaceans to detect small spatial scales in their physical / biological environment. Nevertheless, the location of numerous top predator species representing large consumed biomass seems related at a medium spatial scale to the distribution of primary production, and hence to certain physical processes.

The Mediterranean overall circulation strongly structures its environment and can be characterised by three main features (see details in Millot, this volume; and Millot and Taupier-Letage, 2004) :

1) The anticlockwise along-slope circulation, in both western and eastern basins, of inflowing low-density Atlantic water that tends to become more and more oligotrophic due to the depletion of nutrients by the primary production.
2) The intense, large and long-lived mesoscale turbulences that grow in the southern part of both basins because of the instability of this circulation, which creates significantly enriched zones of primary production that can be predicted up to a few days/weeks in advance only.
3) As surface water becomes saltier through evaporation all along its course, the strong northerly winds that transport cold and dry air masses in winter densify surface water so much that it sinks in some offshore areas of the northern basins. Sinking induces mixing over the whole depth, bringing nutrients into the euphotic zone so that these areas are characterised by an intense spring bloom. These productive areas roughly remain the same from year to year, and top predators appear to remain there all year long.

Investigating simultaneously and systematically the distribution of both primary productivity and cetacean locations across the Mediterranean Sea, starting with north-south transects across the physical and biological features described above, would certainly enhance our understanding of the links between cetaceans and their environment.

3. MEDITERRANEAN CETACEANS

The cetacean fauna in the Mediterranean consists of about 20 species. Of these, only eight are known to maintain regular populations in the region (for recent reviews, see Notarbartolo di Sciara and Demma, 1997; Notarbartolo di Sciara, 2002). They are listed in Table 1 below, along with known aspects of their ecology and presumed conservation status.

Table 1. Cetacean species known to be regular in the Mediterranean.

Regular species	Habitat	Sub-reg. distrib.	Residence	Prey	Estimated numbers	Threats	Conservation status
Fin whale	Mostly pelagic	Mainly W & C, rare in E	Mostly	Euphausiids (small squid, fish?)	Low 1000s	Ship strikes	Least concern
Sperm whale	Deep water. Shelf edge	E, W	Maybe females resident, males observed also in Strait of Gibraltar	Deepwater squid, maybe fish	Probably 100s	At least 40-50 killed in driftnets in Italy alone; ship strikes	Vulnerable; ACCOBAMS priority species
Cuvier's beaked whale	Deep water, shelf edge	E, W	Likely	Deep water squid	?	Acoustics; some killed in driftnets	Data deficient
Long-finned pilot whale	Mostly pelagic	W	?	Oceanic squid, fish	?	Killed in driftnets	Data deficient
Risso's dolphin	Shelf edge	E, W	Likely. Movements unknown within photo-identified populations	Coastal cephalopods	?	Killed in driftnets	Data deficient
Bottlenose dolphin	Nearshore	E, W	Resident	Fish, varied species, mostly inshore, some pelagic	?	Fisheries; Pollution?	Vulnerable; ACCOBAMS priority species
Common dolphin	Nearshore and pelagic	E, W	Resident	Varied (fish, cephalopods, mostly oceanic)	?	Fisheries, pollution?	Endangered; ACCOBAMS priority species
Striped dolphin	Pelagic	E, W	Likely	Varied (fish, cephalopods, pelagic crustaceans – pelagic and nearshore species)	Low 100,000s	Epizootics, killed in driftnets	Least concern

Occasional and accidental species, not listed in the Table, include the North Atlantic right whale *Eubalaena glacialis*, the common minke whale *Balaenoptera acutorostrata*, the sei whale *B. borealis*, the humpback whale *Megaptera novaeangliae*, the dwarf sperm whale *Kogia sima*, Blainville's beaked whale *Mesoplodon densirostris*, Sowerby's beaked whale *M. bidens*, the northern bottlenose whale *Hyperoodon ampullatus*, the killer whale *Orcinus orca*, the false killer whale *Pseudorca crassidens*, the rough-toothed dolphin *Steno bredanensis*, and the Indo-Pacific humpbacked dolphin *Sousa chinensis*. At this moment, of all Mediterranean populations, only common dolphins have been assessed as "endangered" in the IUCN Red List.

4. METHODS FOR THE STUDY OF CETACEAN TROPHODYNAMICS

The workshop identified three main categories of investigation:

a) surveys to estimate the abundance and distribution of cetacean populations;
b) methods for the study of cetacean diets;
c) trophodynamic models.

4.1 Surveys

A summary of methods commonly used to conduct surveys to estimate the abundance and distribution of cetacean populations is given in Table 2 below.

Table 2. Methods for estimating abundance and distribution of cetacean populations.

ABUNDANCE/DISTRIBUTION		
Distance sampling		
Method of data collection	**Advantages**	**Disadvantages**
Dedicated shipboard visual surveys	Methodology well developed and documented, can collect data on environmental covariates simultaneously	Expensive to conduct, not good for species that are difficult to see (eg *Ziphius*). Cannot be conducted close to shore.
Dedicated shipboard acoustic surveys	Can detect species that are difficult to sea, less weather dependent than visual surveys, can be conducted at night.	Analysis methods not yet developed
Dedicated aerial surveys	Can cover large areas in a short time	Cannot be conducted in some areas (eg open ocean)
Platforms of opportunity	Cheap, can make repeated measurements to detect seasonal and longer term trends, sometimes possible to collect data on environmental covariates simultaneously.	Cannot be used to estimate abundance (only density), geographical coverage restricted to areas where suitable platforms (ferries etc.) are available.
Capture/recapture		
Method of data collection	**Advantages**	**Disadvantages**
Photo-identification	Relatively cheap to conduct, also provides estimates of demographic rates (survival, migration).	Only suitable for relatively small populations. Requires repeated surveys. Only suitable for species where individuals can be distinguished.
DISTRIBUTION		
Nature of information obtained depends on way surveys are stratified. However, techniques are being developed to generate maps of density distribution from the results of line transect surveys.		

4.2 Summary on methods for the collection of dietary data on cetaceans

In relation to understanding the role of cetaceans in marine ecosystems, dietary data on cetaceans are needed to fulfil several general objectives:

- Identify and quantify trophic links (i.e., who eats whom and how much).
- Provide insight into feeding and foraging strategies.
- Contribute to evaluation of interactions with fisheries.
- Provide estimates of population food consumption.
- Provide insights on threats to status (e.g., dependence on particular prey species).
- Provide input into static and dynamic ecosystem models.
- Estimate (single or multi-species) functional responses.

There are few published data on cetacean diets in the Mediterranean, although unpublished material and grey literature exist. General indications of feeding ecology may be provided by reference to results from other areas but cetacean diet may vary substantially among areas, and therefore new studies are needed to determine the specific diet of Mediterranean populations.

An optimal sampling design to evaluate diet would require directed sampling of cetaceans. Lethal sampling is not desirable. One possible approach is fatty acid analysis from blubber biopsies. However, stomach contents data from strandings and by-catches are needed to fill gaps, improve seasonal and geographical coverage and increase sample sizes.

Stomach contents analysis has well-known biases, to do with digestion and identifiability of prey remains (see Pierce and Boyle, 1991) but remains the most widely used technique for evaluating cetacean diet. Stomach contents data are needed to facilitate interpretation of fatty acids and stable isotopes. Compared to these methods, stomach contents analysis is relatively inexpensive and requires no specialised equipment.

Major advantages of fatty acid analysis are that data can be collected from animals with empty stomachs and (relatively easily) from live animals, and the results indicate average diet integrated over a relatively long time period (Iverson *et al.*, 2004). Quantitative interpretation of fatty acid data to evaluate cetacean diet is possible but some methodological issues remain to be resolved.

Stable isotope analysis can provide data on trophic level as well as other ecological information (e.g. Dubroca *et al.*, this volume), but cannot yield detailed data on diet. Major advantages are the opportunity to work on historical samples and the possibility of reconstructing aspects of an animal’s life history by measuring variation in isotope ratios across tissues that show growth increments.

Other techniques available to determine diet include:

- Collection of faecal samples and prey remains from the water during feeding events;
- Sampling macro-zooplankton or micro-necton (e.g., small fishes) in the vicinity of feeding baleen whales;
- Direct observation of surface feeding and use of underwater video cameras.

All methods of diet analysis require access to reference material on putative prey species and some degree of specialist training (see, for example, Clarke, 1986).

The optimum approach to evaluating diet is probably to use a combination of available techniques. However, a consistent approach is desirable to ensure availability of time series of comparable dietary data. Attention must be given to quantifying and correcting errors and biases inherent in each technique, e.g. weighting applied to individual stomachs, grading prey hard parts according to state of digestion, back-calculation of original prey size. It is necessary to provide measures of uncertainty about diet composition (e.g. by bootstrap methods, see Hammond and Rothery, 1997).

Additional insight can be obtained by considering not only numbers and biomass of prey but also energy content, nutritional value (minerals, vitamins, fats) and contaminant load.

In the Mediterranean, priority should be given to systematic and integrated collection of data and samples from stranded (and by-caught) cetaceans (e.g. stomach contents, tissue samples for fatty acids and stable isotopes for each individual) as well as information on species, location, season, date, time, sex, length, age and maturity, ensuring that data are obtained from all regions. Efforts should also be made to collect dietary data from living individuals (e.g. biopsies, prey remains, visual observations). Attention needs to be given to archiving dietary records.

Dietary data are also needed on other species in the ecosystem (e.g. other non mammalian marine top predators such as swordfish, tuna, and sharks, as well as their prey species).

4.3 Trophodynamic Models

4.3.1 The purpose of models

In simple words, models are abstractions which help us to understand a given phenomenon of interest. Their aim is to represent the phenomenon under study in a meaningful way for the specific question posed. Although a model does not necessarily need to be mathematical (i.e. it can be verbal, pictorial, logical), most ecological models are mathematically framed.

In the process of assessing the roles that cetaceans might occupy within their ecosystem, it is important to recognize two elements. One is the minimum data requirements associated with different potential questions and/or hypotheses of interest (Table 3). The other one is identifying the set of features of any proposed model (Table 4) which will determine the suitability of the model for answering the question posed (Table 5).

The diversity of ecological questions and the potential approaches to answer them is quite large. When it comes to marine mammals, their roles in the ecosystem, and their proper management and conservation, there are some frequently asked questions (FAQs) which are pervasive in virtually every forum. Here we present some of them (Table 3), but the list is by no means complete. Our goal is simply to introduce some FAQs and to provide rather simplified guidelines for the minimum data and kind of models which are required to answer them.

Tables 3-5 provide one possible framework to address issues on the roles of marine mammals in their ecosystems. Here we explore its application to a concrete case: the common dolphin in the Mediterranean. According to Table 3, we need to know the population distribution and have time series of abundance in order to evaluate the population trend. Although there is evidence that this species has declined in the past 30-50 years (Bearzi *et al.*, 2003), there are no direct estimates of abundance, instead stranding records were used as an index. Table 3 also highlights one important caveat to this conclusion: because there is no evaluation of population distribution, we cannot rule out the possibility of a distributional change as the cause for the observed pattern. Clearly, surveying the whole distributional range of common dolphins in the Mediterranean is a priority if we want to distinguish between these two alternative hypotheses.

Under the working hypothesis that common dolphins declined, one proposed cause is competition with fisheries. A reasonable first step is examining if there is any overlap between the diet of the common dolphin and the fisheries. According to Table 3, an average diet composition for the two presumed competitors is the minimum data requirement for the overlap analysis. This information is available for common dolphins and fisheries, and Table 5 indicates that a static model (i.e. an overlap index) can be enough in the simplest possible scenario. Preliminary analyses of this sort have been performed and indicated that common dolphins feed on forage fishes (e.g. European anchovy, European pilchard). which are also targets of the fisheries. Although suggestive, this result does not entitle us to conclude that there is evidence for consumptive competition. According to Table 3, we need time series for the abundances of both presumed competitors to identify a competitive relationship. This is because we need to demonstrate that both competitors have negative effects on each other in order to establish that there is resource competition. Suitable surrogates for the “abundance” of the fisheries can probably be found (e.g. fishing effort, number of vessels, etc), and relatively simple models can be used for the evaluation (Table 5), but we should remember that we are building this case on the assumption that common dolphins have actually declined. According to Table 3, much more information than we have available currently is required to prove that there is competition.

A more achievable goal might be to determine if food availability is a limiting factor for common dolphins in the Mediterranean. This will save us the assessment of the negative effect of dolphins on fisheries (which is a condition for consumptive competition), while still allowing us to explore the possibility that fisheries may be having a negative effect on common dolphin populations. Actually, this is a more accurate description of the hypothesis that has been advanced. The fisheries, by reducing forage fish stocks, are hindering the common dolphin growth rate, but dolphins apparently have had no negative effect on the fisheries. This more restricted goal still requires time series of abundance for the prey, and time series of abundance and diet composition for the common dolphin (Table 3), which we do not have. In addition, if we want to establish the link with the fisheries, we need to determine if any changes in prey abundance are a consequence of fishing.

Although admittedly superficial, this analysis shows that much more information is needed to address this issue. Long-term monitoring programs are clearly lacking, and the existing information is not well integrated. The absence of surveys over the whole distributional range of the common dolphin makes it impossible to obtain a clear picture of the situation. Nevertheless, an application of the precautionary principle might lead us to conclude that, in the absence of evidence to the contrary, the decline of common dolphins in the northern Mediterranean is linked with fisheries activities. This could have important economic consequences, not just for the fishing industry but also for whale-watching and even maritime traffic. Therefore, and in the best interest of common dolphins and human activities, the obvious recommendation would be pursuing the research outlined above that should allow us, at least, to give some empirically-based relative weight to the alternative hypotheses.

Table 3. Illustrative scheme of the minimum data requirements to answer some frequently asked questions on the roles of cetaceans in their ecosystem.

	Data / Information										Component							Nature of data		
Question	Population boundaries / Distribution	Population abundance	Population internal structure	Diet composition	Seasonal distribution	Pollutant levels	Oceanographic	Topographic	Condition / Nutritional status	Parasite load	Focal species	Preys of the focal species	Predators of the focal species	Competitor of the focal species	Main species in the system	Many / All species in the system	Environment	Average / Single measure	Few / Experimental design	Many / Time series
Where does the focal species live?	x										x							x		
How large is the focal species population?	x	x									x							x		
Does the focal species population migrate?	x				x						x								x	
What are the main structural features of the focal species population habitat?	x				x		x	x			x						x		x	
What does the focal species population eat?	x			x							x							x		
What is the prey consumption of the focal species?	x	x		x							x							x		
Is the diet composition of the focal species dependent on prey availability?	x			x							x									x
	x	x										x								x
Is the focal species population growing or declining?	x	x									x									x
Is food availability an evident limiting factor for the focal species population?	x	x		x							x									x
	x	x										x								x
Is predation (or by-catch) an important source of mortality for the focal species population?	x	x									x									x
	x	x		x									x							x
Is there any trophic overlap between the focal species population and another species/component of the system?				x							x			x				x		
Is there any evidence to suggest competition between the focal species population and another population / component of the system?	x	x									x			x						x
Are the focal species population and another population/component of the system actually competing?	x	x		x							x	x	x	x	x	x				x
Is the focal species population exerting a top-down control on a given prey species?	x	x		x							x									x
	x	x										x								x
Has the focal species a major regulatory effect in the trophodynamic of its ecosystem?	x	x		x							x	x	x	x	x					x

Table 4. Schematic features of ecological models.

Feature	Comment	Category	Category description	Example
Dynamic	This feature refers to the kind of dynamic behaviour allowed by the model	Static	No dynamic behaviour is allowed. The system is assumed at equilibrium	Mass-balanced models in general (e.g. Ecopath) Overlap
		Local	The system is assumed near an equilibrium. The density-dependencies are linearized. Allow exploring the dynamic after small perturbations	Local bioenergetic-allometric models (e.g. Benguela model)
		Global	The full nonlinear expressions for the density-dependencies are considered. There is no equilibrium assumption	Global bioenergetic-allometric models (e.g. Patagonia)
Resolution	This feature refers to the degree of resolution of the modeled food web	Key (few) components	Only few populations/components are modeled. It is assumed that these components are enough to describe the phenomena of interest (i.e. imply discarding *a priori* most of the indirect effects)	Punt
		All (many) components	All, or at least most of the populations in the community are modeled. It allows the evaluation of all / most indirect effects	Yodzis 1998 Ecosim
Spatial structure	This feature refers to the explicit incorporation in the model of spatially related processes (e.g. immigration/emigration)	Absent	There is no explicit spatial considerations in the model.	Ecopath with Ecosim Patagonia Benguela
		Present	At least some space-related processes are explicitly described in the model	Gadget Ecospace
Uncertainty handling	This feature refers to the evaluation of sources of uncertainty in the model, and its impact on model predictions / inferences	Ignored	The model does not evaluate uncertainty. In this case, the model is only a source for working hypotheses, but cannot be used to make predictions or inferences about the modeled system	Ecosim
		Parameters	The model allows the evaluation of uncertainty in the parameter values. If this is the only source of uncertainty being evaluated, the use of the model for prediction/inference assumes that the information contained in the structure of the model (i.e. its mathematical form) represents without error the true mechanisms/relationships involved in the phenomenon of interest.	Gadget Ecosim with Ecoranger Punt MSFOR
		Structure	The model allows the evaluation of uncertainty in its mathematical formulation. This effectively means the comparison among several alternative model formulations. If this is the only source being evaluated, the use of the model for prediction/inference assumes that for each alternative formulation, there is no error in the parameter values (i.e. the values correspond to the true parameters)	Punt

Table 5. Minimum required features of ecological models to address frequently asked questions

	Dynamic				Resolution		Spatial Structure			Uncertainty handling		
Question	Static	Local	Global		Key (few)	All (many)	Absent	Present		Ignored	Parameters	Structure
Where does the focal species live?	x				X		X			X		
How large is the focal species population?	x				X		X				x	
What does the focal species population eat?	x				X		X				x	
Does the focal species population migrate?	X				x			x		X		
What are the main structural features of the focal species population habitat?	X					x		x			X	
What is the prey consumption of the focal species?	x				x		x				X	
Is the diet composition of the focal species dependent on prey availability?			x		x		x				x	x
Is the focal species population growing or declining?			x		x		x				x	x
Is food availability an evident limiting factor for the focal species population?		x	x		x		x				x	X
Is predation (or by-catch) an important source of mortality for the focal species population?		x	x		x		x				x	x
Is there any trophic overlap between the focal species population and another species / component of the system?	x				x		x				x	
Is there any evidence to suggest competition between the focal species population and another population / component of the system?		x	x		x		x				x	
Are the focal species population and another population/component of the system actually competing?		x	x			x	x				x	x
Is the focal species population exerting a top-down control on a given prey species?		x	x		x		x				x	x

BOX 1 - Can we distinguish trophic and non-trophic effects on cetacean population dynamics?

Graham Pierce

Analysis of multiple short time series

Analogous to the quantification of overlap between marine mammal diets and fisheries catches as a way of identifying possible resource competition, time series analysis can be used to suggest possible links between different processes over time. In both cases, development of dynamic models and/or experimental manipulation may be needed to test links suggested by the analysis.

Thus we might have several categories of variables, relating to (i) marine mammal abundance, (ii) fish stock size (spawning stock biomass, abundance indices) or fishing activity (e.g. landings) and (iii) the environment (e.g. sea surface temperature, upwelling indices). The general question addressed concerns the effect of prey abundance and environmental change on marine mammal population trends.

Standard multivariate techniques give information on interactions between variables, but no information is revealed about trends and structural changes over time. Solow (1994) and Shapiro and Switzer (1989) introduced a principal component analysis related technique (MAFA, min/max autocorrelation factor analysis) that extracts common trends in a short time series data set. The axes obtained by MAFA are smooth curves, or trends, the first MAF being the most important trend underlying all the original time series, the second MAF the second most important trend, etc. MAFA can be applied to multivariate time series data sets up to 15 or 20 years.

Figure 1 shows an example of MAFA analysis for various time-series related to fishing activity in Scotland (landings of various categories, numbers of licensed vessels, numbers of fishermen etc). Two common trends were extracted and the variables contributing most to these trends are indicated.

If the series are longer, time series analysis techniques like dynamic factor analysis (Zuur *et al.,* 2003a,b; Zuur and Pierce, 2004) can be applied. DFA can be used to estimate common trends, effects of explanatory variables and interactions between N time series. The technique can cope with missing values and non-stationarity.

N time series = linear combination of *M* common trends +
Explanatory variables + level parameters + noise

These techniques cannot of course demonstrate causal relationships between variables but may suggest hypotheses about the variable(s) (in this context prey populations, fishery activity or environmental factors) which best explain the observed trends in a response variable (cetacean population size)

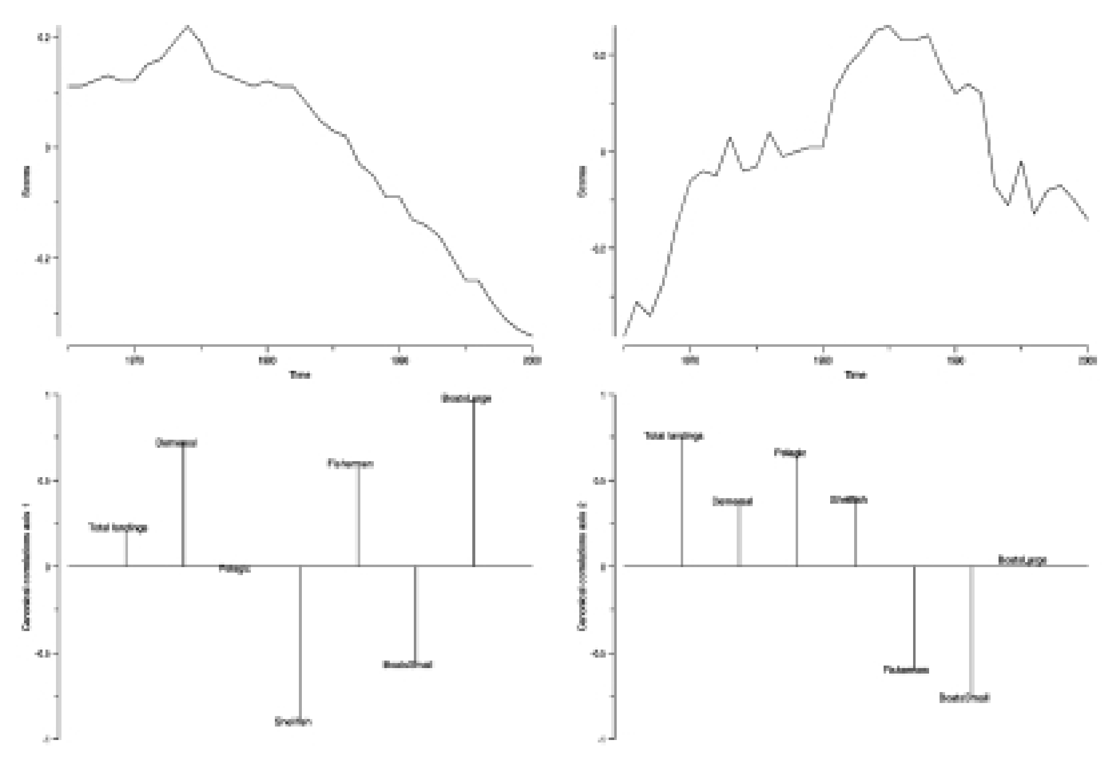

Fig. 1. Results of MAFA for fishing activity data for Scotland. Upper left graph: first MAF. Upper right graph: second MAF, lower left graph: canonical correlations for MAF 1, lower right graph: canonical correlations for MAF 2.

4.3.2 A discussion on the use of models to investigate the roles played by cetaceans in their ecosystem

For the purpose of their use in models, the different roles of cetaceans in their ecosystems can be schematically subdivided into "ecological" (in relation to their environment), and "social" roles (in relation to humans):

- A) Ecological
    - predator
    - prey
    - competitor
    - mutualist
    - detritus
    - host
- B) Social
    - indicator
    - flagship / "special" species
    - competitor
    - mutualist (i.e., as when cooperating with fisheries)
    - resource (when harvested)
    - whale watching

Models are one of several tools for exploring questions about ecosystems and the roles that cetaceans play in them. The limitations of models must be well appreciated: they often reflect a shortage of data or an incomplete understanding of ecosystem processes. While models therefore are not utilized to yield definitive answers to questions, they are helpful to investigate possible or likely answers. They are also helpful for identifying essential areas of research that should be encouraged and promoted.

Understanding ecosystem processes is rapidly improving, but is currently limited by data gaps and complexities that are inherent to ecosystems. Such shortcomings should mandate the implementation of the precautionary principle when there is converging evidence that ecosystem processes are being compromised and can be mitigated by management actions.

Biological communities consist of both short- and long food chains which depict interconnected organisms placed at various trophic levels. Each of the organisms in a food web can fill one or more proximate roles within the ecosystem (e.g., decomposer, filterer, grazer, scavenger, competitor, host, prey or predator). However, all organisms ultimately play structural and/or dynamic roles within their ecosystems (i.e., by providing physical complexity to the environment, or by transferring nutrients and energy, or by regulating abundance of other species).

Quantifying the relative importance of the ecological role played by any one group of organisms within a real ecosystem is still an extremely difficult task. Species may be presumed to significantly or insignificantly affect the dynamics of other species based on their size, abundance and diet. However, presumptions are not always borne out by empirical data or by mathematic calculations that track the logic of such arguments. The effect of one species on the dynamics of another may be simple (linear) but is more likely to be complex (non-linear) and involve indirect pathways that result in counter-intuitive relationships.

Of all the roles that marine mammals play within an ecosystem, the one that garners most attention is "competition with fisheries". It is often and incorrectly assumed that competition occurs when a predator eats the species caught by fisheries (dietary overlap). However, as pointed out previously, dietary overlap is not a measure of competition - it merely indicates the potential for competition to occur. By definition, fisheries and cetaceans compete when the removal of a species by one group negatively affects the other. Competition is not an issue when prey abundance is high, and is only likely to occur when the abundance of species targeted by fisheries and cetaceans is limited. Thus, it is essential to know the amount of prey that is available to fisheries and cetaceans in time and in space. It is equally important to determine the amounts of prey consumed by other predators (such as fish) within the ecosystem.

Mathematical models are currently the only way to quantitatively estimate the extent of competitive interactions between fisheries and cetaceans. However, such models can only demonstrate the probability that competition is occurring - they do not provide absolute evidence that there is or will be competition. Minimum data requirements for these models include numbers of predators and their dietary composition, abundance of prey, and amounts of fish removed by fisheries (see Table 5). Qualitative information that complements and reinforces the quantitative assessments include measures of nutritional quality (e.g., caloric densities of targeted fish), individual health (e.g., cetacean body size and condition) and population demography (e.g., pregnancy rates and birth rates).

5. CONSERVATION AND MANAGEMENT ISSUES

The benchmark on which to base our understanding of the mechanisms at play should be the intrinsic characteristic of the environment rather than potentially shifting baselines caused by anthropogenic effects, and our short-term memory of rapidly deteriorating oceans (Pauly and Christensen, 1995; Jackson *et al.*, 2001). To achieve this objective, we should be able to incorporate historical (qualitative) observations to infer what the past environment was like. Such historical evidence is often available in ancient records and writings, and should be taken advantage of when quantitative time series are lacking (see CIESM Workshop Monograph 22, 2003).

Box 2 - Investigating shifts in the Mediterranean ecosystem: the case of short-beaked common dolphins and striped dolphins

Giovanni Bearzi and Kostantinos I. Stergiou

It has become evident that fishing greatly impacts marine ecosystems (e.g. Jackson *et al.*, 2001; Christensen *et al.*, 2003; Myers and Worm, 2003). One major effect of fishing is the dramatic decline of animals having high trophic levels (i.e., “fishing down marine food webs”). This decline may be accompanied by an increase in highly resilient species such as cephalopods (Caddy and Rodhouse, 1998), myctophids (e.g. Trites *et al.*, this volume), hydromedusae (e.g. Jackson *et al.*, 2001; CIESM, 2001) and bacteria (Jackson *et al.*, 2001; CIESM 2003). Such effects were also observed in some sub-basins of the Mediterranean Sea (e.g. Stergiou and Koulouris 2000), but there is an ongoing debate on whether such a trend has occurred in the whole Mediterranean (e.g. see Pinnegar *et al.*, 2003).

Preliminary analysis of the available diet data of Mediterranean cetaceans indicated that the diet of common dolphins in coastal waters overlaps with fishery targets (e.g. European anchovy, European pilchard). In contrast, the diet of striped dolphins - which are typically pelagic and largely feed on mesopelagic cephalopods and non-commercial fish - suggests low levels of overlap with fisheries (Blanco *et al.*, this volume; Kaschner *et al.*, this volume; Pusineri *et al.*, this volume). Therefore, striped dolphins might be affected mostly or exclusively through indirect food-web competition (*sensu* Trites *et al.*, 1997).

Although overlap between cetaceans and fisheries does not necessarily imply direct competition, it may do so under fishing-induced strong reductions of fish stocks. This may have differential effects on these two dolphin species. It is reasonable to assume that common dolphins in the coastal zone would be negatively affected while striped dolphins in pelagic waters are less likely to be exposed to a detrimental impact, and might be even positively affected.

Striped dolphins have apparently increased in the Mediterranean in the last decades and are currently very abundant in pelagic waters throughout the basin (Aguilar, 2000). In contrast, common dolphins have declined in the past 30-50 years and remain relatively abundant only in a few areas (Bearzi *et al.*, 2003).

The various approaches and technical methods discussed during this workshop would be valuable tools to test such a working hypothesis.

Investigating and understanding the trophodynamics of free-ranging cetaceans not only is a formidable scientific challenge, it is also a fundamental step in assisting conservation efforts of endangered taxa such as cetaceans, and in supporting the responsible management of fisheries in ways that will cause such activities to coexist with a healthy marine environment and a full complement of its biodiversity.

We believe that important progress will be made when the following challenges will have been met:

1. to be able to tell whether change in abundance, density, distribution, social structure or behaviour of a cetacean population is trophodynamically related;

2. to enable the determination of nutritional stress (*sensu* Trites and Donnelly, 2003) in cetacean populations;

3. to explore ways in which management measures can be used (e.g. marine protected areas, time closures, allocation of quotas, limitations in mesh size, gear modification, etc.) to best enhance our understanding and monitoring of the trophodynamic mechanisms involved;

4. to predict the ecological and conservation consequences of removing top predators from their regular habitats (such as foraging, resting or breeding areas), e.g., by acoustic harassment or by culling;

5. to identify geographically-suitable habitats for different species based on their known environmental correlates;

6. to use data on local primary production, trophic level, and estimated trophic transfer efficiency to predict theoretical carrying capacity for top predators (including cetaceans).

Preliminary thoughts

Sidney Holt

I am a little diffident about addressing our gathering: I know something about the great whales but little about the smaller species. However, this is a subject I have thought much about in the thirty years since I began to organise, on behalf of the Food and Agriculture Organisation of the United Nations (FAO) and the newly established UN Environment Programme (UNEP) a major conference on marine mammals which was held in Bergen, Norway, in 1976. Exactly thirty years ago I also attended a remarkable conference in Bloomington, Indians, organised by John Goodman, that brought together scientists, conservationists, poets, musicians, painters, sculptors and other artists and intellectuals, as well as politicians and bureaucrats, to talk about, and in other ways experience - in effect - the role of cetaceans in human society and culture. The reverberations of that illustrious gathering are still with me.

So, I may not be well qualified to offer orientation on certain aspects of this workshop, but I surely am very interested, and have some strong opinions!

The subject-title properly reflects that the role of cetaceans is plural. We cannot assume, *a priori*, that all cetaceans play the same role. Nor does a particular species necessarily play the same role in all places and at all times. Nor, again, does a population necessarily play only one role; “role” is, in our context, a multi-dimensional concept. Then, there may be a problem with defining “the marine ecosystem”. It is, I think, a common, if not universal, belief that there are many linked ecosystems in the marine realm. The cetaceans surely “belong” - if I may use that word - mostly in what are now classed as Large Marine Ecosystems (LMEs). Personally I have some reservations about the validity or usefulness of that convenient classification. But the large whales - by which I mean principally the baleen whales and the sperm whale - have immense ranges, in most cases probably entending to the entire southern hemisphere or to the entire North Atlantic or North Pacific Oceans.

In the first half of the twentieth century, when it was realised that the main target species of the new pelagic whaling industry migrated annually between tropical, subtropical or temperate waters and polar waters, it was natural to think of those species as playing different roles in different locations and at different times - as predators on smaller species of animals in the colder waters in summer and as reproducers when in warmer waters, in winter. However, it is not so simple. At least one of the baleen species and several populations of the others appear not to undertake such vast migrations, and even some individuals within highly migratory populations may be relatively sedentary. Then, while we do not think that baleen or sperm whales give birth (or even copulate) when they are in polar regions, it does seem that they do feed to some extent during migration and/or in the known or presumed breeding areas. To pursue the theatrical metaphor, the same actor can take more than one role in the same play, as characters with complex and perhaps overlapping qualities. We have to be clear, for the purposes of this discussion about what is the play, what is the stage and even in which theatre the show is being performed.

This is perhaps the point for a timely reminder: we do not yet know for sure how many species of great whales there still are. In whaling records through to the 1960s, at least, sei and Bryde’s whales were confused. It is now generally accepted, after much scepticism, given the national origin of the taxonomy, that the blue whale in a diminutive as well as a “normal” form that may be distinct species or at least sub-species. The ”minke” whale is now recognised as two and possibly three species. There is surely greater uncertainty over the identities of the smaller cetaceans, some of which are known only from single specimens from long ago. An example is the reported finding of a Longman’s beaked whale, *Indopacetus pacificus*, stranded in South Africa; this was previously known only from a skull picked up on a Queensland beach in 1882 (later, in 1926, named *Mesoplodon pacificus*) and another found in Somalia in 1955. So we have to be aware that efforts to evaluate the role of particular types of cetacean may, in the present state of knowledge, be confounded by confusion or uncertainty regarding their identities.

The simple logic of old-fashioned biology suggests that we look first at the mass biochemistry of the Extremely Large Marine Ecosystems in which the great whales are actors. It seems natural to consider various phases of the lives of individuals, such as: pregnancy, birth, growth, adulthood and death. One role of birth - apart, that is, from ensuring the continuity of the species or population or tribe - is to provide nutrition for other predators; we have probably all seen dramatic film of Orcas attacking baleen whale newborns and calves.

Unlike most marine animals the cetaceans release metabolic products, particularly carbon dioxide, directly into the atmosphere, thus temporarily removing carbon (and some other gaseous or particulate components) from the oceanic cycle. Another important, biologically generated, “greenhouse gas” - methane - is presumably evacuated from the other end. To the extent that that happens at depth - as it might in the case especially of the sperm whale - the rising, lighter-than-seawater gas may only partially be metabolically intercepted on its way to the surface.

Then there is natural death. Most of the little information we have about this process comes from stranded animals. A few observations have been made of a variety of scavengers feasting on the submerged carcasses of dead whales. It seems that the re-integration of large cetacean bodies into the ocean system is a relatively slow process. This observation can remind us that in considering the role at metabolic level it is necessary not only to look quantitatively and qualitatively at the pathways but also take account of the time frames.

Let me turn to the discipline about which I know rather more - population dynamics. We now have a slightly firmer idea about the parameter values of single populations of several species, considered in isolation than when I began to study whales, in 1960 - but only slightly better. There are some observations of the recovery rates of very depleted whale populations that have been fully or partially protected from further exploitation by whalers. A case in point is that by Peter Best on the apparent rate of increase in number of Southern Right Whales in at least a part of their distribution (feeding grounds in South African waters) - at around 7% annually. Similar rates have been reported for other species and populations, particularly humpbacks, that had been massively depleted by more than a century of intensive whaling. Conventional ideas about population dynamics suggest that such rates are much higher than any that will pertain to the period of increase of the population towards a future stable state. One species for which we have better, long-term data is the gray whale of the Eastern North Pacific. Systematic counts of this species during its migrations between the calving areas, mainly along the coast of Mexico, and the feeding areas in the Arctic, have been made for several decades, and it is regarded as pretty well fully recovered (whatever that means), yet still, in recent years increasing at about 3-4% annually despite considerable so-called “aboriginal subsistence catches” in the far northwestern part of its distribution. Unfortunately, this gray whale (I say “this”, because it is still unclear whether the grey whales in the Northeastern Pacific, and those - now extinct - in the North Atlantic are/were of the same species) has increased to an estimated number far higher - perhaps by as much as two or three times - what was thought to have been the original population at the start of commercial whaling in the nineteenth century, despite the great reduction in breeding habitat, mainly the lagoons along southern California and Baja California. Here is a mystery to which I shall return.

Rates of population growth give us ball-park estimates of the *difference* between rates of reproduction and rates of death. (as, in special circumstances, may rates of decline, under exploitation). They do not allow separation of these two basic parameters, although presumed upper limits to fertility rates, based on general biology (such as the rarity of multiple births, and the delay to sexual maturity) may give some clue. Separation requires at least good estimates of the *absolute* numbers of whales in clearly identified populations, though such estimates may not be sufficient in themselves for this purpose; usually the age and gender structure of the population must also be known. Such structure has been surmised most often in the past from age-determinations of samples from commercial catches; these are inherently very selective. Japanese scientists attempted, through the earlier years of Japan's "scientific whaling" programme, to obtain properly stratified samples for this purpose, but with scant success; the original declared intent of the programme, to obtain better estimates of natural mortality, failed.

Unfortunately, a significant part of the literature on population changes and on attempts at human management of them, contains the assumption - sometimes stated, sometimes implied - that knowledge of the values of the parameters of birth, growth and death would be sufficient for management of sustainable use of those wild populations. This is not so. Calculations of "sustainable catch" and the like depend on estimates of the ways and rates at which those parameters *change* with the size of the population, their so-called *density dependence*. And we know even less about this than about the instantaneous parameter values. There have been speculations about the biological processes involved in such dependence - for example that increases in population may impede access to adequate food and this that will delay sexual maturity - but attempts to verify such speculations from data have not been conspicuously successful. Early work concentrated on examination of samples from commercial whaling, for example, which were as usual confounded by the selectivity of whaling operations, the dishonesty of (some) whalers, and the prevalence of errors in age determination and the identification of ages at sexual maturity and of first successful pregnancy.

Basic parameters are presumed to vary with density, and over time. Little attention has been given to the existence and implications of *spatial* variation. The definitive study of this matter is by Alec D. MacCall, in his "Dynamic Geography of Marine Fish Populations", published in 1990 by the University of Washington Press. MacCall examines, theoretically, "basin" situations in which population parameters take different values in the favoured "centre" of distribution from those at the geographical margins. The geographical pattern of *density* leads to expansion or contraction of the range (consistently occupied area) of the population as its *total number* changes. Assessing the highly migratory species in such a manner is problematic and complicated, but we should expect groups of individuals living near the margins of the species range to play somewhat different roles there than other groups do, living near the more favorable centre. Furthermore, large-scale changes in the ocean environment, especially geographic shifts in currents and so on, would be expected to affect those roles, since the other organisms that interact strongly with the whales, especially their prey, are likely to be affected by the same environmental change in different ways, leading to changes in the *relative* geographical distributions of the predator and prey species and competitors.

Population research has also been confounded when the assumption that a formally "protected" population was not subject to exploitation was incorrect. A notorious example was the revelation, after the political collapse of the Soviet Union, that Soviet expeditions had for years been systematically flouting the IWC's decisions, including taking substantial catches, over several years, of the "protected" southern right whale, now being counted by Peter Best. How far such errors can lead scientists astray, in the context of the subject of this workshop, is illustrated by the story of the blue whales (the "normal" and diminutive ones) in the Antarctic. After "the blue whale" had been "protected" there was no obvious sign, over several decades, of its increasing in number. Most scientists believed, I think, as did I, that estimates of number were too uncertain to allow such detection anyway. But Seiji Ohsumi, a Japanese scientist working with the whaling industry, surmised that minke whales were competing so strongly with the blue whales for krill resources that the recovery of the latter was being impeded. This led to his conclusion that the newly established - but incomplete - protection of the minke whale was a serious mistake in relation to the recovery of the baleen whales of the southern hemisphere and, subsequently, to the demand that the minkes should be “culled” as a management measure. Later it transpired that the Soviet whalers had also been killing, illegally, significant numbers of blue whales (see Yablokov and Zemsky, 2000). [Embarrassingly, this was known to Japanese traders in whale meat, if not to their scientists, since the meat - or some of it - was being transhipped at sea from the Soviet factory vessels to Japanese transports].

The scientific literature concerning baleen whales, and krill in the Antarctic contains another remarkable - and erroneous - story. When interest began to be expressed in a possible large commercial fishery for krill, estimates were made of the “surplus” of krill that was available as a result of the depletion of the whales. These were used to provide indicative figures for a possible future scale of the fishery. Remarkably little attention was given at the time to the likelihood that most or all of the mythical “surplus” would be quickly gobbled up by increases in the populations of the other predators in the system.

Much of the research that is relevant to the subject of this workshop concerns the properties of multi-species population models, with names like MULTISPEC, ECOPATH, BORMICON/GADGET and ECOSIM (see Executive Summary), especially of the kind that is now fashionable in consideration of fisheries management and, increasingly, in discussions about the maintenance and protection of biological diversity. The elements of such models are mostly population models, often very simplified ones, and the links between those modules usually involve the assumption that the driver is predation. What are conspicuously lacking in most publications developing and using these models are sensitivity tests of the often large consequences of relatively small alterations of parameter values (see Blanchard *et al.*, 2002).

Peter Yodzis (2001) has illustrated, with a now-famous diagram, how extremely complex and, indeed, intractable, a predator-prey matrix could be in the sea. In retrospect, my own efforts, with Robert May, John Beddington, Richard Laws and Colin Clark, to model an Antarctic system consisting of just five elements (published in *Science* in the 1970s) look most naive, even though we were trying only to get an idea of the general properties of such a system. A few years ago a small group of scientists, led by David Lavigne, and including Yodzis, as well as me, wrote a *Protocol* outlining a set of rules and procedures that should, we thought, be followed by those considering the culling of marine animals- mainly marine mammals - for the supposed improvement of fisheries (UNEP, 1999). As far as I know it has had little if any discernable effect in international fora where such matters are debated.

Now I offer a couple of supplementary comments on this matter.

The first, mentioned above, is the matter of high sensitivity of output to relatively small adjustments of parameter values. Then there are problems with the internal structures of the models, especially with the form of links between the several single species modules. Most existing models deal with mixed diets, and changing diets of the predator. The universal assumption is that the amount of different dietary constituents eaten by a predator is a rather simple function of the relative abundances of the prey species, and perhaps also of their absolute available abundances. Dietary selectivity is assumed to be constant or, if not, then represented by a simple continuous function. But what if that assumption is not reasonable, judging from our everyday experience. From my admittedly very limited experience with feeding experiments with captive birds, in cooperation with Peter Marler (in the 1940s, unpublished), and in later years with domestic animals, I would suggest that discontinuous “switching” from one “preferred” diet to another may be the norm, at least with the *higher* vertebrates and perhaps with cephalopods, too. I do not think the consequences of such alternative assumptions will necessarily be negligible.

A second point is that we too readily assume that the dominant interaction between larger species and smaller ones is predation. A good recent example of another view has been given by Jaime Gomez-Gutierrez and colleagues, published in 2003 in *Science*. They have suggested that the abundance of Euphausids (“krill”) in the California current system is limited not so much by predation or starvation as by the parasite *Collinia*. Since other krill species, as well as copepods, are thought to be the foundation stones - at secondary production level - of the Antarctic system, as food for penguins, seals, squids and some fishes as well as baleen whales, such findings may turn out to be of major importance in attempts by humans to "manage" that system, and ensure its recovery from excessive human predation.

The simple population models, both those used in single species management scenarios, and as incorporated in reduced form in multi-species models, all contain a single root assumption. This is that, when a population is vanishingly small, its increase can be represented by a simple exponential function. This assumption goes back at least to the time of Thomas Malthus. Since populations do not increase exponentially for ever, a second assumption, dating back to the final decades of the nineteenth century (associated with Volterra and other mathematicians and demographers), is that as a population increases in number (or perhaps in biomass) the "intrinsic rate of natural increase" (***irni***) will be modulated by processes collectively termed *density dependence(s)*. These assumptions, unless further modulated, lead to the conclusion that recovering populations tend to return to an asymptote, a steady state. The modulations that affect that default have been identified in the theoretical literature as (a) delays in reproduction, especially in combination with an intrinsically slow reproductive rate, and (b) involvement in a predator-prey relationship. These both predict cycles of population abundance about a stable point or, *in extremis*, chaotic trajectories that are virtually indistinguishable from random fluctuation. A third modulation is encapsulated in the term "environmental change", in which the subject population mimics (but perhaps with a time delay) various types of change that could be cyclic, apparently random, or complex.

However, a Danish scientist, Lars Witting (2000), working in Greenland has questioned the assumption that the ***irni*** is exponential. His argument, from basic consideration of population genetics, is that it is more likely to be (or, for him, *must* be) something like hypergeometric. This has major consequences when incorporated in population models. Among other things it leads to the conclusion that populations can have intrinsic cycles of abundance that are not due to any of the three factors mentioned above. Interestingly, Witting was encouraged to apply his models to the anomaly of the over-abundant gray whales. In his assessment (IWC, 2001) a couple of years ago, the population is now high, near the top of a slow natural cycle, and will decline - even under protection - in a few years. This, if correct, has of course, enormous implications for the management of any whaling and the interpretation of population changes under protection.

I have commented at some length on population dynamics and multi-species modelling not only because it is my own favorite subject but because at this time it has great practical, political importance. A decade or more after Seiji Ohsumi's claim that baleen whales - especially minke and blue whales - competed with each other for food (mainly Antarctic krill) so strongly that minke whale populations should be reduced to help blues to recover from near extinction, another - and, I think, equally outrageous - claim emerged from the same source: that protection of minke whales should be removed because they were increasing and were affecting or would soon affect adversely the populations of other organisms on which commercial fisheries depend. This doesn't make much sense in the Antarctic because there remains limited interest in development of a major fishing industry for krill. However, the same argument, applied to, for example, areas in the northern hemisphere where at least some of the baleen whales feed, at least some of the time, on fishes, some of which are the targets of commercial fisheries, can have important practical consequences. It is now being used extensively to persuade the world that the current moratorium on commercial whaling (since 1986) should be lifted or modified. In support of this claim documents have been produced comparing - unfavorably, of course, the amounts of "marine living resources" consumed by whales and other cetaceans, with the scale of human catches. Such arguments, while not deserving the title of "science", are persuasive to politicians, fishers, journalists and the lay public. Japanese government representatives have been fairly successful in inserting "warning" resolutions and statements in the proceedings of several inter-governmental bodies, including FAO and its Committee on Fisheries (see Donoghue, 2003).

Attempts to counter this propaganda - for that is what it is - have so far been confined mostly to explanations of the scientific issues, both in technical papers and popular pamphlets. It is not difficult, for example to show that more realistic deductions can even lead to the conclusion that fewer whales in the sea could in certain circumstances lead to reduced, not increased, fish catches. Most simple analyses, however, will conclude that fewer whales could mean more fish for us, if not very much more. This in fact comes, I suggest, from the elementary structures of simple models that (a) do not take proper account of dietary selectivity and (b) do not allow for intrinsic long cycles of abundance à *la* Witting. In the final analysis, however, scientists frequently conclude that it is all very complicated, we need more research, there could be chaotic behaviour in these systems that preclude predictions, and so on. I think a consequence of that is that politicians and the rest (a) may conclude that science is not much help, and, anyway, scientists always want more money for their research, and (b) they will therefore rely on "common sense", which tells them that if the whales eat less then we can get more; simple as that.

It is perhaps worth noting, at this point, that the international law of the sea, as determined by the UNCLOS Convention, does not provide rules for unsustainable depletion of one resource for the intended benefit of another - unless one wishes to interpret the target of "maximum sustainable yield" in a way that was certainly not intended by the drafters of that Convention. It does, however, explicitly mandate the near opposite: with respect to marine mammals and other predators, fisheries for species on which they feed must be managed in such a way as to preclude deleterious effects on the biological productivity and reproductive success of the "dependent" mammals.

There are two interesting sidelines to the above arguments about whales as scapegoats . At first, it was a matter of finding "reasons" to lift or remove the whaling moratorium. These later metamorphosed into a rationale for killing whales in large numbers as "scientific samples", the products from which were - of course - sold to keep the industry alive and to finance the continuing research. This was the third in the "reasons" given for "scientific whaling". The first, mentioned above as a failure, was to estimate natural mortality rates, though not their - crucial - density dependence. The second was to provide information that would "improve" the IWC's preferred management process, the so-called Revised Management Procedure and System (RMP, RMS); this also was rejected by other scientists as not viable. The third, and current, rationale is to improve estimates of the consumption of marine living resources, especially of fishes and other economically valuable species, by whales. This has been used to justify increases in the numbers of what the IWC once quaintly called "scientific whales" - minke in this case, initially, but also an extension of scientific whaling to other species such as the Bryde's whale and the sperm whale (the latter being more firmly protected under IWC regulations than any other species), and to more sea regions. And, most recently, it is offered as the justification for the renewal of what is really commercial whaling, even if under special scientific permits, by Iceland.

To finish this polemic I will suggest that the political issue may not now be only the matter of the whens, hows and ifs of the resumption of full-scale commercial whaling. It could be, I think, that the unstated issue is of the viability and acceptability of the concept of sustainable use of living marine resources (fishes, molluscs, crustaceans, perhaps pinnipeds too, as well as the economically unimportant cetaceans). Consider this scenario. Over-fishing is now a recognised global phenomenon, with some countries having huge stakes in large industrial fleets. There is a rearguard that is reluctant to accept that fishing is the prime cause of the collapse of fish resources. Scapegoats are sought. The first target is, as always, other fishermen, usually either from other countries or using different kinds of gear. Another target is deleterious natural environmental change (and if we cannot do anything to stop that then, so the argument goes, it might be best to get what we can now/soon from the living resources.). Environmental changes caused by human activities can, of course, provide yet another target scapegoat: those "other persons" who are responsible for such changes. And, as virtually a last resort, the other marine animals that prey on fish and other species of direct economic interest to us - especially the whales. The whales are also, of course, a preferred target for such arguments because they are themselves very valuable, at least on a *per capita* basis; there is less enthusiasm for culling "valueless" cormorants that steal" fish from coastal mariculture operations).

Now, an over-capitalised industry, such as the industrial fishing industry, faced with a decline of its renewable resource, has two basic options: to drastically reduce its scale, rather quickly, towards a possibly biologically sustainable level; or to continue operating at a high level of intensity while preparing an orderly phase-out. The first option may be very painful, economically and socially, the second option less so. It is now documented that the British Antarctic whaling industry, or part of it, made the second choice in the 1960s, while paying lip-service to reducing quotas towards biologically sustainable levels (such calculations naturally took into account assessments of the degree to which *other* operators would agree to and abide by the first option). The British pulled out after a planned seven years, having cut losses also by selling vessels to others, along with the national and fleet quotas assigned to them It is worth noting, too, that turning against the notion of biological sustainability does not necessarily imply lack of economic sustainability. The now extinct Norwegian Antarctic industry is an example of that. The profits from that were used to build the city of Sandefjord, and to capitalise the Norwegian ship-building industry; both as long-lasting and as sustainable as any enterprises in this uncertain world. The biggest section of the British whaling industry turned its profits into a large, long-standing road-transport corporation.

Since the UN's Brundtland Commission reported (it was headed, coincidentally by the politician who, as Prime Minister of Norway, authorised her country's resumption of whaling despite the moratorium), followed by many international and national declarations, it has not been easy, publicly, to justify deliberate unsustainable use of renewable resources. True, the debates are mightily prejudiced by, among other things, confusion between biological sustainability and economic/social sustainability, and this is now exacerbated by doubts among ecologists concerning the old, largely theoretical, ideas about stability, continuity and, hence, sustainability. But "multi-species management" arguments, even though based on what are often flawed models, provide an opening for *deliberate, calculated unsustainable* use of certain elements of the marine ecosystems.

The latest fashion in this matter is "ecosystem management" or, for more timid folk "the ecosystem approach to management". This, to many of us, sounds like a great idea. But do we know how to do it, especially in the ocean environment? Will we ever have the capability? And, in the context of the subject of this workshop, is it a concept that can be distorted by those having vested interests in intensive exploitation of particular elements of the systems - such as whales and large predatory fishes? Perhaps the current attacks on the whales and the commercial moratorium are to be seen more as the tip of an iceberg, the vanguard of a concerted effort to avoid the consequences of over-fishing, through the sustainability route, conveniently interpreting the attainment of sustainability primarily as a multi-species or ecosystem management process.

Two recent studies have come to my attention suggesting that removal of top predators, especially cetaceans, may have effects far more dramatic than the "release" of prey species for potential human benefit and a re-adjustment of relative abundances of species. One of these, by Mark Hixon and his colleagues (2002) at Oregon State University, involved the experimental selective removal of some species on coral reefs in the Bahamas which led to unexpected collapses of other species populations. The other, more directly pertinent to our discussion here, is by Alan Springer and his colleagues (2003) at the University of Alaska, Fairbanks.

Springer's team gave its attention to the vast changes in the waters of the Aleutian Island, that closely followed the rapid depletion of large whales by Soviet and Japanese whalers, beginning in the 1940s. The researchers hypothesised that the large whales (presumably mainly the calves) had been preferred prey of orcas; depletion of the whales caused the orcas to prey first on seals, then sea-lions, then sea otters and fish, causing, in the team's words "the longest and most complex ecological chain reactions ever described".

So far I have given my personal reasons for thinking the subject of this workshop is of great importance, practically as well as scientifically. I am aware that I have not begun to touch on "roles" other than as movers and storers of biomass. Others will adress other types of biological/ecological role. What are the marine equivalents of, for instance, the species of wasp whose "role" seems mainly to be to ensure the pollenation of figs? What roles do cetaceans play as transporters of parasites and epizoans? Human bottom-trawling activities change the composition of the benthic fauna; does the benthic feeding of the grey whale physically affect the substrate on which live its prey - worms and molluscs?

I think we need an evolutionary view of our subject, also. One of the great differences between marine and terrestrial ecosystems is in the size distributions of constituent species. This begins with the minute size of the primary producers in the sea compared with the size ranges of photosynthesising terrestrial plants. So, while sperm whales may eat giant squids of the same order of magnitude as themselves, the largest whale, weighing up to 100 tonnes or more prey on herbivorous animals of sizes that would, on land, be consumed by tiny carnivores. The absence of a solid substrate in the biologically most productive zone, except close to shores, has forced the evolution of very different systems from those on land, and not only with respect to adoption of aquatic life-styles.

With respect to the great whales, especially the baleen whales, a critical zone in the Antarctic feeding areas, and probably in the Arctic, too, is the ice edge. Only recently has it begun to become clear just how and why that is critical. Phytoplankters are trapped in and under the ice in winter, being released to become krill feed as the ice melts. The Antarctic convergence is important, but so is the ice edge further south, in spring. Baleen whales, especially the minke, move right into the ice-packs and affect them, at least physically. Similarly, right whales in the Arctic go under the ice and rise to make blow-holes in it that are used by seals and others. How much of this sort of thing is going on, and how important are these “roles”? The Inuit people were long aware of the existence of right whales under the ice, far from its edge, which explained why they could say with assurance that the early counts of right whales made by non-native researchers were gross under-estimates, which were only corrected later by the application of new research techniques.

The baleen whales of the southern hemisphere have evolved in ways that cause them to feed in overlapping but distinct latitudinal zones, ranging from krill furthest south, by blue and minke whales, mainly krill and some copepods by fin whales a little further north, mainly copepods and some small fishes by sei whales further north again, beyond the Convergence; and yet a different diet by Bryde’s whales that feed in temperate waters. Humpback have yet another distribution, closer to land on the whole, especially during the annual migrations. The two sexes of the sperm whale, and different age-groups, occupy distinctly different zones for much of their lives. We know - or think we know - what other krill-eaters the minke and blue whales are competing with, but who is the copepod-eating sei whale competing with? I do not recall a single scientific paper on that subject.

Many of our ideas and presumptions arose from the earlier years of baleen whaling in the Antarctic: the hectic years of the devastating hunt for blue, fin and humpback whales. Sei whaling only began on a large scale in the mid-1960s, and the populations were depleted extremely rapidly by fleets that had been assembled originally for the purpose of hunting the bigger species. We have little more than a snapshot of the demise of those populations of smaller baleen whales, and relatively sparse research results.

The whales are big, eat a lot, are noisy (What role does that characteristic engender, except to other whales of, presumably, the same species?). But some of them are, apparently, clever, as well as communicative. Their communicativeness, especially by underwater sound, determines the geographical scale of their social groups. A baleen whale that looks alone to us is not really alone. This scale must affect the role it plays in the marine system in ways we have perhaps not yet fathomed. So what role does their cleverness generate? Hal Whitehead (2003) and his colleagues have begun to unravel such matters in fascinating studies of the sperm whale, concluding that this species has “culture”. That does not surprise me. And it seems to me this culture will inevitably affect, in many ways, that species’ role in the hemisphere-scale ecosystem it inhabits.

My closing “thought” is about evolution. Species evolve, come and go. Ecosystems evolve, come and go. The roles of cetaceans in ecosystems must change, too. The time-scales of most changes are slow, but when change is accelerated (as it is, now, by human actions) the roles will change, too; the role of the orca has gone rapidly from being, *inter alia*, a regulator of whale populations, to a devastator of very much smaller mammals. So our ecology should be an evolutionary, not static, one.

Methods for dietary studies on marine mammals

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INTRODUCTION

Marine mammals play a key role in marine ecosystems. Information on their diet is needed to fulfil several general objectives:

- Identify and quantify trophic links (i.e. who eats whom and how much)
- Provide insights on threats to status (e.g. apparent dependence on particular prey)
- Provide insight into feeding and foraging strategies
- Contribute to evaluation of interactions with fisheries
- Improve understanding of general biology and ecology of predator and prey
- Provide estimates of population food consumption
- Provide input into static and dynamic ecosystem models
- Estimate (single or multi-species) functional responses

There are few published data on cetacean diets in the Mediterranean (see Bearzi *et al.*, 2003; Notarbartalo-di-Sciara *et al.*, 2003; Blanco *et al.*, this volume) although unpublished material and grey literature exist. General indications of feeding ecology may be provided by reference to results from other areas but details of diets must be specifically determined for the Mediterranean new studies are therefore needed.

The purpose of the present paper is to review the main methods available to collect dietary data in relation to data already available for the Mediterranean.

STOMACH CONTENTS ANALYSIS

The basic methodology for stomach contents analysis in marine predators was described by Hyslop (1980) and applications to piscivorous marine mammals were reviewed by Pierce and Boyle (1991). Stomach contents analysis has well-known biases, especially to do with digestion and identifiability of prey remains (see Table 1), but remains the most widely used technique for evaluating cetacean diet. Stomach contents data are also needed to facilitate interpretation of fatty acid and stable isotope data.

Table 1. Stomach contents analysis: biases and limitations.

Problem	Nature of error or bias	Comments on resolution
Sample source: samples generally from dead animals (difficult to sample live animals)	Results reflect age-specific mortality patterns rather than age structure of population (bias)	Given data on population age structure and age-specific diet, true diet pattern could be reconstructed
Sampling source: stranded animals	Sick animals may not feed normally; bias towards animals feeding in coastal waters	Strandings may include offshore deaths transported to shore by currents; comparisons should be made between "diets" of different cause of death categories
Sampling source: by-catches	Samples biased towards animals feeding in vicinity of fishery (bias)	Rarely if ever demonstrated as a source of bias; comparison should be made between "diets" of different cause of death categories
Many stomachs empty or nearly empty	Lower than expected sample size (random error); little material from which to reconstruct diet (potential bias)	Especially if all stomachs are given equal weighting regardless of contents weight, potential bias towards prey with resistant remains
Time period	Only the most recent meal will be represented	Some remains of earlier meals may be recovered from the intestine
Digestion of prey remains	Identification of partially digested material may be difficult; original prey size must be estimated	Usually biomass is reconstructed from measurements on hard remains
Differential digestion rates for different prey species	Some prey under-represented; size-reduction of hard parts; cephalopod flesh digests more quickly than fish flesh but beaks more resistant than otoliths	Grading of otoliths and application of correction factors can reduce bias in size estimates; loss of prey (or reduction to unidentifiable remains) harder to evaluate; analysis may be restricted to fresh or least degraded remains
Partial ingestion	Hard parts of large fish may not be ingested	Identification of soft remains (proteins or DNA) can aid detection; hard parts other than otoliths also useful
Secondary ingestion	Prey remains from fish stomachs confused with cetacean prey	May be detected by examining size distribution of prey
Identifiability of prey remains	Some prey more easily identified than others, not only due to digestion	Cephalopod beak identification requires specialist training. All prey identification requires experience and access to reference material.
Retention of cephalopod beaks	Due partly to becoming trapped in stomach lining, cephalopod beaks may be retained many days	Independent measure of importance of cephalopods and fish needed, e.g. counts of eye lenses
Selection of parts to use for identification and prey size estimation	Some fish lack otoliths, others have more or less easily identified otoliths; guides available only for lower beaks of cephalopods	Use of other skeletal elements for fish increases detection rate of pelagic fish and may reduce bias due to size reduction.
Back-calculation of prey size	Relationships between otolith size and fish weight vary seasonally and regionally; inherent variability leads to uncertainty and bias in prey size estimation	The combination of otolith length-fish length regressions and seasonal length-weight regressions will cope with seasonal variation; estimated prey size should be adjusted based on variance in regression relationships

Sampling errors and biases associated with use of strandings include the likely overrepresentation of sick animals that may not have been feeding "normally". There is also the general point that the sample set will be representative of the mortality pattern in the population rather than the age structure of the living population. In fact, probably the most serious limitation in published data on stomach contents of cetaceans in the Mediterranean is small sample size (see Table 2 and reviews by Würtz *et al.*, 1992a, Bearzi *et al.*, 2003; Notarbartalo-di-Sciara *et al.*, 2003; Blanco *et al.*, this volume), a problem common to many studies based on strandings and by-catches. Most data exist for the striped dolphin *Stenella coeruleoalba* while for the larger odontocetes there are very few dietary records. Additionally, most studies did not attempt to reconstruct prey biomass and several studies reported only the cephalopod component of the diet (see Table 2).

Table 2. Dietary studies on Mediterranean cetaceans.

Species	**Method**	**Number sampled**	**Reference**
Striped dolphin *Stenella coeruleoalba*	SCA	16	Pulcini *et al.*, 1992
	SCA	23	Würz and Marrale, 1991, 1993
	SCA	28*	Blanco *et al.*, 1994, 1995
Bottlenose dolphin *Tursiops truncatus*	SCA	6	Orsi Relini *et al.*, 1994a
	SCA	14	Salomón *et al.*, 1999
	SCA	16	Blanco *et al.*, 2001
Fin whale *Balaenoptera physalis*	FSN	16+	Orsi Relini and Giordano, 1992
	ID	-	Relini *et al.*, 1992
	FSN	1	Mussi *et al.*, 1999
Common dolphin *Delphinus delphis*	SCA	10	Boutiba and Abdelghani, 196
Cuvier's beaked whale *Ziphius cavirostris*	SCA	2	Blanco and Raga, 2000
	SCA	1*	Carlini *et al.*,1992a
Risso's dolphin *Grampus griseus*	SCA	2*	Carlini *et al.*,1992b
	SCA	1	Bello, 1992
	SCA	1*	Würtz *et al.*, 1992b
Long-finned pilot whale *Globicephala melas*	SCA	1	Orsi Relini and Garibaldi, 1992

The table indicates the method used in each study (SCA = stomach contents analysis, FSN = faecal sampling with a net, ID = inference from distribution), the number of individual cetaceans sampled and the source.

Notes:
* Only the cephalopod fraction of the diet was reported
+ Faecal samples were also obtained from one stranded animal

Given relatively large sample sizes it is possible to obtain good quantitative dietary data from stomach contents analysis. Santos *et al.* (2004) analysed stomach contents of almost 200 harbour porpoises from Scotland (UK) and were able to investigate interannual, seasonal, regional and ontogenetic variation in diets, as well as evaluating possible sampling biases by comparing diets of animals from different cause of death categories. Establishment of a co-ordinated programme of data collection from stranded (and by-caught) cetaceans, including analysis of stomach contents, is a priority for the Mediterranean area.

As shown by simulations, the largest quantifiable source of error in diet reconstruction is probably that due to digestive erosion of some prey remains (Hammond and Rothery, 1996). In many studies it is assumed that there is no digestive erosion or loss of otoliths and it has been argued, based on *in vitro* otolith digestion experiments, that the calculated overall diet composition can be relatively insensitive to size reduction in otoliths (Wijsma *et al.*, 1999). Other authors have derived "calibration coefficients" to account for both size-reduction (e.g. Tollitt *et al.*, 1997) and loss (Bowen, 2000) of otoliths during analysis of pinniped faecal samples. However, to apply these to stomach contents analysis it is necessary to know how long food has been in the stomach. This could be estimated from the proportion of otoliths remaining inside fish heads (Murie and Lavigne, 1986). To account for size-reduction, a better solution is probably to grade otoliths into "digestion categories" based on qualitative morphological features (e.g. loss of lobes) and apply grade-specific calibration coefficients.

Some biases are less obvious. Thus, relationships between otolith length and fish weight are intrinsically variable, obviously leading to uncertainty in back-calculated fish size. Also, if we use regression relationships based on log-transformed data, back-calculated fish weights are biased downwards, the extent of the bias being proportional to the variance associated with the regression line (see Hammond and Rothery, 1996).

Although stomach contents analysis is relatively inexpensive and requires no specialised equipment, it is time-consuming and reliable identification of prey remains requires experience, access to good reference material and, in some cases (e.g. identifying cephalopod beaks, Clarke, 1986), specialist training. Identification of fish remains is facilitated by the existence of various guides aimed at biologists (e.g. Härkönen, 1986; Watt *et al.*, 1997) as well as extensive archaeozoological literature (see Casteel, 1976). Less information is available to assist identification of crustaceans (Mori *et al.*, 1992).

A number of important decisions must be made about prey identification: for instance should only fresh prey be considered? should all hard parts be identified? and so on. Thus, to avoid errors due to digestive erosion and loss of material, one strategy is to identify only "fresh" remains. In practice, many stranded animals have no fresh prey remains in the stomach. Also, if sourced from fishery by-catches, fresh stomach contents may be biased towards prey eaten at particular times of day. If partially digested material is to be identified, this will usually be based on recognition of hard parts such as fish otoliths. However, use of all hard remains can substantially increase the rate of detection, especially for species with small or fragile otoliths, e.g. clupeids or mackerel (Brown and Pierce, 1998; Tollit *et al.*, 2003).

Various issues also arise with respect to quantification, e.g. the use of frequency of occurrence, number of prey or reconstructed biomass. Usually prey biomass is the most informative measure, although additional insights can be obtained by considering energy content, nutritional value (minerals, vitamins, fats) and contaminant load. Very often, "average" diets are obtained by summing prey across all stomachs sampled. This implicitly attaches most importance to the stomach contents of animals that had most food in the stomach. The alternative, which may be desirable for some statistical analyses, is to apply equal weighting, e.g. by expressing biomass of each prey species in each stomach as a proportion of the total for that stomach.

Some multivariate statistical packages (e.g. PRIMER) are well-suited to analysis of patterns in dietary data. One problem in handling dietary data is that there are often many zero values for prey importance. Reliance on non-parametric statistics is one solution; another is use the zero-inflated Poisson distribution, as previously applied in various other contexts, including modelling migration in human populations and modelling the frequency of accidents (Bohara and Krieg, 1996; Shankar *et al.*, 1997; Bohning, 1998). It is important to provide measures of uncertainty about diet composition. Since reconstruction of prey biomass involves many sources of error, bootstrap methods offer the best solution (Hammond and Rothery, 1996; Santos *et al.*, 2001a).

FATTY ACID ANALYSIS

During the last decade, analysis of the fatty acid (FA) composition of blubber has increasingly been used to provide inferences on diet composition. In fact, studies on FAs in marine mammal blubber date back to at least the 1960s. Ackman *et al.* (1963) compared FAs in seal blubber oil and body oils of menhaden and herring, concluding that they were qualitatively similar. The first attempt to provide a quantitative estimate of diet composition based on FAs in predator and prey was probably the work by Knutsen and Vogt (1985a,b) who compared the FA composition of lobster stomach contents with fatty acids in putative prey. They prepared fatty acid methyl esters (FAMEs) and measured the proportions of different components using high performance liquid chromatography. Their analysis then used pattern recognition software developed for taxonomic applications, SIMCA (Soft Independent Modelling of Class Analogy). The current state-of-the-art as described in Iverson *et al.* (2004) is based on a conceptually very similar approach.

Table 3 summarises some of the main advantages and disadvantages of FA analysis as a tool to determine diet composition. So-called quantitative fatty acid signature analysis (QFASA) is described in detail by Iverson *et al.* (2004). These authors identified those FAs considered to be wholly or mainly of dietary origin in marine mammals and provide experimentally-derived "calibration coefficients" to account for differential synthesis, uptake or deposition rates of different FAs by pinnipeds. A major uncertainty at present is whether these calibration coefficients are applicable to cetaceans. It is very likely that some calibration coefficients will be needed, however, to allow quantitative interpretation of cetacean blubber FA profiles. Thus, Olsen and Grahl-Nielsen (2003) found that FA profiles of minke whales were unlike those of the whales' fish prey. However, Hooker *et al.* (2001) found that fatty acid profiles of northern bottlenose whales and their main prey, adult squid *Gonatus fabricii*, were very similar.

Table 3. Advantages and disadvantages of using fatty acid analysis to determine diet composition.

Topic	Advantages	Disadvantages
Origin of FAs in blubber	Most FAs are of dietary origin ("you are what you eat"); identities of FAs of exclusively dietary origin are known	Shorter chain FAs are biosynthesised; uptake rate differs between FAs
Other lipids	Standard methods can also take account of other lipid classes of dietary origin, e.g. fatty alcohols	
FA profiles of prey	Different prey taxa can be distinguished (at least, quantitatively)	FA profiles of closely related taxa tend to be very similar; prey FA profiles vary seasonally, regionally and ontogenetically
General ecological interpretation	FAs vary between habitats, e.g. marine *vs* freshwater	
Chemical analysis	Preparation of FAMEs and GCFID is straightforward; identity of components confirmed by MS	FAMEs are unstable; identification of FAs by MS is not exact
Sampling from live animals	Blubber biopsies can be used; lipids can be obtained from other tissues, e.g. chylomicrons in blood	Blubber is stratified; usually it is necessary to analyse the inner blubber layer to determine diet
Sampling from dead animals	Samples can be obtained from animals with empty stomachs	As above; also FAs become oxidised as the animal decomposes
Sample storage	Samples can be preserved at –70ºC	FAs become oxidised over time, even at –20ºC
Time-scale of dietary data	Results will indicate average diet over (at least) several months	Precise time-period unclear; will vary between tissues
Quantitative interpretation	Proportions of different prey in diet can be calculated. "Calibration coefficients" are available for pinnipeds	FA profiles are needed for all putative prey; computation is time-consuming; calibration coefficients required to account for differential uptake.
Use in models	Even if the diet composition cannot be quantified, proportions of fatty acids can themselves be used as predictor variables, e.g. for contaminant burdens	Interpretation may be dificult

FA = fatty acid; FAME = Fatty acid methyl ester; MS = mass spectrometry; GCFID = gas chromatography with flame ionisation detection

More research is needed on the process of FA deposition in marine mammal blubber to determine the effect of diet composition and nutritional state on FA update and to identify differences, in FA uptake and deposition, between different marine mammal species. Some technical issues also remain to be addressed. Thus, Wetzel and Reynolds (2003) proposed the use of fatty acid picolinyl esters (FAPEs), which are more stable than FAMEs, due to the presence of the heavy pyridine ring. Identification of the FA components using gas chromatography and mass spectrometry (GC-MS) is easier, e.g. allowing double bond isomers to be distinguished, and can be accomplished without reference to standards (Wetzel and Reynolds, 2003).

Learmonth *et al.* (2003) measured FA profiles in the blubber of harbour porpoises, based on samples taken from animals stranded in Scotland (UK), as well as FA profiles of likely prey species (Santos *et al.*, 2004). They applied standard methods: lipid extraction (Hanson and Olley, 1963), production of FAMEs, quantification using gas chromatography with flame ionization detection (GC-FID) and identification of fatty acids using GC-MS. Proportions of SFs were arcsine transformed to normalize the data. Analysis of prey data using PCA showed that prey could be reliably separated at least to family level, although some pairs of species were very similar (Figure 1). Seasonal, regional and size-class differences in porpoise FA profiles were qualitatively consistent with expectations based on the FA profiles of the most prominent prey species of different sub-sets of porpoises (c.f. stomach contents data in Santos *et al.*, 2004). In terms of quantitative interpretation, PCA plots indicate that porpoise FA profiles are significantly displaced from prey FA profiles along the first PC axis. Restriction of analysis to the subset of "mainly dietary" FAs identified by Iverson *et al.* (2004) brings the two groups closer together, while application of calibration coefficients (also from Iverson *et al.*, 2004) results in almost complete overlap of prey and predator FA signatures, suggesting that the calibration coefficients were, at least to some degree, appropriate.

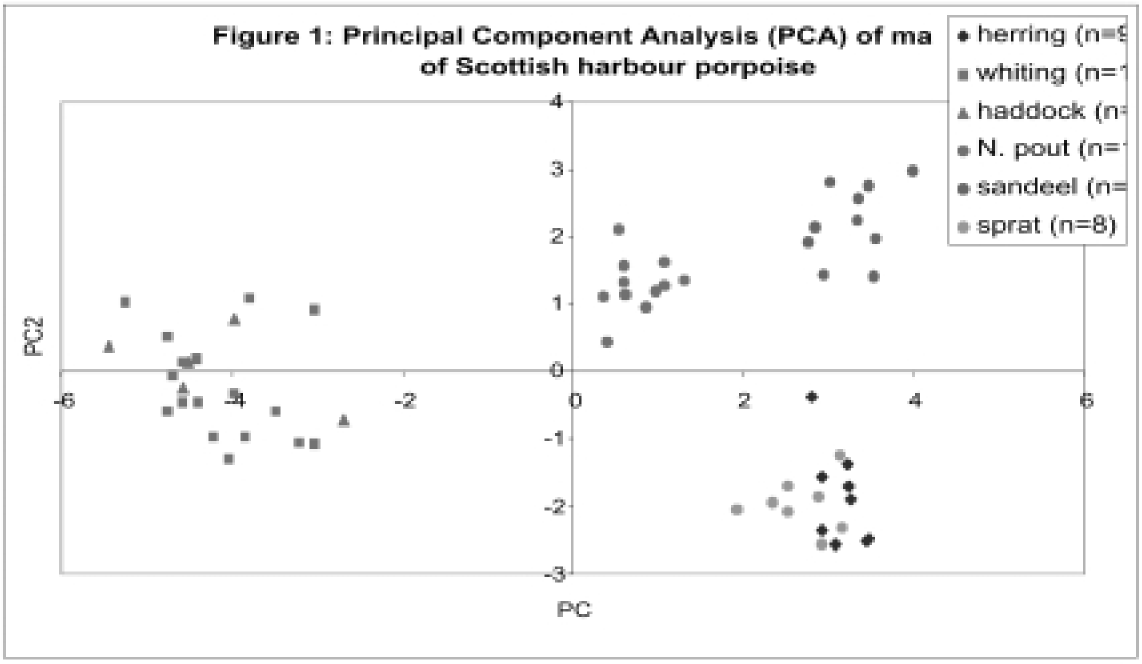

Fig. 1. Principal Component Analysis (PCA) of main prey species of Scottish harbour porpoise.

The general approach to quantitative determination of the diet from fatty acid profiles (i.e. QFASA) is based on evaluating goodness of fit for different hypothetical diets. This may be thought of as equivalent to fitting a series of simultaneous equations, where the unknowns are the proportions of the different prey species that would produce the FA profile observed in the blubber. In practice, there may be no analytical solution, only a closest approximation established numerically. Iverson *et al.* (2004) considered several alterative goodness of fit measures, electing to use the Kulback-Leiber distance rather than the more familiar squared error distance.

In a preliminary application for harbour porpoise data (Pierce *et al.*, unpublished), we have used a simple least squares procedure, coded in BASIC, to evaluate goodness of fit of different putative diets (up to 200,000 combinations tested). The resulting best-fit diets estimated using uncorrected data were generally less plausible than best-fit diets estimated after applying calibration coefficients to the porpoise FA blubber profiles. However, experimental data are needed to provide validation.

STABLE ISOTOPE ANALYSIS

Stable isotope analysis is another tool now routinely used to provide data on trophic interactions, often in tandem with fatty acid analysis. The general assumption of the approach is that there is a predictable relationship between the isotopic composition of a consumer and its food. The most commonly analysed isotopes are those of carbon (12C and 13C) and nitrogen (14N and 15N). The latter provides the most useful dietary information since ?15 nitrogen levels show a stepwise enrichment of 3 –5 ‰ with each rise in trophic level. Carbon is transferred rather conservatively, so that carbon isotope ratios can be used to trace different sources of primary productivity, i.e. to infer the identity of the ecosystem in which an animal feeds.

One limitation is that stable isotope can provide only rather coarse data, i.e. indicating trophic level rather than detailed diet composition. Sample processing can be relatively straightforward (e.g. freeze drying followed by mass spectrometry) but is expensive. Processing and storage of samples may affect isotope determinations (e.g. Feuchtmayr and Grey, 2003). Schmidt *et al.* (1994) review other problems related to the underlying principles of the method. They note that isotopic fractionation is not constant but can vary depending on food quality and nutritional stress, and that different species feeding on the same food source can show different isotope values. For a summary of advantages and disadvantages of stable isotope analysis as applied to dietary studies, see Table 4.

Table 4. Advantages and disadvantages of using stable isotope analysis to determine diet composition

Topic	Advantages	Disadvantages
Origin of stable isotopes in predator tissues	Stable isotopes in predator tissues reflect those in the prey	Isotopic fractionation depends on food quality and nutritional stress
Trophic relationships	Trophic level can be determined	Detailed dietary cannot be obtained. Isotope data for prey are needed for comparison.
General ecological interpretation	SI ratios can be characteristic of particular ecosystems (C, S), latitude (C), environ-mental conditions (O) or related to exposure (Pb).	Interpretation is not straightforward, e.g. due to multiple food sources, variable growth rates, isotopically changing food web baseline
Processing samples		Extraction and storage methods may affect results
Chemical analysis	Mass spectrometry is relatively straightforward	Results must be expressed relative to calibration standards to be meaningful. Regular calibration necessary. Expensive
Sampling from live animals	Biopsy samples can be used	
Sampling from dead animals	Samples can be taken from animals with empty stomachs. Historical material (e.g. bones of museum specimens) can be used	Certain storage methods preclude SI analysis
Time-scale of dietary data	Results will indicate average feeding over (at least) several months	Precise time-period unclear; will vary between tissues

SI = stable isotope

Perhaps the most interesting aspect of stable isotope analysis is the prospect of following changes in diet over time. Stable isotope ratios can be measured using museum specimens - thus Hobson and Montevecchi (1991) were able to study trophic interactions in great auks. Walker *et al.* (1999) showed that coastal bottlenose dolphins had similar diets over a 100-year period. Another exciting possibility is reconstructing aspects of individual life histories by following changes in isotope ratios across tissues that show incremental growth layers, e.g. baleen of fin whales (Dubroca *et al.*, this volume). Using high spatial resolution microprobes this approach can be extended to smaller structures such as teeth, using e.g. ion microprobe/secondary ion mass spectrometry (SIMS) or (b) laser ablation inductively coupled plasma mass spectrometry. To date, most applications of laser ablation to mammalian teeth have been to measure isotopes of heavy elements such as lead or strontium (e.g. Uryu *et al.*, 2003).

Experimental work on captive squid (Stowasser *et al.*, 2003) showed that individuals feeding on crustaceans had lower ?15N ratios than those fed on fish or mixed diets, and these changes were detectable after only seven days. There have however been few experimental studies to validate stable isotope analysis in higher animals. Hobson and Clark (1992) experimentally validated use of carbon isotope ratios to make inferences about feeding in Japanese quail and American crows.

OTHER APPROACHES TO DIET ANALYSIS

Other techniques available to determine cetacean diets include collection of faecal samples and prey remains from the water during feeding events (e.g. Orsi Relini and Giordano, 1992), sampling macro-zooplankton (etc) in the vicinity of feeding baleen whales (e.g. Relini *et al.*, 1992), direct observation of surface feeding, and use of underwater video cameras.

There have also been various approaches to identifying soft remains of prey, from electrophoresis of proteins in eye lenses (Barrett and Williams, 1967) and raising antisera to fish proteins (Pierce *et al.*, 1990) to identification of prey DNA (Jarman *et al.*, 2002). The optimal strategy to build up a qualitative and quantitative picture of diet is probably to use several techniques. In this way, trophic links missed or poorly quantified by one method may be detected or more adequately quantified using another method. Thus, direct observation may reveal feeding on large fish prey, such as salmonids or cartilaginous fish, not detected from analysis of stomach contents or faeces (Brown and Mate, 1983; Condit and LeBouef, 1984; Carter *et al.*, 2001).

FROM DIET TO MODELS AND EVALUATION OF COMPETITION WITH FISHERIES

As other papers in this volume (Harwood and MacLaren, this volume; Koen-Alonso and Yodzis, this volume) make clear, simply to demonstrate an overlap between the diet of a cetacean and the target species of a fishery does not prove that there is competition. Similarly, observation of opposite temporal tends in fishery landings and dolphin abundance does not prove that there is a causal link.

Due to indirect trophic interactions, and the important trophic role of predatory fish, there may be no negative effect of marine mammal predation on fisheries or vice versa. As Furness (2002) comments in the context of marine mammal and seabird predation on sandeels in the North Sea, the “overwhelming influence of predation on food-fish by predatory fish may be a feature of many marine food webs worldwide”.

Modelling the dynamics of food webs provides a means to demonstrate the likely interactions occurring between marine mammals and fisheries. To parameterise such models requires more than just dietary data: information on diet composition must be coupled with information on energy requirements. While it is common to apply standard equations relating energy requirements to body weight, or to make inferences based on energy requirements in captive animals, it should be recognised that this subject requires at least as much attention as the subsequent partitioning of predator energy intake between the various prey species in the diet.

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Modelling interactions between marine mammals and fisheries: model structures, assumptions and data requirements

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1. INTRODUCTION

There is no doubt that marine mammals can expert important influences in their ecosystems (Bowen, 1997), but how do we evaluate this influence? In particular, how do we assess the potential effects of a change in prey abundance caused by fisheries on marine mammal numbers, or of changes in marine mammal abundance on fisheries yields? In this paper we review the model frameworks that have been used for these purposes, focussing particularly on models that have been used to investigate the interactions between seal populations and commercial fisheries because there is better information on the diet of seals than for most other marine mammal species. In many cases, these frameworks are extensions of multispecies approaches that have been developed for fisheries management. As a result, the focus has been on the potential impact of marine mammals on fisheries. In a final section we discuss whether or not the same approach can be used to assess the impact of fisheries on marine mammals. Although ecosystem-based approaches are being actively promoted for fisheries science in general (e.g., ICES, 1997; CIESM, 1999), total allowable catches for exploited fishes are still largely based on single-species models.

So far, none of these valuable attempts to develop multispecies approaches has provided unequivocal evidence that fisheries produce negative impacts on marine mammal abundance or foraging behaviour, or that marine mammals affect fisheries yields. The issue is complicted by the fact that "...on a short time scale we might predominantly observe the effect from the shorter pathway (an increase in fisheries yield), with the contribution of the longer pathway making itself felt only on a longer timescale, possibly leading to a reversal of the response (a decrease in fishery yield)" (Yodzis, 2001 [p. 80]).

2. STATIC-FLOW MODELS

Whipple *et al.* (2000) provide a useful discussion of the different methodologies that have been used to analyse predation mortality in aquatic ecosystems. They distinguished between static-flow models that provide a "snapshot" of the system at one moment in time, dynamic models that attempt to track variations in population size over time, and spatially explicit models that attempt to take account of variation in space as well as time.

2.1 Surplus yield calculations

The simplest static-flow models involve a calculation of the quantities of each fish species consumed by a marine mammal species, these are then compared with the quantities taken by commercial fisheries. It is then assumed that reduction of either the marine mammal population or fisheries catches by, say X%, will result in an equivalent "surplus yield" becoming available to the competing consumer.

These surplus yield calculations have been used primarily to calculate the potential benefits to a fishery of a reduction in marine mammal numbers, or to assess the potential for competition between marine mammals and fisheries. For example, Tamura (2003) concluded that estimates of the consumption of fish, cephalopods and crustaceans by cetaceans in various oceans were similar to the quantities of these groups removed by commercial fisheries and concluded that there was "probably direct competition between cetaceans and commercial fisheries in the North Pacific and North Atlantic".

Although surplus yield calculations, if performed correctly, may provide a reasonable estimate of the short-term consequences of a change in predator abundance, they are unlikely to provide a realistic estimate of the longer-term consequences. In addition, it is important that uncertainties involved at each stage of the calculation are adequately accounted for. When this is done, the potential benefits to fish stocks may be less clear cut than a simple calculation might imply. For example, McLaren *et al.* (2001) calculated the potential effects on the northern cod stock of removing 750,000 harp seals from the North-West Atlantic stock over a five year period. The mean estimate was that this would reduce the quantities of cod consumed by around 4,000 t per year. This is roughly equivalent to the effect of closing the current commercial fishery. However, the 95% confidence limits on this estimate were wide (± 40%) and the consequences for the Canadian seal industry of the resulting decrease in harp seal abundance would be dramatic, with a high probability that this fishery would have to be closed.

2.2 Mass balance approaches

More sophisticated static-flow models use mass-balance principles to estimate flows of organic matter or energy among components of an ecosystem using data on diets, estimated assimilation efficiencies, metabolic demands, etc. Formal implementations of this approach include the use of Ecopath software (Christensen and Pauly, 1993, available at http://www.ecopath.org) and inverse-modelling (Savenkoff *et al.*, 2001). It is particularly useful for identifying deficiencies in knowledge about the system. Some authors have attempted to use Ecopath to investigate the impacts of changes in one component of an ecosystem by manipulating the biomass of that component and re-balancing the system. However, Ecopath **assumes** that energy flows are in balance so it cannot, on its own, be used to draw conclusions about effects of changes in exploitation rates or predation. Dynamic models, such as Ecosim (see below), are required for this.

3. PREDATOR FUNCTIONAL RESPONSES

Many model implementations have combined static-flow models for higher predators and dynamic models for prey populations. This approach allows predator dynamics to be ignored. This may be useful when considering the potential impact of predators on fisheries yields, but it is clearly inappropriate when considering the potential impacts of fisheries on predators.

If such models are to be even moderately realistic they must take account of the way in which the number of individuals of each prey species consumed by a predator varies with prey abundance (the predator's functional response). The functional response of generalist predators, which consume many different prey species, will be affected by changes in the abundance of any, or all, of its prey. However, most work on functional responses has focussed on the response of individual predators to changes in only one prey species.

Data on what form the functional responses of marine mammals may take are equivocal. Stenson and Perry (2001) found no significant change in the proportion of Atlantic cod in the diet of harp seals off the east coast of Newfoundland over a period when the size of the cod stock declined by a factor of 100 times. This suggests that the functional response of harp seals to cod is highly non-linear. The Ecosim computer package has the facility to mimic the effects of predator functional responses by providing a "refuge" where some prey are unavailable to predators. Ironically, when this package was used to model interactions between cod and harp seals in the same area, the best fit to the time series of fish abundance data was obtained when cod had no refuge from seal predation (Bundy, 2001), implying a linear functional response.

Other authors have documented large changes in diet composition from region to region that appear to be related to the availability of prey. For example, there have been marked shifts in the diet of harp seals in the Barents Sea following changes in the abundance of capelin, their preferred prey (Bogstad *et al.*, 2000). This kind of switching between prey species is characteristic of a particular form of functional response. Similarly, Lindstrom *et al.* (2002) documented a non-linear relationship between the importance of herring in the diet of minke whales in the Barents Sea and herring abundance.

4. MINIMUM REALISTIC MODELS

One way to improve the realism of simple surplus yield calculations is to incorporate predator mortality directly into models of the dynamics of target fish stocks. Such models have been referred to "minimum" realistic models (MRMs, for short) – Butterworth and Plaganyi (in press). They may be fully dynamic (where continuous changes in the abundance of both predator and prey are modelled), or combine dynamic models of the fish stocks with static-flow models of predator consumption. There are now a number of examples of spatially-explicit models of this kind.

The incorporation of additional sources of predation may have counter-intuitive consequences for the predicted response of the target fish stock to a change in predator abundance. Perhaps the most oft-quoted example is an analysis conducted by Punt and Butterworth (1995) who developed an age-structured model of the interactions between Cape fur seals and the South African hake fishery. When they included only a single, cannibalistic hake species in their model, a decrease in fur seal numbers resulted in increased hake catches. However, when they took account of the fact that there are actually two hake species in South African waters, and that the species preferred by fur seals is a major predator on the younger stages of the species that is predominantly taken by the commercial fishery, they reached the opposite conclusion: a reduction in fur seal numbers had a negligible or negative effect on the commercial catch of hake. This is a classic example of "mesopredator release" (Courchamp *et al.*, 1999; Crooks and Soulé, 1999).

The results of Punt and Butterworth's analysis led UNEP (1999) to recommend the use of MRMs for evaluating the potential effects of culls of marine mammals on fisheries yields, and to suggest that MRMs should attempt to incorporate at least 80% of the natural predation on the target fish stock. There have been a number of attempts to apply MRMs to marine mammal-fisheries interactions since the original meetings that led to the UNEP guidelines.

4.1 Multspec, Bormicon and Gadget

MULTSPEC is a spatially-explicit, mixed static-flow and dynamic modelling package (Bogstad *et al.*, 1997; Tjelmeland and Bogstad, 1998) which has been used to investigate interactions between three fishes (capelin, herring, cod), harp seal, and minke whale (*Balaenoptera acutorostrata*) in the Barents and Norwegian Seas. Marine mammal numbers are assumed to remain constant over time, unless they are harvested. Bogstad *et al.* (1997) tentatively concluded that herring stocks would be reduced by increased whale numbers, whereas increased harp seal numbers would most heavily affect the capelin and cod stocks. These conclusions were generated by removing portions of the mammal populations and comparing the results with those from a "reference run." However, the lack of any functional response by either predator to changes in the relative abundance of alternative prey, and the fact that the dynamics of the system are largely driven by variations in spring-spawning herring (which are controlled by events outside the Barents Sea) suggests that alternative formulations of the model might produce different conclusions.

BORMICON (Bjoernsson, 1997) is another spatially-explicit, mixed static-flow and dynamic modelling package which has been used to investigate the interactions among Icelandic cod, capelin, shrimp and baleen whales and fisheries yields. Preliminary application of this model

(Stefánsson *et al.*, 1997) suggested that “the impact of the three baleen whale species on the development of the cod stock is uncertain, but may be considerable”. GADGET (Stefánsson, in press) is an elaboration of elements of BORMICON and MULTSPEC.

4.2 Grey seals and cod on the Scotian Shelf, Canada

There have been two recent attempts to develop MRMs of the interactions between grey seals and Atlantic cod on the Scotian Shelf, off the east coast of Nova Scotia.

Mohn and Bowen (1996) modelled the functional response of the seals in two ways: a linear response and a “constant ration” model (which assumed that the proportion of cod in the seals’ diet was independent of cod abundance). They found that the model results were highly dependent on the form of the functional response, but concluded that “seals were not a major factor in the recent [1993] collapse of this stock”.

Fu *et al.* (2001) assumed that mortality on cod was proportional to grey seal abundance (which had been increasing exponentially over the 25 years of their modelling exercise). They used the same two functional responses as Mohn and Bowen (1996), but allowed mortality from other causes to vary between years. They conclude that high natural mortality of immature and adult cod, much of which appears to be due to grey seal predation, and low recruitment since the mid-1990s have prevented the recovery of this stock.

4.3 Multispecies Virtual Population Analysis (MSVPA)

A number of studies have incorporated marine predation into the MSVPA framework. Livingston and Jurado-Molina (2000) developed an MSVPA model of the Bering Sea ecosystem involving six prey species and six predators, including northern fur seals. They found that the resulting estimates of total mortality for the prey species were higher than those obtained from single-species VPAs, but drew no conclusions about the effects of fur seal predation on prey dynamics.

The ICES Multispecies Working Group (ICES 1997) implemented an MSVPA model for the entire North Sea, involving a large number of fish prey species and their predators. Estimates of species- and size-specific fish consumption by grey seals, seabirds and cetaceans (mainly harbour porpoise and minke whales) were included in this analysis. The estimates of prey consumption by fish predators were based on large-scale stomach sampling programmes conducted in 1981, 1985-87 and 1991. Like Livingston and Jurado-Molina (2000), they also obtained higher estimates of natural mortality, particularly for younger age-classes, than those obtained from conventional single-species VPAs. Hildén (1988) had shown that shifts in predators preference for prey over time, caused by their functional response, could undermine the reliability of MSVPA calculations. However, the Working Group found very little evidence of such shifts in the data from the North Sea studies. It concluded that the predictions of MSFOR (a multi-species model that uses values from MSVPA and assumptions about stock-recruitment relationships for individual fish species to predict future changes in stock sizes) were quite similar to those obtained from single species models, but that single species models may underestimate the time that depleted stocks take to recover. They also noted that predator stocks and prey stocks may follow very different trajectories as a system recovers from over-fishing. However, grey seals do not appear to be a particularly important source of mortality for most of the fish stocks considered by the Group. The Group also concluded that inadequacies in the available catch data were probably more important than inadequacies in the diet data.

4.4 Steller sea lion and Alaskan pollock

Hollowed *et al.* (2000) developed a MRM of predation on pollock in the Gulf of Alaska incorporating three predators, one of which was the Steller sea lion, and pollock cannibalism. As with other MRMs, they obtained estimates of natural mortality on pollock that were higher than those from single species models but drew no conclusions about the importance of this predation for pollock stock dynamics.

5. FOOD WEB MODELS

Pimm and Rice (1987) reviewed the way in which food web models could be used in the management of marine resources, and concluded that they were more useful for broad comparisons among ecosystems rather than for providing specific advice. They also noted that such models often had serious problems in situations where many predators consumed the same prey species. However, there have been substantial improvements in the sophistication of marine food web models since their work (Trites, 2002).

Yodzis (1998, 2000, 2001) used an extended food-web model of the Benguela Current ecosystem, of which the interaction of the fur seal with hakes studied by Punt and Butterworth (1995) is a part, to investigate the usefulness of MRMs. He found that he could capture most of the important features of the system if he excluded all links that represented less than 10% of consumption both by and of any species. In this way, he could ignore 91 of the 203 links in his system and still make similar predictions to those obtained with the full system. However, most of the data that are available to fisheries scientists only provide information on the proportions of different prey species in the diets of individual species in the system. He concluded that this was a less satisfactory way of identifying weak (that is, less important) links in the system, but he concluded that most of the important properties of the system could be preserved if all links that contributed less than 5% of a predators diet were ignored. This reduced the number of links in the system from 203 to 106. Unfortunately, this is still a much more complex system than any of the MRPs that have been used so far. These results also imply that MRPs which follow the guidelines in UNEP (1999) and account for 80% of the predation on the prey species of interest may not capture all of the important indirect interactions in the system.

6. ENERGY FLUX MODELS

Given the enormous difficulties in obtaining enough information for the complex, age-structured population models of the kind developed by Yodzis, an alternative modelling approach for complete food webs is to use information on biomasses and the flow of organic matter among components. The Ecosim software (Walters *et al.*, 1997; Pauly *et al.*, 2000) provides a methodology for investigating the consequences of changes in fishing and predation ecosystems using this kind of information, although its limitations and assumptions must be clearly recognized. There have been a number of attempts to use Ecopath-with-Ecosim to investigate the consequences of changes in marine mammal numbers on commercial fish stock.

6.1 Steller sea lions and Alaskan pollock

Trites *et al.* (1999 in Yodzis 2001) used Ecosim to investigate the role of fisheries for Alaskan pollock and commercial whaling for fin whales on the decline of the Steller sea lion population in the Bering Sea. However, they were "unable to account for the differences between what was observed in that system in the 1980s and the best available reconstruction of the state of the system in the 1950s."

6.2 Harp seals and cod on the Newfoundland-Labrador shelf

Bundy *et al.* (2000), compiled available information and indirect estimates of biomass, consumption, production, and diet of major species and species groups on the Newfoundland-Labrador shelf during the period 1985-1987. The biomasses and flows of organic matter among components were balanced using Ecopath. They found that the two most important predators of small cod were harp seals and large cod, although they concluded that the former was less important than the latter.

The system has changed radically since the 1980s, most obviously through the great diminution of cod and other groundfish stocks and an approximate 70% increase in the harp seal population. The possible impact of these changes between 1985 and 2005 was explored by Bundy (2001) using Ecosim. She concluded that her results were consistent with the hypothesis that the collapse of the northern cod stocks was due to excess fishing, and "also support the hypothesis that the recovery of cod is currently being retarded by … predation by harp seals on cod." It should be recognized that these simulations take no account of uncertainties in the estimates of energy flows between components of the system and that Ecosim is likely to be more effective at simulating the effects of small deviations from initial equilibrium conditions, than the very large changes that have occurred on the Newfoundland-Labrador shelf.

7. CONCLUSIONS

None of the model frameworks described above is ideal for determining the role of marine mammals in marine ecosystems or for predicting the consequences of changes in any component of this system. All require large amounts of data, although this may not be as difficult to obtain as was once thought (Trites *et al.*, 1997). MRMs can capture many of the biological characteristics of particular interactions but they ignore the effects of diffuse links in the ecosystem, which may have important long term consequences. Energy flux models can capture some of these diffuse effects, but they require the user to accept a particular phenomenological approach to the structuring of marine ecosystems.

Modelling food webs: a bioenergetic-allometric approach

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INTRODUCTION

Solutions to the problems posed by marine mammals/fisheries interactions, like any other problem that arises from the interplay of components in exploited ecosystems, can be achieved only if we understand how these multispecies systems work. We pursue that goal, among other paths, through mathematical modelling. Presently, there is not one right way for modelling food webs, and we are still exploring different approaches. This paper briefly summarizes one of them, a bioenergetic-allometric approach (Yodzis and Innes, 1992; Yodzis, 1998).

In a very general bioenergetic setting, the dynamics of any species in a food web can be represented by

$$\frac{dB}{dt} = B(-T + J) - L \qquad (1)$$

where B is the population biomass, T and J are mass specific respiration and ingestion rates respectively, and L represents the losses to mortality other than starvation. Although equation (1) is conceptually simple, its actual implementation requires the estimation of many parameters, and their number grows with the complexity of the model.

One way to address this issue is to build bioenergetic-allometric models (Yodzis and Innes, 1992). This approach takes advantage of the observation that many vital rates are allometrically scaled to individual body mass (Peters, 1983; Innes *et al.*, 1987; Brown *et al.*, 1999). Then many of the parameters in the model can be estimated from allometric relationships or constrained to be proportions (hence bounded between 0 and 1). Food web modelling requires two types of equations, basal and consumer equations. A basal equation represents the biomass growth rate of a species whose resources (food) are not explicitly described in the model as

$$\frac{dB_j}{dt} = \left\{ r_j \frac{B_j}{K_j} \left[K_j - B_j - \sum_c \alpha_{jc} B_c \right] \right\} - \sum_i B_i F_{ji} - m_j B_j - H_j \equiv g_j \qquad (2)$$

where B_j , B_i and B_c are the biomasses of species *j* (the focal species), *i* (a predator of *j*) and *c* (a competitor of *j*); K_j is the carrying capacity of *j*; α_{jc} is the competition coefficient of *c* on *j* (the summation over *c* indicates all competitors of *j*); F_{ji} is the functional response of *i* preying on *j* (the summation over *i* indicates all predators of *j*); m_j is the "other mortality" rate of *j*, and H_j is the harvest rate of *j*. The intrinsic production/biomass ratio (r_j) is estimated as $r_j = f_{rj}a_{rj}w_j^{-0.25}$ where f_{rj} is a proportion, a_{rj} is an allometric coefficient which depends on metabolic type (endotherms, vertebrate ectotherms, invertebrates or phytoplankton), and w_j is the mean individual body mass of *j* (Yodzis and Innes, 1992).

A consumer equation describes the dynamic of those species which are feeding on species included in the model as

$$\frac{dB_j}{dt} = B_j\left\{-T_j + \sum_k e_{kj}F_{kj}\right\} - \sum_i B_iF_{ji} - m_jB_j - \mu_jB_j^{v_j} - H_j \equiv g_j \qquad (3)$$

where the mass-specific respiration rate of species *j* (T_j) is estimated as $T_j = a_{Tj}w_j^{-0.25}$ with a_{Tj} another allometric coefficient (Yodzis and Innes, 1992), e_{kj} is the assimilation efficiency of *j* eating prey *k*, F_{kj} is the functional response of *j* preying on *k* (the summation over *k* indicates all preys of *j*), and the term $\mu_jB_j^{v_j}$ corresponds to density-dependent mortality of *j*. All the other parameters were described in equation (2).

The functional response F_{kj} has a very strong influence on the behaviour of any trophodynamic model, but there is no hard evidence to determine its actual form. For this reason, we do not assume *a priori* any particular form for it; instead, we prefer to explore a range of plausible forms. The details of this exploration will vary with the nature of the particular model. The only general property is that its maximum asymptotic value J_j can be estimated as $J_j = f_{Jj}a_{Jj}w_j^{-0.25}$ where f_{Jj} is a proportion and a_{Jj} is another allometric coefficient (Yodzis and Innes, 1992).

A dynamic food web model can be local (the density-dependencies are linearized in the neighbourhood of an equilibrium) or global (the density-dependencies are fully described) (Yodzis, 2001). The relative appropriateness of these two modelling approaches depends upon the data available and the question being addressed.

LOCAL MODELS

Local models can handle complex food webs, and do not require time series data. They can be built using average biomasses, catches and diets (Yodzis, 1998). These models assume that the system is near equilibrium and that any departure from it is small enough to reasonably approximate the density dependencies with linear functions. Therefore, the dynamic of the system is governed by the Jacobian matrix

$$A_{ij} = \left[\frac{\partial g_i}{\partial B_j}\right]_e$$ where g_i are the right-hand sides of equations (2) and (3), and the subscript *e*

indicates that the derivatives are calculated at equilibrium (Yodzis, 1996, 1998). The Jacobian matrix determines the long term response to small press perturbations. For instance, the change in equilibrium biomass B_i^e of any species in response to a change in the harvest rate of species *j* is

$$\frac{\partial B_i^e}{\partial H_j} = \left(A^{-1}\right)_{ij} \tag{4}$$

which is the inverse of the Jacobian matrix at the original equilibrium before the perturbation.

Within this framework, Monte Carlo techniques can be used to explore model uncertainty and to determine how a given perturbation affects the final equilibrium of the system. In this way, probability distributions of the expected response of the system to the perturbation can be produced, allowing us to incorporate both our knowledge and our ignorance of the system into the analysis. Yodzis (1998) has addressed in this way the influence on the fisheries of a proposed cull of Cape fur seals in the Benguela ecosystem, using a food web with 29 species. He found that the total yield to all fisheries would more likely decrease than increase in response to a cull.

As well, Yodzis (1998) found that relatively little of the food web structure can be eliminated without increasing the probability of getting different answers than the full model. Further analysis showed that, although a modular approach is still possible, the modules of the system that should be used for "minimum-realistic" models were not always obvious from previous knowledge of the system (Yodzis, 2000).

GLOBAL MODELS

Global models can describe the dynamics of a system far from equilibrium and under large perturbations. This broader capability does not come for free. The data requirements are larger because time series of biomass and catches are required. These models also need to be fitted to the time series with all the practical problems associated with model fitting. In addition, time series for all the species in the food web are usually unavailable. This implies building comparatively simpler models and considering only those species with enough data. There is no *a priori* assurance that such "maximum-feasible" models will be capable of capturing the behaviour of the full system. An ideal modelling process might involve initial local models with high food web resolution to serve as test-benches for smaller, truly "minimum-realistic", global models.

Furthermore, global models also require precise definitions of certain components such as functional responses. Therefore, as in local models, any implementation of global models should also address the issue of model uncertainty.

One clear advantage of global models is that they do not rely on precise diet data. Unlike local models where diet matrices are used to parameterize the functional response, in global models all that is required, in principle, is presence/absence dietary information. The parameters of the functional responses are estimated by fitting the full dynamic model to the time series. Therefore, the fitted model can be used to predict consumption. If reliable quantitative diet data become available, they can be used to validate the model by comparing diet information with model predictions.

Currently, there is no primary publication fully describing the approach to global models sketched above. Therefore, we will give some additional details on the implementation of a simple global model and the path that we followed to explore model uncertainty.

A MODEL FOR SOME COMPONENTS OF THE PATAGONIA MARINE COMMUNITY, SOUTHWESTERN SOUTH ATLANTIC, ARGENTINA (based on Koen-Alonso and Yodzis manuscript)

The Patagonia food web has the anchovy, the squid and the hake as central components. They appear in the diet of many top predators, including marine mammals (Koen-Alonso *et al.*, 1998, 1999, 2000, 2001, 2002). The hake feeds on anchovy and squid, although zooplankton is also an important component of its diet (Angelescu and Preski, 1987; Prenski and Angelescu, 1993). Anchovy and squid feed mainly on zooplankton (Angelescu, 1982; Ivanovic and Brunetti, 1994). Among marine mammals, the southern sea lion is currently the most abundant species (Reyes *et al.*, 1999; Dans *et al.*, in press). However, its population was depleted by harvesting between 1930-1960 and it is still recovering (Crespo and Pedraza, 1991). From a fisheries perspective, hake and squid are also important fishery targets. The squid is considered fully exploited whilst the hake stock is virtually collapsed (Aubone *et al.*, 1999; Brunetti *et al.*, 1999).

We explored the joint dynamics of squid, anchovy, hake, and sea lion with a global model based on equations (2) and (3) (Figure 1). The impact of the functional response was evaluated by fitting the same structural model (Figure 1) with five different functional responses (Table 1). These models were fitted to the time series data by minimizing the negative log-likelihood and assuming lognormal multiplicative errors. The best models were selected using the corrected Akaike's information criterion (Burnham and Anderson, 2002) (Table 1).

Table 1. Functional responses considered in the Patagonia models. When applicable, these functional responses assume a single and prey-independent maximum asymptotic consumption rate. The corrected Akaike's information criteria (AIC_c) correspond to θ_{MLE}

Functional response	Equation	AIC_c
Multispecies Holling Type II with predator interference [(a)]	$F_{kj} = J_j \dfrac{a_{kj}B_k}{J_j\left(Q_j + B_j\right)^{q_j} + \sum_K a_{kj}B_k}$	2011.9
Multispecies generalized *laissez-faire* Holling [(b)]	$F_{kj} = J_j \dfrac{a_{kj}B_k^{b_j}}{J_j + \sum_K a_{kj}B_k^{b_j}}$	1965.7
Frequency-dependent predation [(c)]	$F_{kj} = J_j \dfrac{p_{kj}a_{kj}B_k^{1+b_j}}{J_j \sum_K p_{kj}B_k^{b_j} + \sum_K a_{kj}B_k^{1+b_j}}$	2073.1
Evans [(d)]	$F_{kj} = J_j \dfrac{a_{kj}B_k\left(1 + b_jB_k\right)}{J_j + \sum_K a_{kj}B_k\left(1 + b_jB_k\right)}$	1963.6
Ecosim [(d)]	$F_{kj} = \dfrac{a_{kj}v_{kj}B_i}{v'_{kj} + v_{kj} + a_{kj}B_j}$	2205.9

F_{kj}= functional response of predator *j* on prey *k*, B_k = biomass of prey *k*, B_j = biomass of predator *j*,

J_j= maximal ingestion rate of predator *j*. In the corresponding equations, a_{kj}, p_{kj}, v_{kj}, v'_{kj}, Q_j, q_j, and b_j are positive coefficients.

(a) This form is based on equation (10) in Yodzis (1994). It allows from a *laissez-faire* Holling type II ($q_j = 0$) to high predator interference (Q_j and $q_j \rightarrow \infty$) including the classical ratio-dependent formulation ($Q_j = 0$ and $q_j = 1$).

(b) This form allows both Type II ($b_j = 1$) and Type III ($b_j > 1$) functional responses.

(c) This form was derived by Yodzis (unpublished) and corresponds to a *laissez-faire* Type III shape which reduces to a Holling Type II if $b_j = 0$ or if only one prey species is available. In this functional response the $\sum_K p_{kj} = 1$.

(d) This form was derived by Evans (unpublished, cited in Evans and Garcon, 1997), and correspond to a *laissez-faire* Type III shape if $b_j > 0$. This form has both linear and non-linear effects in the capture rate (the two terms in the numerator).

(e) This form is the Ecosim functional response (Walter *et al.*, 1997; Walters and Kitchell, 2001)

In this way the Evans and generalized Holling models were selected for further analysis. Both models had *laissez-faire* Type III shaped functional responses, but the Evans functional response allows for linear and non-linear effects in the attack rate (*sensu* Yodzis, 1994) while the generalized Holling only has non-linear effects (see equations in Table 1). Disturbingly, the functional response that has been most widely used of late in marine food web models, the Ecosim functional response (Walters *et al.*, 1997; Walters and Kitchell, 2001), was the one that showed the worst performance (Table 1).

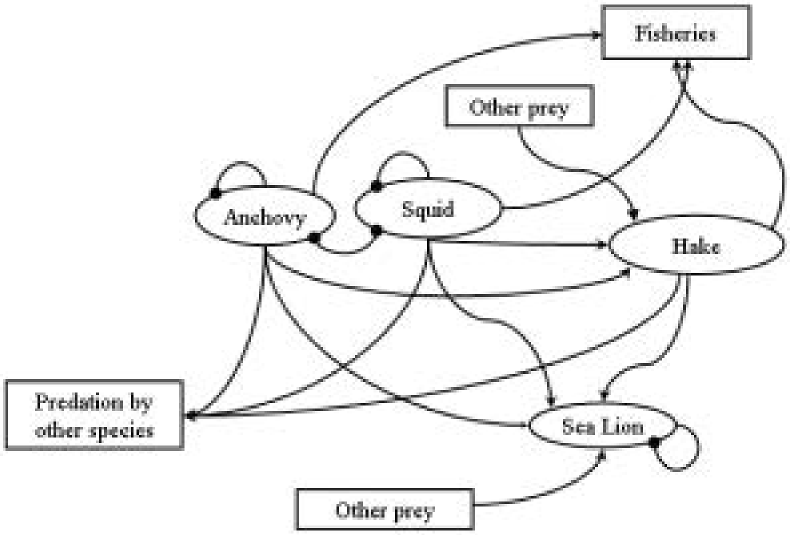

Fig. 1. Structure of the Patagonia model. The ovals represent dynamic equations (basal for squid and anchovy and consumer for hake and sea lion) and the boxes correspond to effects included as constant rates (predation by other species) or elements (other prey is modeled as an additional fixed food source in the functional responses). The observed annual catches were used as annually updated harvest rates H_j for fitting purposes. The negative self loop in the sea lion corresponds to density-dependent mortality, while the double negative link between anchovy and squid indicates Lotka-Volterra competition. The negative self loops on anchovy and squid correspond to the self limitation imposed by their carrying capacities.

We explored the behaviour of the selected models under exploitation using bifurcation and continuation analysis (Doedel, 1991a, 1991b, 1998). Our results indicated that despite their similarities in goodness-of-fit, the behaviour of the models can be substantially different in some exploitation scenarios. For this reason, we implemented the sampling-importance-resampling algorithm to explore how parameter uncertainty affects the conclusions (Gelman *et al.*, 1996). We considered uniform priors within the range $\theta_{\mathbf{MLE}} \pm 0.5\theta_{\mathbf{MLE}}$ where $\theta_{\mathbf{MLE}}$ is the vector of maximum likelihood estimators of the parameters. Using the approximated posterior distributions we selected four parameter sets with the lowest likelihoods within the 95th percentile region. These are the worst, but still presumably plausible, parameter sets. We performed the bifurcation analyses with them, trying to capture some of the extreme behaviours of these models under exploitation. The idea behind this approach is simple. Any conclusion that holds considering both $\theta_{\mathbf{MLE}}$ and the "extreme" sets for the selected models should be fairly robust to model uncertainty.

Regarding the impact of harvesting hake on sea lion, the most likely response was consistent between models and indicated that harvesting hake increases the equilibrium biomass of sea lion. This suggests that the hake fishery not only causes no harm, but actually boosts sea lion equilibrium biomass (Figure 2). However, when parameter uncertainty is considered, the range of plausible behaviours also includes the possibility that harvesting hake can drive sea lions to extinction (Figure 2). Therefore, the response of sea lions to a harvest of hake cannot be predicted in a robust manner. Of course, as in the local model, if a specific harvesting scenario is proposed, the approximated posterior distributions can be used to produce probability distributions for this response.

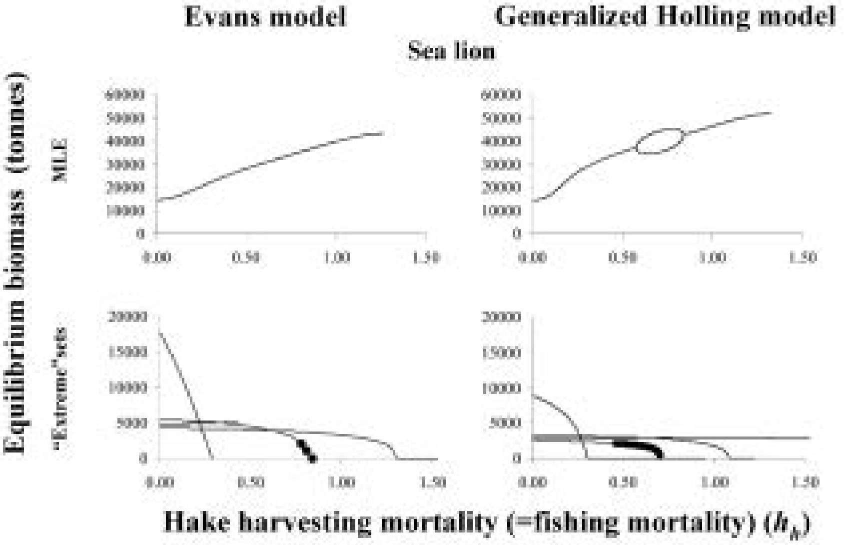

Fig. 2. Bifurcation diagrams of the equilibrium biomass of sea lion with the hake harvesting mortality as bifurcation parameter. In these analyses the harvest rate of hake (H_h) was represented as $H_h = h_h B_h$ where h_h is the hake harvesting mortality (=fishing mortality) and B_h is the biomass of hake. These analyses started with the system at equilibrium in absence of harvest; h_h was increased until hake extinction. The other species in the model remained un-harvested. MLE indicates the bifurcation diagrams using $\theta_{\mathbf{MLE}}$. The blob in the MLE diagram of the generalized Holling model indicates a region with oscillatory behaviour; the vertical dimension of the blob corresponds to the amplitude of the oscillations. All these attractors (point and periodic) are stable. The filled circles in the "extreme" sets diagrams correspond to stable periodic attractors, although in these cases the circles do not represent the amplitude of the oscillations.

On the other hand, the most likely response to a harvest of sea lions was an increase in hake, but also a decrease in squid equilibrium biomass (Figure 3). The inclusion of parameter uncertainty shows that driving sea lions to extinction may very well have no impact on hake (Figure 3).

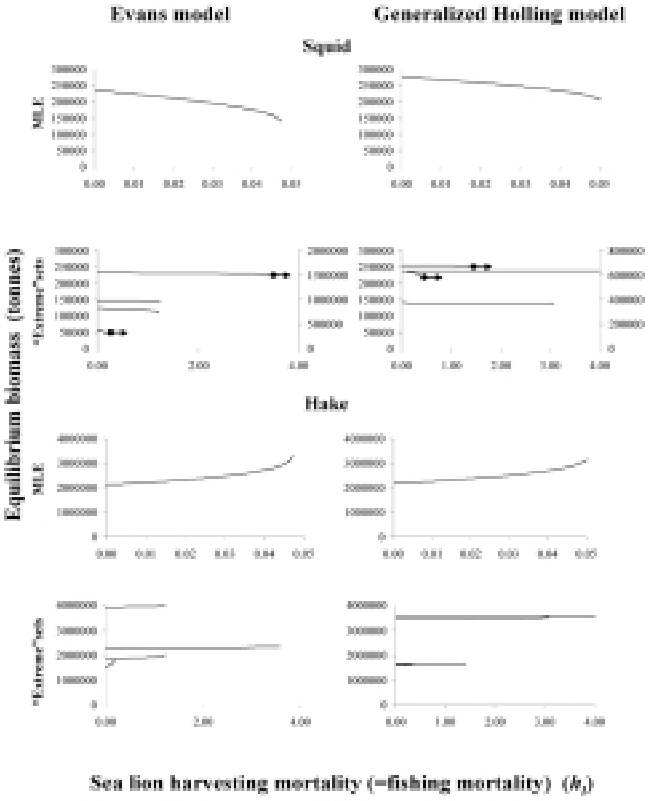

Fig. 3. Bifurcation diagrams of the equilibrium biomass of squid and hake with the sea lion harvesting mortality as bifurcation parameter. The harvest rate of sea lion (H_l) was represented as $H_l = h_l B_l$ where h_l is the sea lion harvesting mortality (=fishing mortality) and B_l is sea lion biomass. These analyses were performed in a similar way as described in Figure 3. The arrows indicate which bifurcation diagrams should be read in the right hand-side axes. All equilibria are stable.

Overall, these results indicate that model uncertainty cannot be dismissed. Results from a single model configuration and parameterization are likely to be misleading. However, the explicit consideration of model uncertainty allowed us to reach some general conclusions. For example, the effects of culling sea lions, if they are large enough to be non-trivial, will not be beneficial to all fisheries in the region. They will negatively affect squid as much as they positively affect hake. Also, and from a marine mammals conservation perspective, there is no strong evidence from these models that the effect of the hake fishery is surely detrimental for sea lions. On the contrary, the most likely effect appears to be beneficial, but still a precise definition of the harvesting scenario is required to calculate the full probability distribution.

Trophic levels of marine mammals and overlap in resource utilization between marine mammals and fisheries in the Mediterranean Sea

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INTRODUCTION

Most species of marine mammals are located near or at the top of marine food webs (Pauly *et al*., 1998b; Trites, 2001; Froese *et al*., in press) and may therefore be utilizing the same or similar food resources as those exploited by fisheries (Beddington *et al*., 1985; Trites *et al*., 1997; Northridge, 2002; Trites, 2003). The extent to which this may result in direct or indirect competition between these two groups of apex predators is difficult to assess due to the lack of data on total abundance and accessibility of the specific prey sources available to either group. However, determining the degree of trophic overlap between different marine mammal species and individual fisheries is a useful starting point to analyze the potential for food competition to occur. Moreover, quantifying the spatial overlap in resource use of fisheries and marine mammals would facilitate management decisions regarding conservation measures to protect endangered populations of marine mammals. Ultimately though, other factors such as temporal dimension of overlap as well prey sizes targeted and prey switching abilities of either group should also be considered.

In this report, we estimate the trophic position of twelve marine mammal species that occur in the Mediterranean. Trophic levels were calculated based on published diet information using an approach similar to Pauly *et al*. (1998b) and Trites (2001). We also estimated the degree of overlap between known marine mammal diet components and fisheries catches of different Mediterranean subareas using multivariate analyses.

MATERIAL AND METHODS

Estimation of trophic levels

The fractional trophic level (TROPH) of a species (i) was defined according to Pauly and Christensen (2000):

$$TROPH_i = 1 + \sum_{j=1}^{G} DC_{ij} * TROPH_j \ ,$$

where $TROPH_j$ is the fractional trophic level of prey (*j*), DC_{ij} is the fraction of *j* in the diet of *i* and G is the total number of prey species.

Dietary information of marine mammals from around the world has been extracted from published sources (i.e. primary literature, reports, conference publications) and compiled in a global marine mammal database that forms part of the "Sea Around Us Project" and will be made available online in the near future (~ 1 year) (www.seaaroundus.org; see also Pauly and MacLean, 2003). Information stored in the database includes sources, quantitative or qualitative diet descriptions and the level of confidence in the data based on the data collection method and sample size in addition to information about the specific area and time period during which the data were collected.

Out of the 21 marine mammal species whose presence has been documented in the Mediterranean and Black Seas (http://www.accobams.org/species/index.htm), only ten species occur regularly in these waters. Of these, only three are found in the Black Sea, of which the harbour porpoise, *Phocoena phocoena*, is almost exclusively restricted to this area. Quantitative or qualitative diet information specifically obtained from the Mediterranean Sea was available for twelve marine mammal species, including the ten most common species as well as two species for which there are only occasional records of occurrence in the Mediterranean, the killer whale, *Orcinus orca,* and the Northern bottlenose whale, *Hyperoodon ampullatus*. A total of 45 datasets were extracted, consisting of 35 qualitative and ten quantitative diet descriptions (a list of sources can be obtained from the first author). The majority of available diet information was based on stomach content analyses of stranded animals, supplemented by some direct feeding observations and/or analysis of fecal samples. Reported diet percentages were mostly based on wet weight measurements. Sample sizes were generally low (~ 1–2 animals/fecal samples/observations) except in a few cases of mass strandings of up to 16 bottlenose dolphins, *Tursiops truncatus,* or 28 striped dolphins, *Stenella coeruleoalba* (e.g. Blanco *et al*., 2001; Meotti and Podesta, 1996; Würtz and Marrale, 1993). TROPHs and standard errors (SE) were calculated for each dataset using the appropriate routines dealing with qualitative or quantitative datasets, respectively, in TrophLab (a standalone Microsoft Access routine: Pauly *et al*., 2000; downloadable from www.fishbase.org).

In both routines, estimation of consumer TROPHs relies on available information about prey species' TROPHs. Stergiou and Karpouzi (2002) served as the primary source for TROPHs of Mediterranean fish species, but these were supplemented by TROPH values extracted from FishBase (Froese and Pauly, 2003; www.fishbase.org) when necessary. TROPH values for various cephalopods and crustaceans were extracted from the SAUP database (http://saup.fisheries.ubc.ca/catchrate/map/trophic_levels.htm). Default TrophLab values were used for fish and cephalopod prey reported at taxonomic levels higher than genus as well as for all remaining prey taxa.

TROPHs of individual marine mammal species were calculated as the mean of TROPH values estimated for all available datasets for a particular species

Overlap in resource use between marine mammals and fisheries

Overlap in exploitation of food resources between marine mammals and fisheries was investigated by comparing species-specific marine mammal diet composition with catch compositions of different Mediterranean (and Black Sea) fisheries using multivariate analysis.

The catch composition (species or groups of species; henceforth called species) for each GFCM[1] subarea (i.e., Balearic, Gulf of Lions, Sardinia, Adriatic Sea, Ionian Sea, Aegean Sea, Levantine Sea, Marmara Sea, Black Sea) was extracted from the GFCM fisheries catches database (using Fishstat Plus ver. 2.30; both downloadable from www.fao.org) for the years 1970-2001. Average (1970-2001) catch per species was subsequently calculated. In this study only species contributing more than 0.5% of the mean total catches per GFCM subarea were considered. For marine mammals, a common prey list was constructed from all datasets and combined with the list of species targeted by the GFCM fisheries.

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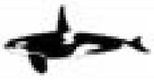
[1] General Fishery Council for the Mediterranean.

Multivariate analysis was applied on a presence-absence matrix, because the majority of marine mammal diet data was of qualitative nature. The matrix contained 21 consumer columns (nine GFCM subareas and twelve marine mammal species) and 152 prey rows (species consumed/caught by either or both a marine mammal or in GFCM fisheries/subarea). Subsequently, the triangular matrix of Bray and Curtis' (1957) similarities between all pairs of columns were computed and subjected to clustering (group-average linking) and multidimensional scaling (MDS) using PRIMER 5 (Car 1997).

RESULTS AND DISCUSSION

Mean estimated TROPHs of Mediterranean marine mammal species ranged from 3.23 for the fin whale *Balaenoptera physalus* to 4.71 and 5.5 for the bottlenose dolphin and the killer whale, respectively (Table 1). Not surprisingly, given the predominance of fish and squid-eating carnivorous odontocetes in our datasets, the majority of Mediterranean marine mammals appear to be top-level predators with TROPHs between 4.3 and 4.6 (Table 1, Figure 1a).

Table 1. Trophic level (mean, TROPH, range and standard error, SE, of mean) estimated from the different datasets (N) for each of the 12 marine mammal species in the Mediterranean Sea. The last column (SE) is the mean SE of the TrophLab estimates.

	SPECIES	COMMON NAME	TROPH	RANGE	SE	N	SE
	*Balaenoptera physalus*	Fin whale	3.23	3.20-3.30	0.03	4	0.41
	*Stenella coeruleoalba*	Striped dolphin	4.36	3.50-4.60	0.07	16	0.45
	*Monachus monachus*	Mediterranean monk seal	4.40	4.29-4.50	0.06	3	0.51
	*Ziphius cavirostris*	Cuvier's beaked whale	4.46	4.38-4.50	0.04	3	0.34
	*Grampus griseus*	Risso's dolphin	4.46	4.39-4.50	0.03	4	0.35
	*Globicephala melas*	Long-finned pilot whale	4.50	-	-	1	0.37
	*Hyperoodon ampullatus*	Northern bottlenose whale	4.50	-	-	1	0.37
	*Physeter macrocephalus*	Sperm whale	4.50	-	-	1	0.37
	*Delphinus delphis*	Short beaked common dolphin	4.53	4.50-4.60	0.03	4	0.42
	*Phocoena phocoena*	Harbour porpoise	4.62	4.43-4.80	0.19	2	0.39
	*Tursiops truncatus*	Bottlenose dolphin	4.71	4.43-4.92	0.10	5	0.53
	*Orcinus orca*	Killer whale	5.50	-	-	1	0.29

However, a large number of biases likely impact our estimates. These are mainly due to the difficulties associated with obtaining diet information for marine mammals directly, reliably and in sufficient sample sizes in the wild (e.g. Barros and Clarke, 2002). Diet composition estimates that are based on stomach content analysis tend to be biased towards cephalopods as hard parts of this taxonomic group are less affected by digestion than those of other prey species (Pierce, this volume). Such biases may be addressed by applying correction factors that allow to compensate for differential effects of digestion on different types of prey species (Tollit *et al.*, 1997, 2003). The assessment of the overall importance of a prey species in the diet of a marine mammal is very dependent on the type of measurement unit used (wet weight, volume, numbers, frequency of occurrence, etc.) when reporting proportions (see e.g. Pusineri *et al.*, this volume). Since the majority of datasets used in this analysis is based on a single type of measurement, namely wet weights, the impact of different measurement units may be negligible here. Nonetheless, this bias should be recognized and corrected for when attempting diet meta-analyses based on more heterogeneous datasets. 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 stomach contents may only represent the coastal components of diet spectrum (Pierce, this volume). Ideally, to compensate for these biases, diet compositions should be derived from samples that are representative of the population/species in question using a broad array of different techniques following standardized routines as well as including the appropriate digestion correction factors such as outlined by Pierce (this volume). Finally, there may be substantial small-scale regional and seasonal variation in the diet composition of marine mammal species (e.g. Bowen *et al.*, 1993; Haug *et al.*, 1995; Pierce, this volume; Pusineri *et al.*, this volume) which may also introduce additional biases. Restricting our analysis to diet records known to have been collected in Mediterranean substantially decreased the number of available data sets. Consequently, the information used in this analysis most likely only represents a subset of the total diet spectrum of each marine mammal species in the area and may be skewed towards a predominance of squid species in the diet. Analyses results should be interpreted keeping this in mind.

Estimated Mediterranean TROPHs for species were similar to average global TROPHs as computed by Pauly *et al.* (1998b), though Mediterranean TROPHs tended to be slightly higher for most species. These discrepancies may be due to a number of factors, the individual impact of which will be difficult to determine. Factors include differences in assumed prey TROPHs in the different analyses, the effect of using averaged TROPHs for diverse food groups in the global analysis or differences in actual diet compositions of individual species or a combination of all three of these. To determine the extent to which the observed discrepancies represent regional dietary specializations of species deviating from the "average" global diet composition would require further examination and a careful investigation of biases affecting both analyses.

Comparing of TROPHs estimated based on individual marine mammal datasets with those based on diet datasets of Mediterranean fish species (from Stergiou and Karpouzi, 2002) indicated that marine mammals tend to be positioned higher in the food web than most fish species in this region (Figure 1b). Froese *et al.* (in press) also compare the TROPHs of different marine organisms in the Mediterranean Sea. They report that the TROPHs of fish, cephalopods, seabirds and marine mammals (the latter based on the global analysis by Pauly *et al.* (1998b)) range between 2-4.5, 3.4-4.6, 3.3-4.5 and 3.4-4.5, respectively. Similarly to our findings, their estimated modal TROPHs of cephalopods (~3.7), seabirds (~4.0) and marine mammals (4.3) were all higher than that of Mediterranean fishes **(3.2)**

Multivariate analysis applied on the mean standardized catches of the nine GFCM subareas indicated three main groups of subareas (figures not shown): (a) Balearic, Gulf of Lions, Sardinia, Adriatic, Ionian and Aegean, (b) Levantine and (c) Marmara and Black Seas. The species composition of the three groups differed considerably from each other. The first was dominated by the small pelagic fish *Engraulis encrasicolus* and *Sardina pilchardus,* making up from 20 to ~50% of all catches, depending on subarea. In contrast, the Levantine mean catch was more evenly distributed among species, with *Sardinella* spp., Natantia, Mugilidae, Atherinidae, *Boops boops* and *Sphyraena* spp. making up ~33% of the total. Finally, the last group was characterised by the predominance of *E. encrasicolus* (67% and 27% for the Black and Marmara Seas, respectively) followed by *Sprattus sprattus* and *Trachurus mediterraneus*, for Black Sea, and *Scomber japonicus*, *T. mediterraneus*, *S. pilchardus*, *Pomatomus saltatrix* and *Micromesistius poutassou*, for the Marmara Sea.

The initial multivariate analysis applied to the presence-absence matrix of consumer/prey species was strongly affected by a single outlier, represented by the only mammal-eating consumer in the system, the killer whale. Some populations of killer whales are known to feed exclusively on other mammals in other areas of the world (Ford *et al.*, 1998). In the Mediterranean, however,

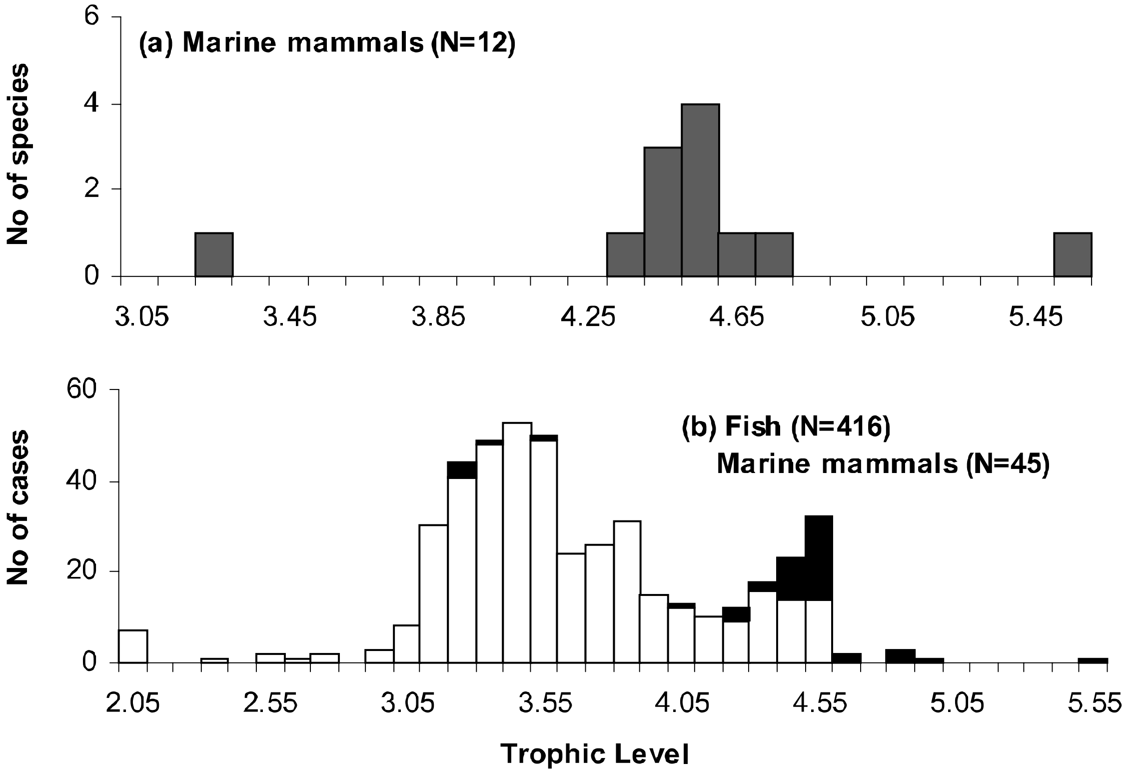
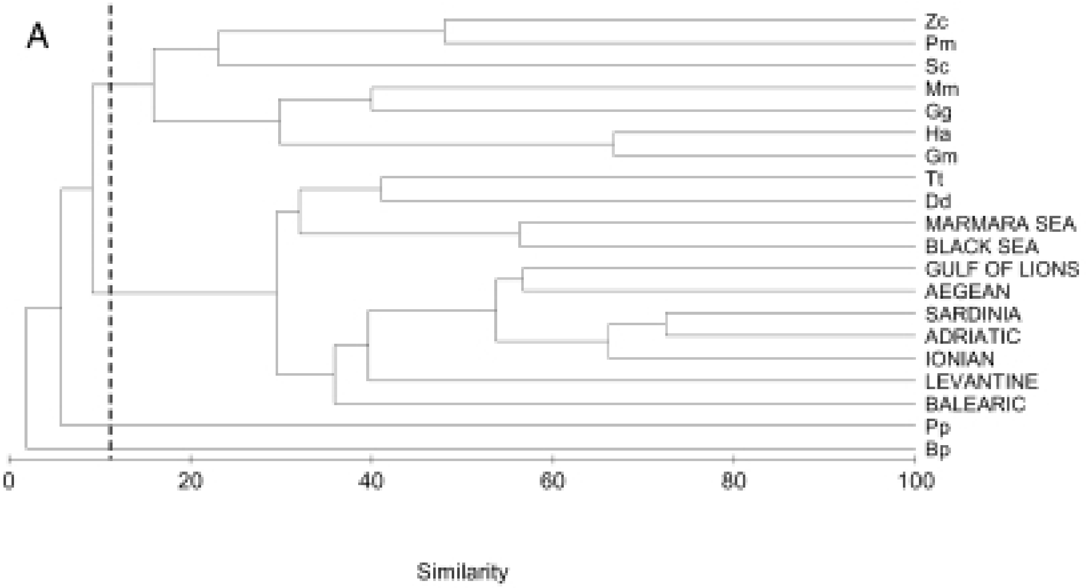


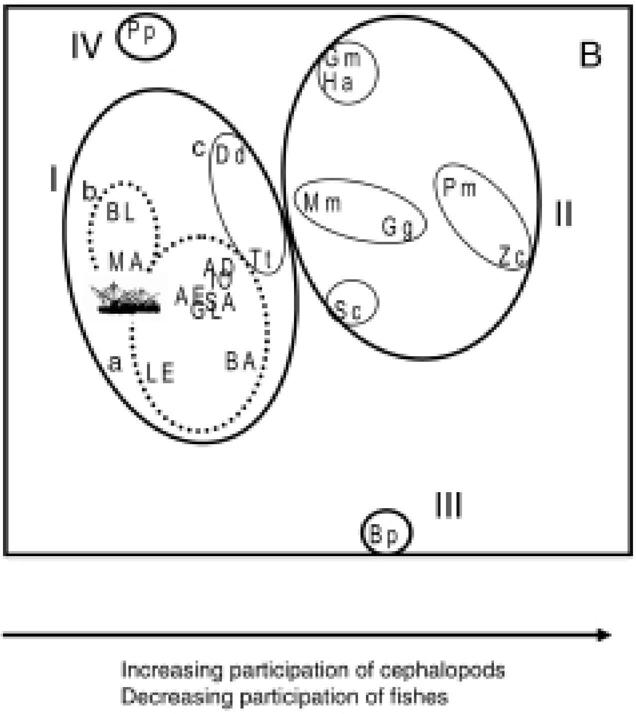
Fig. 1. Mediterranean Sea. Distribution (a) of the number of marine mammal species per trophic level class and (b) of 416 fish (white bars) and 45 marine mammal datasets (black bars) per trophic level class.

where killer whales only occur sporadically, a similarly specialized population has not been documented to our knowledge. Given our low sample size for this species (a single observation of a killer whale feeding on a Cuvier's beaked whale *Ziphius cavirostris*; Notarbartolo-di-Sciara, 1987) it is unlikely that we have captured the full dietary spectrum of the killer whale in the Mediterranean. To reduce this bias and since the 100% dissimilarity between the killer whale and all other consumers masked the formation of other groups, we re-ran multivariate analyses after excluding this species. The results of both, cluster and MDS analyses, fully agreed (Figure 2). In combination with a low MDS stress value of 0.09 this allowed an adequate representation of the MDS inter-column relationships in a two-dimensional graph (Clarke and Warwick, 1994).

Multivariate analyses revealed four main consumer groups in terms of prey/target species composition (Figure 2A, at a similarity level of 15%, Figure 2B): Group I consisted of all Mediterranean fisheries and two delphinid species, the short-beaked common dolphin, *Delphinus delphis,* and the bottlenose dolphin. Group II was made up exclusively of marine mammal species, namely the Cuvier's beaked whale, the sperm whale, *Physeter macrocephalus*, the Northern bottlenose whale, the long-finned pilot whale, *Globicephala melas,* the Risso's dolphin, *Grampus griseus,* the striped dolphin and the only Mediterranean pinniped, the Mediterranean monk seal, *Monachus monachus*. Finally, the fin whale and the harbour porpoise each formed a separate group by themselves (Groups III and IV, respectively: Figure 2A and B). At a higher similarity level (30%), Group I was further divided into three subgroups consisting of (a) all Mediterranean fisheries, (b) the Marmara and Black Sea subarea fisheries, and (c) the two marine mammals in this group.

Interestingly, the qualitative species composition of diets and catches within the groups identified through multivariate analyses differed greatly. For instance, though the short-beaked common dolphin and the bottlenose dolphin (Group Ic) were both characterized by a mixed cephalopod-





Group Ic

Tursiops truncatus (*Octopus vulgaris, Eledona moschata, Loligo vulgaris, Todarodes sagittatus, Engraulis encrasicholus, Sardina pilchardus,Phycis blennoides, Trachurus, Pagellus erythrinus, Ophidion, Cepola rubescens, Conger conger, Merluccius merluccius, Micromesistius poutassou, Lepidopus caudatus, Dentex dentex*)

Delphinus delphis (squids, Clupeidae, Mugilidae, *Trachurus*, Syngnathidae, *Engraulis encrasicolus*)

Group II

Ziphius cavirostris, Physeter macrocephalus, Hyperoodon ampullatus, Globicephala melas (various squids and/or flying squids)

Grampus griseus (various cephalopod taxa);

Stenella coeruleoalba (Euphausiacea, Sergestidae, Sepiida, Ommastrephidae, Teuthida, *Loligo vulgaris, Loligo forbesi, Illex coindetii, Todarodes sagittatus sagittatus, Engraulis encrasicolus, Boops boops, Belone, Merluccius merluccius*, Sparidae, *Micromesistius poutassou, Hygophum, Diaphus rafinesquii, Chauliodus sloani, Maurolicus muelleri, Ceratoscopelus maderensis, Lampanyctus crocodiles, Lobianchia gemellarii, Stomias boa boa*, Gonostomatidae)

Monachus monachus (lobsters, squids, octopuses, common cuttlefish, other cephalopods, fishes, sponges, plants)

Group III

Balaenoptera physalus (*Meganyctiphanes norvegica*, benthic shrimps)

Group IV

Phocoena phocoena (*Engraulis encrasicolus*, Gobiidae, *Odontesthes regia*)

Fig. 2. Results of (A) cluster and (B) multidimensional scaling analyses applied on the presence-absence matrix [(152 rows) X (20 columns)]: (152 species contributing in the marine mammal diet and in GFCM catches/subarea) X (9 GFCM subareas and 11 marine mammal species). Groups identified, at different similarity levels, are also shown (dotted ellipses in B indicate GFCM fishing subareas). The box at the right shows marine mammal species participating in the groups together with their main prey items in parentheses. The dotted line in (A) indicates the similarity level at which the four main groups are formed. GFCM subareas for (B): Balearic, BA; Gulf of Lions, GL; Sardinia, SA; Adriatic, AD; Ionian, IO; Aegean, AE; Levantine, LE; Marmara Sea, MA; Black Sea, BL. Marine mammals: *Delphinus delphis* , Dd; *Tursiops truncatus*, Tt; *Ziphius cavirostris*, Zc; *Physeter macrocephalus*, Pm; *Hyperoodon ampullatus*, Ha; *Globicephala melas*, Gm; *Stenella coeruleoalba*, Sc; *Grampus griseus*, Gg; *Monachus monachus*, Mm; *Balaenoptera physalus*, Bp; *Phocoena phocoena*, Pp.

fish diet, the available diet composition data for the bottlenose dolphin was much more diverse and showed a higher similarity to the species composition of the GFCM fisheries catches than that of the short-beaked common dolphin (Figure 2). In contrast, diet composition of species belonging to Group II ranged from foraging specialists almost exclusively feeding on different squid and/or flying squid taxa (Cuvier's beaked whale, sperm whale, Northern bottlenose whale, and long-finned pilot whale), to the more universal teuthophagous Risso's dolphin and finally to generalistic foragers such as the striped dolphin and the Mediterranean monk seal. Striped dolphins appeared to feed on a mixed diet made up of various crustaceans, cephalopods and fishes while monk seals seemed to have an even more diverse diet made up of lobsters, cephalopods, fishes, sponges and plants (Figure 2). Finally, the extreme ends of the spectrum were represented by the fin whale (Group III) with a diet exclusively composed of crustaceans and the exclusively ichthyophagous harbour porpoise (Group IV) (Figure 2). The majority of the taxa occurring in the diet of all of the above mentioned marine mammal species (see box in Figure 2) are either not targeted by the Mediterranean fisheries (i.e., Group Ia-b) or contribute at very low levels to the catches of the different GFCM subareas. This suggests that, with the exception of the bottlenose dolphin and - to a lesser extent - the short-beaked common dolphin, the overlap between marine mammal prey species and those targeted by fisheries in the Mediterranean and Black Seas is very low.

Investigations of the extent to which human consumers and marine mammals actually rely on the same or similar food resource represent just one of many important aspects to consider when assessing potential conflicts in terms of food competition. Therefore, studies such as ours help to illustrate that "crude estimates of overall food consumption by marine mammals […] recently bandied about in support of various 'culling programs', misinform rather than inform the public and indeed, completely miss the complex geography underlying interactions between fisheries and marine mammals" (Pauly and MacLean, 2003; pp. 61).

Despite the likely low trophic overlap between the two groups in the Mediterranean, some competition between marine mammals and fisheries may nonetheless occur in this area, as regional and temporal aggregations of marine mammals in highly productive areas are likely to coincide with high density fishing areas (Kaschner *et al*., 2001; Bjørge *et al*., 2002; Cañadas *et al*., 2003; García-Tiscar *et al*., 2003). Negative impacts of fisheries on Mediterranean marine mammal populations may result, especially if populations are already vulnerable or in decline, such as in the case of the Mediterranean monk seal. The consideration of spatial and temporal dimensions of overlap in the exploitation of marine food resources by marine mammals and fisheries is therefore crucial. Spatially explicit food consumption models of various temporal and spatial scales have been shown to be useful tools to investigate some of these aspects (Bjørge *et al*., 2002; Cañadas *et al*., 2003; García-Tiscar *et al*., 2003; Kaschner *et al*., 2001).

The identification of large scale patterns of potential hotspots of high trophic overlap in the Mediterranean may be useful in the context of establishing marine reserves, as discussed by Hooker (this volume) and Brownell (this volume). The application of a generic approach to map marine mammal distributions (Kaschner *et al*., 2003a, b) to produce spatially explicit food consumption estimates may be a helpful and cost-efficient starting point to identify such patterns. In this modeling framework, species-specific marine mammal distributions are generated by relating published information about habitat preferences with respect to some basic environmental parameters to locally averaged oceanographic conditions in a high resolution GIS raster. By linking the maps thus generated to available information about species abundance, mean body weights, feeding rates and diet composition, estimates of regional food consumption densities may be obtained as demonstrated by Kaschner *et al*. (2001) in a preliminary analysis of trophic overlap in the North Atlantic. Marine mammal food consumption densities may then be compared to corresponding disaggregated fisheries catches using modeling techniques like those developed by Watson and Pauly (2001). This very simplistic approach cannot, by any mean, fully capture the complexity of existing marine mammal-fisheries interactions and is affected by all the shortcomings of other modeling approaches as reviewed by Harwood and MacLaren (this volume) and by the IWC (2003). Nonetheless, the large-scale visualization of potential areas of conflict between fisheries and marine mammals, like those proposed here, may help focus future research efforts and aid in the identification of data demands and boundaries for more detailed small-scale models.

ACKNOWLEDGEMENTS

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Study of dietary overlap between small cetaceans and fisheries in the Bay of Biscay from stomach content analysis

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INTRODUCTION

The Bay of Biscay and the adjacent Atlantic Ocean are highly harvested by fisheries that exploit the same habitats as several top predator populations (small cetaceans and seabirds). Particularly abundant in the area, these two groups mainly comprise protected species. The challenge is therefore to manage habitat and resources so as to ensure the conservation of these species in exploited ecosystems. More generally, this objective is part of the broader issue of managing fisheries in a manner that would preserve its biodiversity and the integrity of its functioning. Understanding the functioning of these pelagic ecosystems, and notably the relationships among the upper trophic levels, is central in this context. It is even more so when some of these relationships may lead to conflicts as they often do between marine mammals and fisheries. Indeed, many studies report that a significant number of cetaceans are caught incidentally by fisheries while marine mammals are reported to occasionally damage nets and to deplete fishery resources (see Smith, 1995). If operational interactions have already been documented in the region (Goujon, 1996), evidence for resource overlap between marine mammals and fisheries is not always obvious (Yodzis, 2001). In the Bay of Biscay, important fisheries target either small pelagic fish, which include the anchovy *Engraulis encrassicolus*, the sardine *Sardina pilchardus*, the horse-mackerel *Trachurus trachurus*, and mackerel *Scomber scombrus* are also prey of small cetaceans, or large predatory fish such as the albacore *Thunnus alalunga*, that seems to share prey with small cetaceans (Aloncle and Delaporte, 1975). In this study, we will assess the dietary overlap between fisheries and small cetaceans in the Bay of Biscay and adjacent Atlantic Ocean.

In this context, our study area should be divided into distinct neritic and oceanic regions (Figure 1). The neritic area is geographically constrained to the continental shelf from the seafloor to the surface. Four species of cetaceans are observed in this area: the common dolphin *Delphinus delphis*, the striped dolphin *Stenella coeruleoalba*, the bottlenose dolphin *Tursiops truncatus*, and the harbor porpoise *Phocoena phocoena*. Other top predators mainly consist the sea bass *Dicentrarchus labrax*, and the hake *Merluccius merluccius*. The trophic relationships between marine mammals and fisheries in the area mainly involve small cetaceans feeding on fishery targets. The oceanic area is defined as the pelagic waters between 40°-50°N and 10°-25°W. The main top predators in the area are: the striped and common dolphins, the swordfish *Xiphias gla-*

dius, the blue shark *Prionace glauca,* and immature albacore tunas, *Thunnus alalunga*, that spend the summer months in the oceanic Northeast Atlantic. The main trophic relationship between marine mammals and fisheries in the area involve dolphins feeding on preys of the main commercial species: the albacore tuna.

Our objectives will be to: 1) determine the diets of the small cetaceans in both neritic and oceanic areas, 2) determine the albacore diet in the oceanic area, 3) identify and quantify the dietary overlap between fisheries and small cetaceans in the neritic area and between dolphins and albacore in the oceanic area, 4) compare consumed biomasses between the major components of the neritic and the oceanic ecosystems.

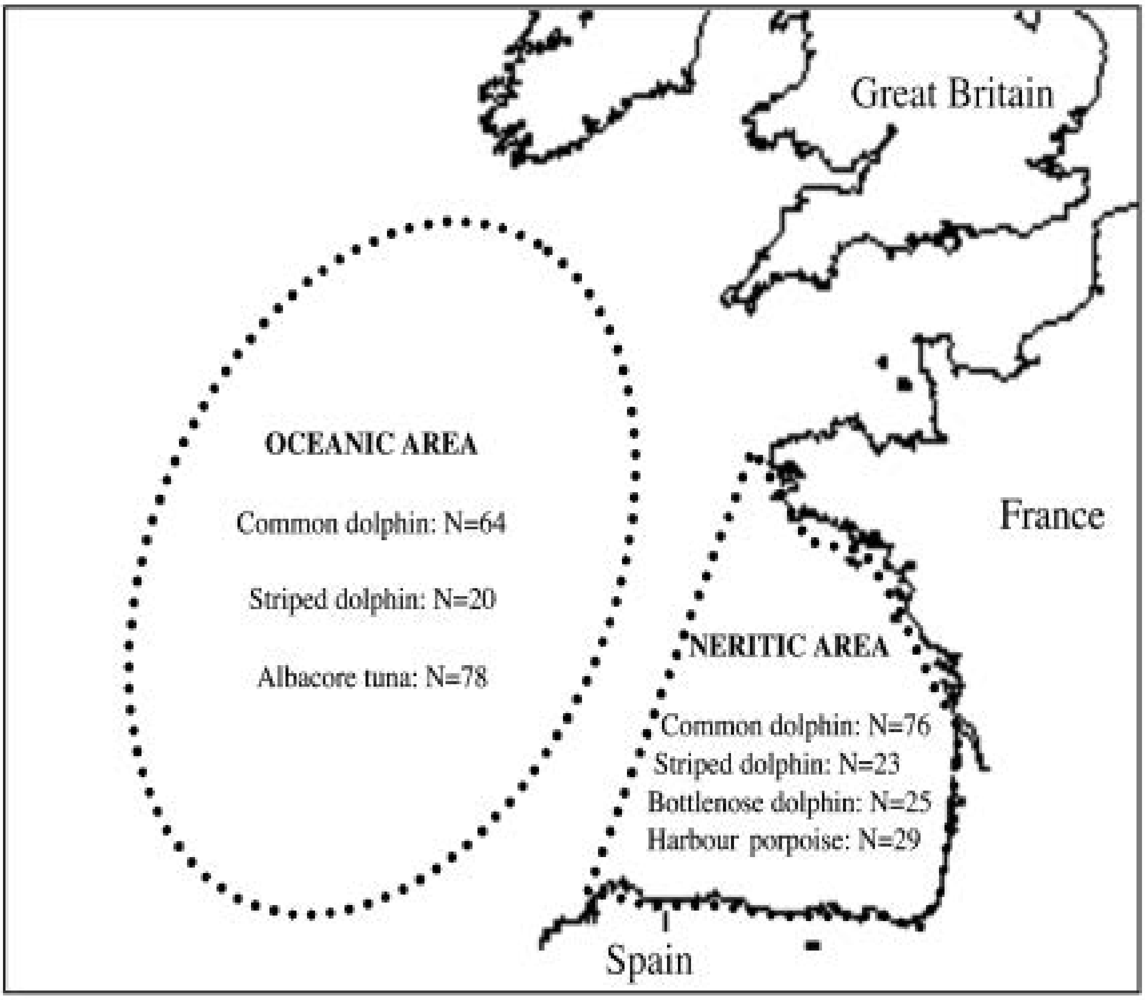

Fig. 1. Localisation of the two study areas and number of stomachs collected for each top predator species.

MATERIAL AND METHODS

Sampling

In 1992-93, the GERDAU programme was carried out by Ifremer to study the ecological impact of the albacore drift-net fishery on small cetaceans. Scientists onboard tuna drift-netters collected stomachs of top predators from the area 40°-50°N and 10°-25°W, between June and September (Figure 1). This set of samples constitutes the only source of data for the oceanic Bay of Biscay. Stomachs of stranded dolphins were collected by the CRMM (Centre de Recherche sur les Mamifères Marins) from the 1980's onwards along the coasts of the Bay, constituting a permanent record for the neritic Bay of Biscay. In both cases, samples were frozen for further analysis in the laboratory.

Diet analysis

Analytical procedures are standard and follow protocols published in recent works (*e.g.* Pierce and Boyle, 1991; Santos *and al*., 1998). Each stomach was weighed and its contents washed through a sieve of 0.2 mm mesh-size. Intact prey were identified, measured and weighed. Bones, otoliths, cephalopod beaks and exoskeletons of crustaceans were sorted and identified at the lowest taxonomic level. For identification, we used Härkönen (1986) and Clarke (1986) and a reference collection of specimens caught by both commercial and scientific trawlers off the French coast (CRMM data base). All prey remains were stored in 70% ethanol, except otoliths and bones stored dry. The number of fish species was determined by the half number of otoliths rounded up to the integer, whereas the number of cephalopod species was estimated by the maximum number of upper or lower beaks (Pierce and Boyle, 1991). For crustaceans, individuals were counted from the carapace or from the telson. To describe the diet, four standard indices were used: percentage occurrence, percentage by number, percentage by reconstructed mass and body size. The reconstruction of individual prey body length and body mass was based on the measurements of hard diagnostic parts. When more than 30 fish otoliths, jaw bones or cephalopod beaks were present in a stomach, a random sub-sample of 30 was measured. Relationships from the literature (Clarke, 1986; Härkönen, 1986; Reid, 1996; Whitehead *et al.,* 1986) or computed from our reference collection allowed body length and mass to be back-calculated.

Dietary Overlap Analysis

Three measures of dietary overlap were computed between the fisheries and small cetaceans in the neritic area and between dolphins and albacore in the oceanic area: the number of shared species, the Pianka (1973) niche overlap index and the compared approximate yearly consumed biomass.

The Pianka niche overlap index is a measure of the resource overlap between two species:

$$Ojk = \Sigma(Pij * Pik) / \sqrt{\Sigma Pij\_ * Pik\_}$$

where Pij and Pik are the proportions of the resource i (here proportion by mass of prey i) in the diet of species j and k. This index varies between 0, when there is no niche overlap, and 1, when the overlap is total.

The following equation was used to estimate the consumption of small cetaceans and albacore:

$$Q = P * T * M * F * N$$

where P_i is the proportion by weight of prey species i in the diet (see Tables 1 and 2). T is the number of days when the predator is in contact with prey i. T is assumed to be 365 days for the cetaceans (supposed to be resident in the area), whereas T is set at 120 days for the albacores known to migrate through the area in the summer only (May to September). M is the average estimated body mass of the predator and was set at 90 kg for the common dolphin, 100 kg for the striped dolphin, 250 kg for the bottlenose dolphin and 6,5 kg for the albacore. F is the estimated proportion of its body mass that a predator consumes daily. It was established at 0.04 for a marine mammal and 0.05 for the albacore. N is the estimated predator population size: 40,000 common dolphins, 1,000 bottlenose dolphins, 0 striped dolphin and porpoise in the neritic area, 74,000 striped dolphins, 62,000 common dolphins (Goujon, 1996) and 8 millions albacore in the oceanic area.

The catches by the fisheries were estimated from landings as reported in Ainsworth *et al*. (2001) for the year 1998.

Table 1. Overall importance of prey species identified from oceanic common dolphins (DD, N=64), striped dolphins (Sc, N=20) and albacore tunas (TA, N=78). Importance is expressed as % frequency of occurrence, % number and % mass.

Prey species	% Frequency			%Number			%Mass		
	DD	SC	TA	DD	SC	TA	DD	SC	TA
FISH									
Bathylagidae	1.6						0.1		
Bramidae	4.8						0.8		
Gadidae	4.8								
Gempylidae	6.3						0.2		
Myctophidae	90.3	62.5	2	81.1	20.2		44.6	9.2	
Nomeidae	17.5			0.3			1.8		
Paralepididae	35.5	25	55.1	1.1	7.3	4.8	1	20.4	6.4
Alepocephalidae		5			0.3			0.3	
Platytroctidae	1.6						0.3		
Scomberesocidae	30.2	12.5	48	0.8	0.1	2.1	3.3	0.1	37.2
Sternoptychidae	44.4	12.5	46	5.7	0.1	78.5	1		20.3
Stomidae				0.3	3.7		1.2	2.2	
Unidentified fish	16.1	12.5		0.4	1.16		0.1	0.5	
CEPHALOPODS				8.8					
Brachioteuthidae	71.4	100		3	20.3		2.2	6	
Cranchiidae	69.8	50	4	3.5	15.1		18.7	28	0.3
Gonatidae	63.5	100	20	0.9	6.3	2	12.2	23.2	31.4
Histioteuthidae	45.2	62.5		0.8	4		7	3.5	
Pholidoteuthidae	3.2	5			0.1		0.2	0.2	
Octopoteuthidae	12.7	5	2	0.1	0.2	0.4	0.4	0.5	2.4
Ommastrephidae	1.6	5			0.1		0.2	0.3	
Onychoteuthidae	53.2	87.5	12	0.5	1.6	0.2	3.9	0.9	0.7
Sepiolidae	1.6	12.5		0.1					
CRUSTACEANS									
Euphausiidae	12.7	12.5	4	0.3	0.6	7.3			1.2
Oplophoridae	9.7	25		0.2	1.6		0.2	0.3	
Pasiphaeidae	6.4	50		0.2	3.9		0.1	1.5	
Peneaeidae	11.1	12.5		0.1	0.8		0.1	0.2	
Sergestidae	30.7	37.5		0.7	12.7		0.5	3.8	
Hyperidae	4.8		18			5.1			0.1

RESULTS

Diet composition

Oceanic albacore 78 stomachs of albacore tuna were analyzed (Table 1). Four families of fish, four families of cephalopods and two families of crustaceans were identified. Fish dominated the diet, accounting for 85% by number and 64% by mass. The most prominent families were: the Sternoptychidae, the Scomberesoxidae, the Paralepididae and the Gonatidae

Oceanic striped dolphins Six families of fish, nine families of cephalopods and five families of crustacean were found from stomach samples of striped dolphins by-caught in the French albacore drift-net fishery in 1992-3 (N = 20; Table 1). Squids dominated in both number or reconstituted mass, with 48 % and 63 % respectively of the diet. The main families were the Cranchiidae, the Brachioteuthidae and the Gonatidae. Fish were the second prey type and represented 33% both by number and mass of the diet. The dominant species were a variety of mesopelagic fish that included several lanternfishes and the barracudinas. Crustaceans contributed the higher proportion among all species/habitats studied here with 20% by number and 6% by mass. The dominant species belonged to the mesopelagic shrimps Sergestidae and Pasiphaeidae.

Table 2. Overall importance of prey species identified from neritic common dolphins (DD, N=76), neritic striped dolphin(SC, N=20), neritic bottlenose dolphin(TT, N=25), neritic harbor porpoises (PP, N=29). Importance is expressed as % frequency of occurrence, % number and % mass.

Prey Species	%Frequency				%Number				%Mass			
	DD	TT	SC	PP	DD	TT	SC	PP	DD	TT	SC	PP
FISH												
Atherinidae	4.2	4.8	13.1	7.7	0.5	0.1	14.6	0.3	0.2		15.9	0.1
Clupeidae	81.3	28.6		30.8	11.8	15.4		2.3	40.3	4		21.3
Engraulidae	56.3	14.3	4.4	15.4	16.9	2.4	0.1	0.5	11.7	0.2	0.1	0.3
Gadidae	65.9	80.9	52.9	68.0	19.8	24.2	25.5	49.9	13.8	7.3	25.2	45.5
Merluccidae	19.7	52.4	8.7	11.5	0.6	20.2	1.3	0.3	2.2	40.8	1.8	1.4
Carangidae	70.4	57.1		26.9	15.5	15.6		5.2	18.3	13.2		27.6
Scombridae	23.9	9.5		3.8	0.6	0.9		0.1	6.2	2.3		0.9
Ammodytidae	8.5	9.5			0.7	2.6			0.7	0.1		
Argentinidae	11.3	4.8			0.1	0.2			0.1			
Gobiidae	59.2	9.5	17.4	23.1	24.8	0.3	48.2	21.5	1		3.6	1.1
Soleidae	4.2	4.8			0.1	0.2			0.1	0.3		
Scophtalmidae	5.6	14.3			0.1	0.3				0.2		
Belonidae	1.4								0.1			
Labridae	2.8											
Cepolidae		4.8				0.2				0.1		
Mugilidae		19				4.5				12.1		
Sciaenidae		4.8				0.1				0.1		
Serranidae		9.5				4.2				5.5		
Sparidae		23.8				2.8				4.6		
Alepocephalidae			4.3				0.1					
Myctophidae			8.7				1.7				0.4	
Sternoptychidae			4.4	3.8			0.5	0.2				
Unidentified fish	2.8	9.5	26.1	23.1		0.4	1.3	4.1				
CEPHALOPODS												
Ommastephidae	4.2		8.7	3.8	0.1		0.5	0.1			22.1	0.2
Histioteuthidae			4.4				0.1				0.1	
Gonatidae			4.4				1.3				24.2	
Loliginidae	43.9	42.8	8.7	32.0	2.1	3.6	1.1	0.8	3.5	9.3	5.7	0.6
Brachioteuthidae			4.4				0.2				0.1	
Sepiidae	1.4	4.8	8.7			0.1	0.2				0.5	
Sepiolidae	46.5		8.7	23.1	6.3		2.6	1.7	1.3		0.3	0.2
Octopotidae				3.8				0.1				0.7
Unidentified cephalopods	1.4		8.7	7.6			0.2	0.2				
CRUSTACEANS												
Oplophoridae			4.4				0.1					
Pasiphaeidae		4.8				0.2						
Crangonidae	1.4	4.8	4.4			1.5	0.1					
Unidentified shrimps		14.3	13.1			0.4	0.3					
Euphausiacea				11.5				12.7				0.2

Bay of Biscay neritic striped dolphin Eight fish families, seven cephalopod families and two crustacean families were found in the stomachs of neritic striped dolphins collected along the coasts of the Bay of Biscay (N=23; Table 2) with both neritic and oceanic species. Fish were the most important taxa by number making up 94% by number and 47% by reconstituted mass. The Atherinidae and the Gadidae were the main families eaten. Small numbers of oceanic species were found: lanterfish, Ommastrephidae and Gonatidae. These two latter groups made a significant part of the diet by reconstituted mass. The score reached by gobies (48% by number) was not relevant because 90% of them came from only one stomach. Cephalopods represented 6% by number and 53% by mass and also included neritic and oceanic species as well.

Oceanic common dolphin Eleven fish families, nine cephalopod families and six crustacean families were identified from the stomach of oceanic common dolphins, by-caught in the French albacore drift-net fishery in 1992-3 (N = 64; Table 1). The prey species were epi- and mesopelagic taxa, known from the surface to a few hundred meters. Fish represented the main part of the diet with 90% by number and 54% by mass and were characterised by an overwhelming dominance of lanterfish. Cephalopods formed a regular part of the diet accounting for 9% in the numbers and 45% of the reconstituted mass, the main families being the Cranchiidae and the Gonatidae.

Bay of Biscay neritic common dolphin Fourteen fish families, four cephalopods families and one crustacean family were identified from the stomach of neritic common dolphins, sampled along the Atlantic coast of France (N = 76; Table 2). The preys were mostly pelagic and epi-benthic species. Fish represented the main part of the diet with 92% of the total by number and 95% by mass, with a dominance of gadids and small pelagic species (clupeids, engraulids, carangids and scombrids); gobies were abundant but, due to their small body size, negligible in mass. Cephalopods represented 9 % by number and 5% by reconstituted mass, the main prey being loliginids and sepiolids.

Bay of Biscay neritic bottlenose dolphin Seventeen fish families, two cephalopod families and two crustacean families were identified from the stomach samples of bottlenose dolphins stranded along the French coast (N = 25; Table 2). Fish represented as much as 94% by number and 91% by mass of the diet, with large-sized Merluccidae (41% by mass), Carangidae (13%) and Mugilidae (12%) being the most important prey taxa. Cephalopods represented 4% by number and 9% by mass and were almost entirely composed of Loliginidae. Crustaceans were a minor component of the food with only 2% by number and negligible amounts by mass.

Bay of Biscay and Western Channel neritic harbour porpoise Nine fish families, three cephalopod families and one crustacean family were found from the stomach of harbour porpoises stranded along the French coast of the Bay of Biscay and western Channel (N = 29, Table 2). Fish represented 84% of the total by number and 98% by mass, shared almost equally between three dominant prey families: the clupeids, gadids and carangids. Cephalopods represented 3% by number and 2% by mass. Crustaceans were found in three samples and represented 13% by number but only trace amounts by mass because they were made of the small-sized euphausiid *Meganyctyphanes norvegica*.

Dietary overlap

Dietary overlap between fisheries and small cetaceans in the neritic area The cetaceans and the fisheries shared from 10 to 19 preys (Table 3). This overlap is asymmetric: the shared preys make most of the cetaceans diet diversity (38 to 63 %) but only a minor part of the fisheries diversity (11 to 21 %). The Pianka Index was high between the common dolphin and the fisheries (0.72), reduced between the striped dolphin and the fisheries (0.03), and intermediate between the two other cetaceans species and the fisheries (0.32-0.53). The fisheries caught 66% of the total consumed biomass in the neritic area, and this varied from 36% to 75% of target species consid-

Table 3. Dietary overlap between small cetaceans (DD: Common dolphin, SC: striped dolphin, TT: bottlenose dolphin, PP: harbour porpoise) and fisheries (F) in the neritic area, and between dolphins (DD, SC) and the main commercial species (TA: albacore tuna) in the oceanic area.

Index	Neritic area				Oceanic area	
	DD-F	SC-F	TT-F	PP-F	DD-TA	SC-TA
Nb shared species	17	10	19	10	9	8
% nb shared species / total cetacean diet diversity	56.6	38.5	63.3	52.6	19.6	26.7
% nb shared species / total fishery (or tuna) diet diversity	19.3	11.4	21.6	11.4	75.0	66.7
Pianka's niche overlap index	0.72	0.03	0.32	0.53	0.23	0.36

ered (Figure 2). The common dolphin consumption was of the same order of magnitude: this species consumed 32% of the total prey biomass consumed in the area and this proportion varied from 18% to 63% according to prey species. Comparatively, the bottlenose dolphin consumption was low: it consumed 2% of the total harvested biomass but as much as 22% of consumed hake.

Diet overlap between dolphins and albacore tuna in the oceanic area The tuna shared eight preys with the common dolphin and nine with the striped dolphin (Table 3). This overlap is asymmetric, as the shared species made most of the tuna diet diversity (46% to 75) but only a minor part of the dolphins diversity (19 to 41%). The Pianka index was intermediate between the tuna and the two dolphin species (0.36-0.23). Sixty-two percent of the total prey consumed biomass were harvested by the tuna, 21% by the striped dolphin and 16% by the common dolphin (Figure 3). The two main albacore preys: the Sternoptychidae and the Scomberesocidae are seldom consumed by the dolphins (0-2%). On the contrary, the consumption of cephalopods and Paralepididae by the dolphins and by tuna are of same order of magnitude.

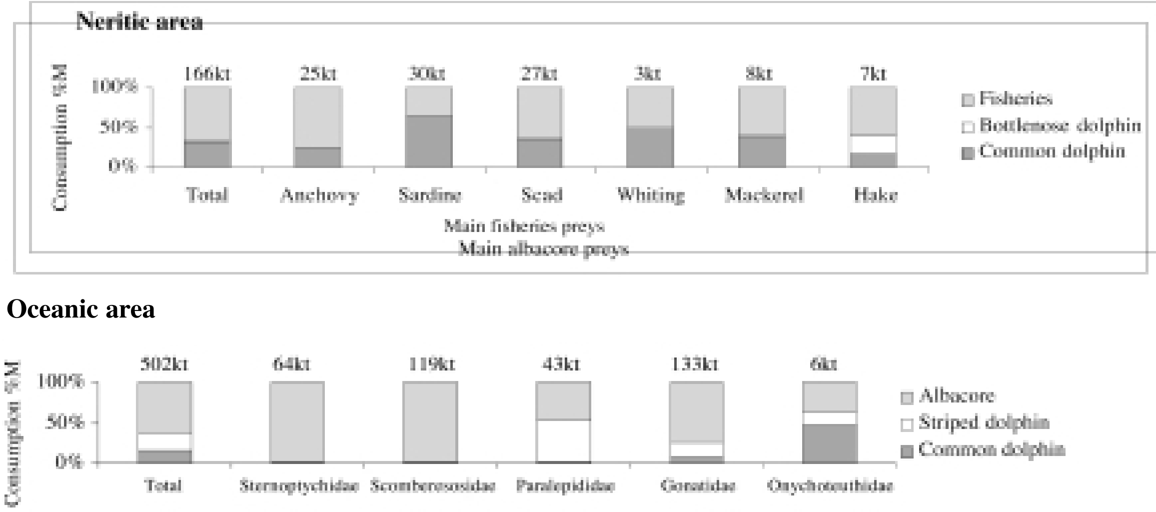

Fig. 2. Comparison of consumed biomass between fisheries and the two main species of small cetaceans in the neritic area, and between the main commercial species and the main small cetaceans species in the oceanic area.

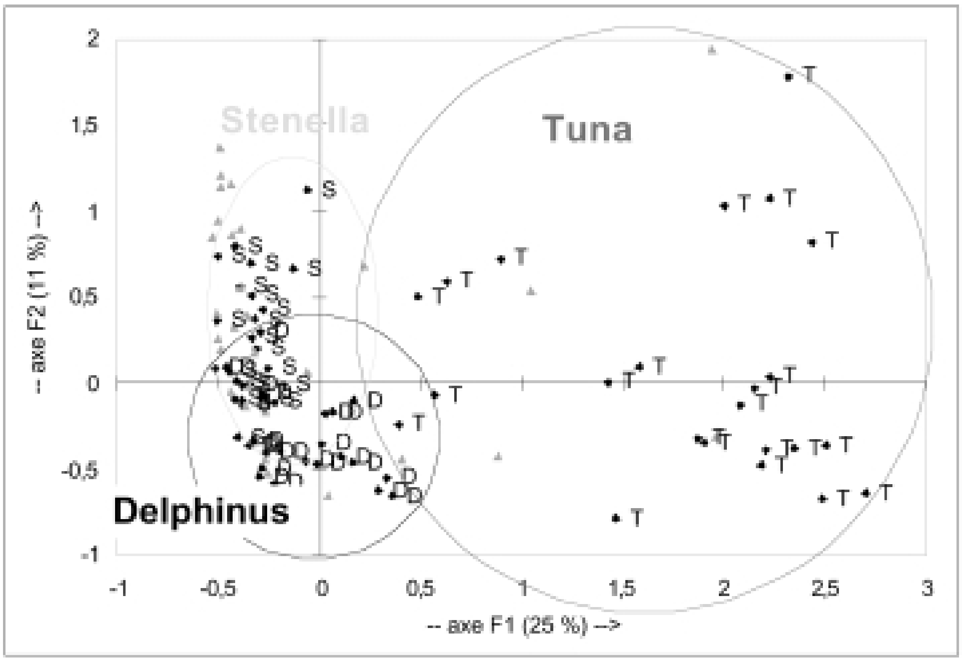

Fig. 3. Factorial analysis of oceanic species diet composition by number.

DISCUSSION

Diet composition

Neritic area The common dolphin feeds on truly pelagic fish species of the continental shelf, with mainly clupeids and anchovy. This is consistent with many other studies that showed that clupeids are one of common dolphin main preys (Gess, 1984; Young and Cockroft, 1994; Sekiguchi *and al*., 1992). The bottlenose dolphin is not a genuine pelagic predator as its diet is dominated by large sized epi-benthic species such as hakes, and sea breams. The diet of the porpoise combined true pelagic species with benthic coastal ones, such as the sandeels. Some oceanic species were also found, as in Bjørge *et al*. (1991). As this species is essentially observed in the neritic area, it is supposed that the oceanic preys have been caught during occasional foraging bouts on the slope. Striped dolphin's diet includes mostly small epi-benthic species, notably the atherine and some gadids. Some oceanic species were also found in several stomach contents; they were not significant by number, but two species of cephalopods made a large part of the diet by weight. A mixed diet has been observed in other studies: Gess (1984), Würtz and Marrale (1993). As this species is seldom observed on the continental shelf it is hypothesised that the striped dolphin population is oceanic and performs only scarce incursion in the neritic area.

Oceanic area Mesopelagic fish, especially myctophids, appear to be the main prey of common dolphins, while striped dolphins feed on a more balanced share of cephalopods and fish, and include a substantial part of crustaceans. A similar striped dolphin diet was recorded off the Japanese coast by Miyazaki *et al*. (1973), but such a strictly oceanic diet is rarely documented for common dolphins. The albacore displays the lower dietary diversity and its diet is mostly concentrated on epi-pelagic species such as sauries and macro-planctonic crustaceans. Mesopelagic species only include the barracudinas and the Sternoptichidae. The dietary niche of the albacore characteristically excludes the lanternfish. A study conducted, over the years 1968-1971, in the same area reported a similar diet (Aloncle and Delaporte, 1975).

Diet overlap

Neritic area. The diet of the common dolphins, mainly constituted of small pelagic fish species, overlaps significantly with fishery landings. Furthermore, because of its large population, its consumption is of the same order of magnitude than fisheries. The bottlenose dolphin shows an intermediate dietary overlap with fisheries and, because of its lower population, its overall consumption is negligible compared to that of fisheries and common dolphins. However, it is not negligible when one considers only the hake. The porpoise diet significantly overlaps with fishery landings, but because of its reduced population in the area, its predatory pressure is negligible. As the striped dolphin consumption by weight is mainly made of atherine and oceanic preys, it shows a very low overlap with fisheries, and because of its reduced population, its consumed biomass is negligible in the area. Hence, there is a significant overlap between fisheries and small cetaceans in the neritic area, but only the common dolphin shows a quantitative impact similar within an order of magnitude to that of fisheries on their shared resources.

Oceanic area The albacore tuna diet largely relies on dolphins' preys, but the reverse is not true as dietary diversity is much higher in both dolphins than it is in the albacore. As regards the consumed biomass, it is of the same order of magnitude for the dolphins and the tuna. Hence, the two dolphin species have an impact that is similar to that of tuna on their shared dietary resources.

CONCLUSION

We found a high dietary overlap and biomass consumption within the same order of magnitude between common dolphin and the fisheries in the neritic area, and between both common and striped dolphins and the main commercial species (albacore tuna) in the oceanic area. Similar results have been found in other parts of the world, where marine mammals have been shown to either have a diet that overlaps with fisheries resources (Scott and al., 1983; Trites and al., 1997), or a biomass consumption similar to landings (Bax, 1991). However, this alone does not provide evidence of trophic competition between marine mammals and fisheries. For competition to occur, resources should be limited, and we have no evidence of that in the Bay of Biscay and the adjacent Atlantic Ocean.

Assessing trophic interactions of some dolphins in the Balearic subbasin, Western Mediterranean Sea

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From recent published studies on the diet of some dolphins from the western: we know some aspects of the diet of *Stenella coeruleoalba* (Blanco *et al.*, 1995; Meotti and Podestá, 1997; Pulcini *et al.*, 1992; Würtz and Marrale, 1993), *Tursiops truncatus* (Blanco *et al.*, 2001; Orsi Relini *et al.*, 1994a), *Ziphius cavirostris* (Blanco and Raga, 2000; Podestá and Meotti, 1991; Würtz *et al.*, 1993), *Grampus griseus* (Bello, 1992; Carlini *et al.*, 1992b; Podestá and Meotti, 1991; Würtz *et al.*, 1993), *Globicephala melas* (Orsi Relini and Garibaldi, 1992b) and *Delphinus delphis* (Orsi Relini and Relini, 1993) coming from the western basin of the Mediterranean Sea. However, some ecological aspects of dolphin populations remain unknown; the preferential feeding area, the trophic interactions among dolphins and the trophic interactions between cetacean and fish or cephalopod populations are essential points in order to establish trophic interactions between cetacean population an fisheries; this study focuses on the trophic interactions among dolphins as a first step to understand it; the degree of similarity in the diet between two or more species will condition the level of interactions between these predators; only some attempts have been made to this aim in odontocetes from the Pacific and Atlantic areas (Dolar *et al.*, 2003; MacLeod *et al.*, 2003).

Among the questions arising this paper shall focus on the following: is there an overlapped diet between dolphin species? How can this be evaluated? The data to answer the first question should be selected to avoid misinterpretation; the diet of dolphins must be constant in order to compare data coming from different periods. Similarly we could ask about the validity of data coming from different geographical areas of western Mediterranean.

To answer these questions we have selected the striped dolphin. The diet of this species has been published from some areas of the western Mediterranean: south-central Tyrrhenian Sea (Pulcini *et al.*, 1992), Ligurian Sea (Würtz and Marrale, 1993), Balearic subbasin (Blanco *et al.*, 1995) and western Ligurian Sea (Meotti and Podestá, 1997). The number of both sampled dolphins and period of strandings in each study are shown in Table 1; contribution of cephalopods, fishes and crustaceans to diet are also shown. If we reject data from the Balearic subbasin, for which only cephalopod prey are known, the similarity of sample data may be assumed; despite the fact that, there are obvious differences in general composition of feeding habits of striped dolphin according the geographical distribution; dolphins coming from the Tyrrhenian Sea prey on cephalopods preferentially; on the contrary, those coming from Ligurian prey specially on fish and those from the west Ligurian have a mixed cephalopod and fish diet. In the same way, differences in the contribution of the most quantitative important families of both fishes and cephalopods may be found

(Table 2). The fish component of the diet of dolphins in the western Ligurian focuses on myctophids while those of the Ligurian on gonostomiatids and gadids preferentially; only sparids made up the scarce fish component in the diet of dolphins from the Tyrrhenian. Variability in the composition of cephalopod component of the diet according to the geographical area can also be seen when the most important families are considered; Ommastrephidae, Histioteuthidae and Onychoteuthidae families which are common prey in the four studied areas are quantitative the most important families in the Ligurian and Tyrrhenian Seas; by contrast, both Brachioteuthidae and Enoploteuthidae which are important components of the diet in the Balearic subbasin are not found in Tyrrhenian nor in Ligurian diets; the most diverse contribution of cephalopods to the diet of this dolphin in the Balearic subbasin agrees with the highest diversity of cephalopod population in the western Mediterranean (Salman *et al.*, 1998). Differences in fish prey are more obvious than in cephalopod prey reflecting supposedly the richnest fish fauna in the Mediterranean Sea.

According to these results we may assume a diverse diet of this dolphin according to the geographical area due possibly to different ecological factors. The presence of subbasins (see definition in Millot, this volume) could clarify the zonation in the Mediterranean Sea. Therefore, it is advisable to specify the exact area of sample origin in ecological studies to preclude misinterpretation of data.

Table 1. Sample data of studies on the diet of striped dolphin in western Mediterranean; numerical percentage contribution of fish, cephalopods and crustaceans.

	N	period	cephalopod	fish	crustacea
Tyrrhenian	16	1986-91	96.7	2.0	1,1
Ligurian	23	1983-91	7.0	91.0	2.0
west Ligurian	24	1987-91	39.4	57.4	3.2
Balearic subbasin	25	1990	-	-	-

N: dolphin number

Table 2. Contribution (numerical percentage)of the most important cephalopod and fish families in the diet of *Z. cavirostris, S. coeruleoalba* and *T. truncatus* in the Balearic subbasin.

	Tyrrhenian	Ligurian	W Ligurian	Balearic subb
fish				
Myctophidae		15.5	57.4	-
Gonostomiatidae	23.8	7.6	-	
Gadidae		31.2	0.9	-
Sparidae	100,0	2.9	4.6	-
cephalopods				
Brachioteuthidae				21.9
Enoploteutidae			1.7	29.3
Onychoteuthidae	8.5	19.3	28.3	25.7
Histioteuthidae	55.5	18.0	23.8	1.7
Ommastrephidae	12.2	47.0	10.4	10.2

The variation in composition of the diet of striped dolphin according to different areas forces to focus on a concrete area where studies on trophic interactions among dolphin species are concerned. We have selected the Balearic subbasin of western Mediterranean where the diet of three dolphin species are known; a teuthophagous species in the Mediterranean Sea, Cuvier's beaked whale (Blanco *et al.*, 2000; MacLeod *et al.*, 2003) and two mixing cephalopod and fish diet, bottlenose (Blanco *et al.*, 2001) and striped dolphins (Blanco *et al.*, 1995). Since the contribution of fish to the diet in the last dolphin species is unknown, the study focuses on trophic interactions of cephalopod prey among these dolphin species. The comparison of the diets is represented in

Table 3 which shows the number of both exclusive and overlapped cephalopod species and their numerical contribution to the diet for each dolphin species. When a mixed cephalopod and fish diet occurs as in both striped and bottlenose dolphins, the contribution to the complete diet has been estimated. The highest diet component of the three dolphins belongs to exclusive prey which are not represented in the diet of the other dolphins; only *Todarodes sagittatus* is a common prey in the diet of the three dolphins; in addition to *T. sagittatus* there are five cephalopod species which overlap in the diet of Cuvier's beaked whale and striped dolphin and only two species, *Todaropsis eblanae* and *Loligo* sp. between the latter and the bottlenose dolphin; no interaction excluded *T. sagittatus* occurs between *T. truncatus* and *Z. cavirostris.* The contribution of these prey to the complete diet is preferentially low when a mixed diet occurs.

Table 3. Species number (N) of overlapped prey (ov) and their contribution to the diet of Cuvier's beaked whale (Z)and both striped (S) and bottlenose dolphins (T). Numerical percentage of overlapped prey respect to cephalopod fraction and total diet (within parentheses) in the Balearic subbasin.

	own prey	N	ov Z-S-T	ov Z-S	ov S-T	ov Z-T
N			1	5	2	0
Z. cavirostris	75.5	3	5.0	19.5	-	
S. coeruleoalba	73.6 (29.0)	9	5.3 (3.0)	21.0 (8.2)	5.3 (2.1)	-
T. truncatus	60.0 (1.9)	4	16.0 (0.5)	-	20.0 (0.6)	

N: species number; ov: overlap, Z: *Ziphius cavirostris*, S: *Stenella coeruleoalba*, T: *Tursiops truncatus*

The degree of trophic interactions previously quantified decreases when sizes of overlapped prey are considered; the individual sizes (lower rostral beak length (LRL)) of *T. sagittatus,* the single common species prey of the three dolphins are represented in Figure 1; differences in the size of prey eaten by dolphins are shown, being higher in Cuvier's beaked whale in which this prey is a more important component of the diet; the biggest size of individuals preyed by this dolphin may be associated with ontogenic migration of this cephalopod species (Guerra, 1992). *Histioteuthis bonnellii*, *Chiroteuthis veranii*, *Ancistrocheirus lesueurii* and *Ancistroteuthis lichtensteinii* contributed to the diet of *S. coeruleoalba* and *Z. cavirostris*; the sizes of these species are represented in Figure 2, which shows that the last dolphin preyed also on much larger individuals than the striped dolphin; so, the degree of ineractions between both dolphins, Cuvier's beaked whale and striped dolphin, decreases when the size of the prey are considered. Size differences in prey occur in other odontocetes (Dolar *et al.*, 2003; MacLeod *et al.*, 2003) and would limit direct interactions among dolphins. The scarcity of individuals of overlapped species in both striped and bottlenose dolphins diet precludes a comparative analysis of size prey; whatever the size may be, the contribution of these species to the complete diet is very low.

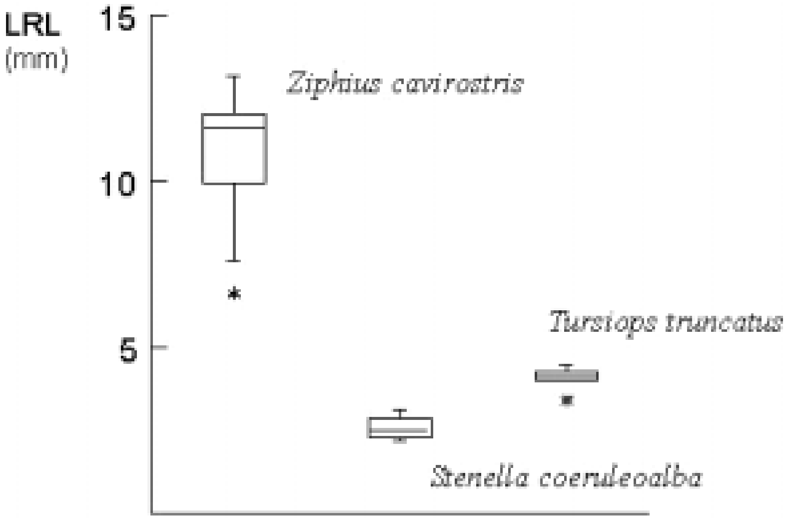

Fig. 1. Distribution of size (lower rostral beak lengthh) (LRL) of *Todarodes sagittatus* preyed by *Z. cavirostris*, *S. coeruleoalba* y *T. truncatus*.

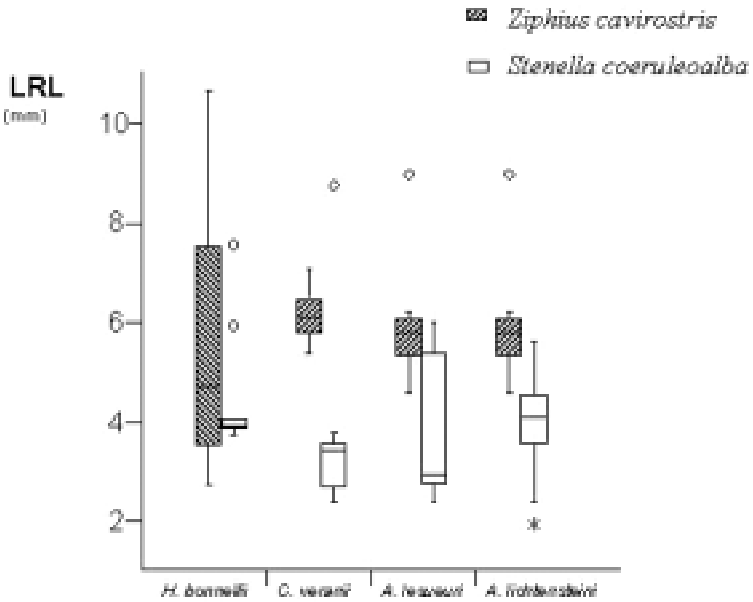

Fig. 2. Distribution of size of overlapped cephalopod species in the diet of *Z. cavirostris* and *S. coeruleoalba*.

Therefore, comparison of diet of these three dolphins suggests a most particular diet for the bottlenose dolphin for the scarcity of overlapped species and their low contribution to its diet. The striped dolphin and Cuvier's beaked whale, which have a higher number of common cephalopod prey, fed upon individuals of very different sizes; the distinctive resources utilization by these three dolphins implies a segregation of niches in the Balearic subbasin.

The cephalopod distribution (Quetglás *et al.*, 2000; González and Sánchez, 2002) in this area may clarify the segregation of niches. The distribution of the prey of bottlenose dolphin could indicate a feeding area more coastal than for both striped dolphin and Cuvier's beaked whale. A similar offshore feeding area may be considered for the last two dolphins according to the oceanic character of cephalopod prey and the high number of common species prey; nevertheless, the separation of both niches may be due to differences in the size of prey. Segregation of niches along prey size and/or space has been observed in some beaked whales (MacLeod *et al.*, 2003) and dolphins (Dolar *et al.*, 2003).

Investigating food-web interactions between Mediterranean coastal dolphins and fisheries in "natural laboratories"

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INTRODUCTION

This paper aims (1) to summarize current knowledge about the potential impact of prey depletion and nutritional stress[1] in Mediterranean cetaceans, (2) to make recommendations about how to investigate this problem into further detail, and (3) to propose the semi-enclosed waters of the Amvrakikos Gulf, north-western Greece, as a promising "natural laboratory" where ecological interactions between common bottlenose dolphins (*Tursiops truncatus*) and fisheries can be investigated.

CETACEAN PREY DEPLETION IN THE MEDITERRANEAN SEA

Jackson *et al*. (2001) argued that "ecological extinction caused by overfishing precedes all other pervasive human disturbance to coastal ecosystems, including pollution, degradation of water quality, and anthropogenic climate change". This lesson may also apply to the Mediterranean, where fisheries have had major direct and indirect impacts on ecosystem dynamics (e.g. CIESM, 2000; FAO, 2000).

The poor state of several Mediterranean fish stocks and the inadequacy of the current exploitation pattern to secure sustainable fisheries have been repeatedly pointed out by the scientific community. Although Mediterranean fisheries statistics are incomplete and unreliable, and there is an acute lack of historical data (CIESM, 2000, 2003), unsustainable harvesting has led to the decline of many fish stocks (Caddy and Griffiths, 1990; De Walle *et al*., 1993; Stanners and Bourdeau, 1995; CIESM, 2000; FAO, 2000), with potentially serious ecological consequences (cf. Dayton *et al.,* 1995; Jackson *et al*., 2001). A recent document by the EC concludes that overall production and catch rates in the Mediterranean have been steadily decreasing, despite the increase in fishing effort, as compared with yields obtained 20 or more years ago. For example, in some of the most productive areas such as the Adriatic Sea and the strait of Sicily, overall catch rates per unit of effort were said to have diminished by more than 60% (EC, 2003).

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[1] Trites & Donnelly (2003) defined nutritional stress as a negative physiological and/or behavioural state resulting from suboptimal quantity or quality of food available to an animal. Effects of and responses to nutritional stress in terrestrial and marine mammals include reduced body size, reduced birth rates, increased neonate mortality, increased juvenile mortality, behavioural modifications (e.g. longer foraging bouts), and changes in blood chemistry and body composition.

The mean trophic level of Mediterranean catches was reported to have declined significantly and quite steadily since the late 1950s, although aggregate fishery landings have increased (e.g. Pauly and Palomares, 2000; Stergiou and Koulouris, 2000). Although there is an ongoing debate on whether such a trend is occurring in the whole Mediterranean (e.g. see Pinnegar *et al*., 2003), a pervasive and large-scale "fishing down" impact on marine food webs (Pauly *et al*., 1998a) would have a profound impact on ecosystem dynamics, ultimately affecting top predators.

Overfishing, as well as habitat degradation, has been proposed as a factor that may significantly contribute to the decline of Mediterranean cetaceans - particularly coastal dolphins - by reducing the availability and/or the quality of their prey (Bearzi, 2002). As stressed by Chapman and Reiss (1999), the lack of sufficient food to maximise reproductive potential may be the most important regulator of population size in animals. Unfortunately, it is highly difficult to determine to what extent nutritional stress is a contributing factor to the decline of any particular population. The "nutritional quality" of a diet is a complex matter and the effects of different diets on animal health are particularly difficult to assess in free-ranging cetaceans. Just how large the nutritional deficit must be to noticeably affect blood chemistry, behaviour, growth, survival and reproduction is not known; nor is it known if these changes occur in progressive and predictable manners (Trites and Donnelly, 2003).

However difficult it may be to establish a clear, mechanistic link between fisheries exploitation and the decline of some cetacean species, such a link provides one of the most plausible contending hypotheses for coastal odontocetes (Bearzi, 2002). Exploitative competition with fisheries represents a source of concern in all the Mediterranean areas where short-beaked common dolphins *Delphinus delphis* have been studied consistently, including the eastern Ionian Sea, the south-eastern Tyrrhenian Sea, and the Alboran Sea (Bearzi *et al*., 2003). Prey depletion resulting from overfishing and habitat degradation is also one of the likely causes that prompted the disappearance of common dolphins from the northern Adriatic Sea, where these animals used to be regular until the 1970s (Bearzi *et al*., in press).

When mass mortality events occur, prey depletion and xenobiotic contamination are often mentioned as potentially contributing factors having compounding effects. For example, inadequate nutrition may have compromised animal health and made Mediterranean striped dolphins *Stenella coeruleoalba* more susceptible to the epizootic that caused a large die-off in 1990-1992 (Aguilar and Raga, 1993; Aguilar, 2000).

In the Black Sea, reduced prey availability has been cited as a factor affecting the abundance of common dolphins and harbour porpoises *Phocoena phocoena* (Bushuyev, 2000). Of two mass mortality events involving Black Sea common dolphins in 1990 and 1994 (Krivokhizhin and Birkun, 1999), only one was recognised as being the result of a morbillivirus epizootic (Birkun *et al*., 1999). Most stranded animals (dead and alive) examined during both die-offs were emaciated (A. Birkun, pers. comm.). Although such emaciation could be a result of the disease, both die-offs coincided with steep declines of European anchovy *Engraulis encrasicolus* and European sprat *Sprattus sprattus* stocks, the main prey of Black Sea common dolphins (Birkun, 2002). Overfishing, combined with the consequences of eutrophication (e.g. water hypoxia) and the concurrent irruption of the introduced ctenophore *Mnemiopsis leidyi*, has been blamed for the rapid decline in anchovy and sprat stocks (Zaitsev and Mamaev, 1997). The total commercial catch of anchovies experienced a 12-fold decline (from an absolute maximum of 468,800 tonnes in the 1987-1988 fishing season to 39,100 tonnes in 1990-1991), while landings of sprat fell by a factor of nearly eight (from 105,200 tonnes in 1989 to 13,800 tonnes in 1993; Prodanov *et al*., 1997). This suggests a close relationship between large die-offs of Black Sea common dolphins and prey scarcity (A. Birkun, pers. comm.).

Mediterranean fisheries are now exploiting most of the fish and fishing grounds available down to a depth of more than 800 metres. The gradual extension of fishing activities to off-shore fishing grounds, exploiting either new stocks or new parts of already over-harvested stocks, have the potential for threatening the food resources of pelagic cetacean species which so far may have been relatively unaffected by prey depletion. Exploitation of deeper fishing grounds would be particularly dangerous, due to the low productivity of such biological systems (which makes deepwater fish more vulnerable to fishing) and to the presence of important but not yet well identified habitats (EC, 2003).

INVESTIGATING NUTRITIONAL STRESS IN CETACEANS

Work done on pinnipeds in recent years is especially valuable to indicate how the issue of nutritional stress may be approached. For instance, research conducted in Alaska by Trites and Donnelly (2003) has shown that declining Steller sea lion (*Eumetopias jubatus*) populations were nutritionally compromised because of the quality of prey available to them (chronic nutritional stress), rather than because of the overall quantity of fish *per se* (acute nutritional stress). This suggests that prey *quality* is at least as important as *quantity* when it comes to evaluating the potential impact on the animals - a consideration that so far has been overlooked in most cetacean studies.

Energetic requirements of top level predators can be used to infer the probable ecosystem structure. Energy consumption by cetaceans can be based on the number of individuals present in a given area at any time, their trophic level, the food requirements of each individual, and the rates of energy transfer between trophic levels (Hooker *et al*., 2002a). Although it is difficult to perform studies on cetaceans similar to those carried out on pinnipeds (e.g. based on blood chemistry, accurate body size measurements etc.), viable research approaches can be identified to evaluate nutritional stress in free-ranging cetaceans through non-invasive techniques. To this regard, a multi-disciplinary approach based on a combination of research methods may provide valuable results.

A variety of different methods can be used to gain insight into what cetaceans eat. These include the following ones, each presenting advantages and disadvantages (e.g. see Barros and Clarke, 2002):

1) Intestine and stomach contents in stranded or bycaught animals can be studied to identify the structures representing a typical meal, e.g. fish bones and the jaws of cephalopods. Fish otoliths and lower cephalopod beaks, in particular, are diagnostic structures in the identification of prey (Barros and Clarke, 2002).

2) Systematic behavioural sampling and the study of surfacing patterns by focal individuals may provide insight on preferred prey type (e.g. epipelagic vs. demersal), and help assessing the time devoted to feeding and the related energy investment as compared with temporal and environmental variables (Fortuna *et al*., 1998; Bearzi *et al*., 1999).

3) Isotopes in biopsy samples can be analysed to obtain information on cetacean prey preferences (e.g., Todd *et al*., 1997), as well as on food preferences by other ecosystem components (Das *et al*., 2000; Polunin and Pinnegar, 2000; Lesage *et al*., 2001). Remotely-obtained skin biopsies may be used in isotope analysis and thus provide an alternative to the examination of stomach contents to delineate diet. Dietary evaluations based on analyses of assimilated tissues implies that the data reflect dietary information integrated over a longer period of time, as opposed to the instantaneous sampling of recently digested food items. With the added possibility of re-sampling photo-identified individuals between seasons or years, isotope analysis may also be used in longitudinal studies of foraging behaviour (Todd *et al*., 1997). Stable isotope analyses performed on teeth from museum collections and stranded individuals may provide comparative insight on the diet of modern *versus* historical cetacean populations (Walker and Macko, 1999; Walker *et al*., 1999).

3) Fatty acids analysis can be useful in reconstructing changes in diet (e.g. Hooker *et al*., 2001), although this method presents shortcomings related to fat stratification in the outer and inner blubber layer, which may yield misleading results of dietary information (Barros and Clarke, 2002).

4) Finally, biochemical analyses of lipid contents/structure in blubber from biopsies may, in the future, help detecting starvation or nutritional stress.

Information collected through “traditional” studies can also be directly or indirectly relevant to nutritional and ecosystem studies. For instance, individual photo-identification (Hammond *et al*.,

1990) may help assessing population numbers and dynamics, habitat use, immigration rates, calving and survival rates, and a number of other key biological features including information on the physical appearance of known individuals over time (e.g. emaciated vs. well-fed, Politi *et al*., 2000). Genetic studies performed on swabbed skin samples (Harlin *et al*., 1999) or stranded animals may help assessing - among other things - genetic variability and the degree of isolation of a given cetacean community, which can represent relevant background for food-web studies.

In addition to the approaches described above, ecosystem modelling has been proposed in recent years as a viable tool for understanding the complex ecological interactions between cetaceans, fisheries and other ecosystem components (e.g., Smith, 1995; Earle, 1996). For effective conservation policy it is widely recognized that an ecosystem-level approach is more effective than that at species-level (Agardy, 1994; Jones, 1994). However, such an approach is often difficult. Theoretically, an ecosystem should encompass all the linkages between species within a defined habitat, but the spatial boundaries of marine ecosystems are mostly nebulous. Ideal "natural laboratories" for ecosystem studies focusing on coastal cetaceans may be represented by semi-closed systems with low rates of immigration and emigration, where cetacean numbers, age classes and diet, as well as prey quantity and removal rates by fisheries can be determined more precisely than in open systems.

With proper development and implementation, and applied on systems for which sufficient information exists, software tools such as "Ecopath-Ecosim" (Christensen and Pauly, 1992) may increase our understanding of food-web dynamics and future cetacean management. Models can provide information on food consumption of cetaceans as compared with fisheries catches, and indicate the degree of resource overlap (Kaschner *et al*., 2001). This approach to the study of marine food webs and cetacean-fisheries interactions may help identify areas of conflict and serve as a useful management tool in the context of defining critical habitat for cetaceans.

DEALING WITH COMPLEXITY

As discussed above, the complexity of marine food webs and a troublesome access to the relevant data make it difficult to provide conclusive evidence that nutritional stress represents a threat to cetaceans. Prey depletion may be a subtle and scarcely noticeable threat, and the impacts may go unnoticed owing to inadequate research effort (e.g. monitoring changes in reproductive success or survival rates). Even in places where the research effort has been extensive, it is difficult to find simple cause-effect relationships between dolphin trends and prey availability.

For instance, bottlenose dolphins and common dolphins were studied intensively around Kalamos, north-western Greece (Figure 1), between 1993-2003. A total of 25,000 km of navigation on effort conducted during 800 boat surveys allowed to document a significant and continuous decline in the density of common dolphins since 1997, and generally low densities of bottlenose dolphins. The most likely causal factor to explain the observed trends appears to be a decline in prey availability over time (Politi and Bearzi, in press; Bearzi, 2003). However, the open character of this marine ecosystem makes it difficult to relate changes in prey abundance and dolphin trends. Food-web studies are complex in this area due to factors including *inter alia*: 1) the observed dolphin move-

Fig. 1. The semi-enclosed Amvrakikos Gulf and the open waters surrounding the island of Kalamos, north-western Greece. The areas where dolphin studies have been conducted are indicated in light grey.

ments in and out of the main study area, making actual movement ranges by the dolphins unknown; 2) a documented presence of transient bottlenose dolphins using the area on occasional bases; 3) possible “food-web” competition between the two dolphin species; 4) presence of other top predators (tuna, swordfish etc.) overlapping in diet with common dolphins; 5) high and largely unpredictable rates of immigration/emigration for most pelagic species; 6) difficulties to monitor fishery trends (e.g. landings refer to a wider fishing area, and CPUE data are unavailable); and 7) poor or absent background information on other trophic levels, e.g. to implement ecosystem models.

In conclusion, despite the abundant longitudinal data collected on dolphins, it is currently difficult to bring conclusive quantitative evidence that overfishing in the area of Kalamos - a well-documented fact (Papaconstantinou *et al*., 1985a,b; Papaconstantinou *et al*., 1988; Papaconstantinou and Stergiou, 1995; Stergiou *et al*., 1997) - is responsible for the observed decline of common dolphins. So far, such an hypothesis rests upon consistent indirect evidence and common sense. Part of the difficulties relate to the fact that the area of Kalamos does not represent an ideal “natural laboratory” for this kind of studies.

THE AMVRAKIKOS GULF, GREECE: A “NATURAL LABORATORY” FOR THE STUDY OF FOOD-WEB INTERACTIONS BETWEEN BOTTLENOSE DOLPHINS AND FISHERIES

Although the inherent complexity of food-web dynamics often makes it difficult to investigate the role of cetaceans in the ecosystem and to evaluate the ecological significance of competitive interactions with fisheries, insightful studies can be conducted in semi-closed marine systems.

The Amvrakikos Gulf, situated in north-western Greece (Figure 1), is virtually a closed basin whose only channel to the open Ionian Sea is a narrow and shallow canal 600m wide, which renews the waters of the Gulf very slowly through a process that takes nearly one year to complete. The Gulf - roughly 400Km^2 - stretches over an area of approximately 60Km, and its waters have a maximum depth of 60m. As a result of the high input of nutrients due to river runoff, the Gulf is among the most productive coastal areas of Greece.

Research conducted by the Tethys Research Institute since 2001 in the context of a long-term monitoring programme confirms that an abundant bottlenose dolphin “community” (*sensu* Wells *et al*., 1987) lives in the Gulf. Based on three years of photo-identification work (>2,500 dorsal fin photos filed and about 60 individuals identified between 2001-2003), these dolphins show high levels of site fidelity[2]. Individual movements in and out of the Gulf appear to be limited, probably owing to dramatic differences between the shallow, highly productive, turbid waters of the Gulf and the deep, oligotrophic, limpid Ionian Sea open waters. The bottlenose dolphin community living in Amvrakikos clearly benefits from abundant prey resources, as shown by behavioural observations within the Gulf. Conversely, in the nearby open waters of the eastern Ionian Sea bottlenose dolphin densities are low (Politi *et al*., 1992) and prey shortage is an issue (Politi *et al*., 2000; Bearzi, 2003). The data collected so far indicate that bottlenose dolphin densities in Amvrakikos are one order of magnitude higher than those recorded at Kalamos.

Bottlenose dolphins in Amvrakikos - as well as the locally abundant sea turtles *Caretta caretta* - are blamed for inflicting damages to fishing gear, thus causing significant loss to local fishermen. Dolphin and turtle attacks are claimed to have increased in the last decade, together with depredation by cormorants *Phalacrocorax carbo* (Athanassopoulos *et al*., 2003), but no compensation mechanism has been put in place by the Greek government. Gear and fish losses embitter the problems experienced by local fishermen, who lament that the local production has declined and the cost of fishing has become excessive in recent years (Conides *et al*., 2001). Artisanal fishermen claim that commercial overfishing jeopardizes the resources in the Gulf. Illegal fishing by non-local fleets, in particular, is blamed by some for the decline of the shrimp *Penaeus kerathurus*, one of the most profitable fishery targets. Pollution from rivers has also been related to shrimp decline (Conides *et al*., 2001).

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[2] Consistent results were obtained by Zafiropoulos & Merlini (unpublished abstract, see http://www.efmsts.org/files/Zafiropoulos.pdf).

Jackson and Sala (2001) argued that, today, our ecological understanding of most marine systems is biased by a misperception of what was their pre-exploitation state. Because of a phenomenon described by Pauly (1995) as the "shifting baselines" syndrome of fisheries, it is difficult to frame ecosystem changes into the right context once its original state has been dramatically changed by overfishing. Although some evidence of habitat degradation has been recorded in the last decade, the Amvrakikos Gulf is a very productive area where the "fishing down" phenomenon, if present, is likely to be in its early years. Compared with the Mediterranean scenario, particularly as far as lagoons and coastal systems are concerned, the Amvrakikos Gulf still sustains abundant resources and a large community of top predators. Therefore, this semi-closed basin may be particularly appropriate for conducting longitudinal studies aimed at investigating food-web interactions and changes in dolphin population dynamics.

Ecosystem studies highlighting the roles of cetaceans would be relatively simple here as 1) there is only one cetacean species; 2) there seem to be no large top predators with diets overlapping those of the dolphins; 3) shark predation on dolphins is probably insignificant; 4) bottlenose dolphins appear to be present year-round, and their movement ranges are probably limited to the Gulf area; 5) rates of immigration/emigration are absent or low for many of the other species living in the Gulf; 6) it is easy to study dolphins due to their high densities; 7) it should be relatively easy to monitor fishery landings and trends within the Gulf area; and 8) reasonably good background information exists on other trophic levels, which facilitates ecosystem modelling.

Therefore, the semi-closed Amvrakikos Gulf appears particularly appropriate for conducting studies aimed at investigating food-web interactions and changes in dolphin population dynamics based on the methods described elsewhere in this volume. This would result in increased understanding of trophodynamics which might benefit cetacean and ecosystem studies in other areas. For instance, data obtained in the Gulf can be compared with information on the well-studied bottlenose dolphins living outside the Gulf, in the oligotrophic waters around Kalamos. Comparisons between these geographically contiguous but likely separated bottlenose dolphin communities may focus on diet differences, nutritional status (including relative occurrence of emaciated individuals; Politi *et al*., 2000) and proportions of time spent in feeding-related activities.

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Summer fin whales *(Balaenoptera physalus)* distribution in relation to oceanographic conditions : implications for conservation

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ABSTRACT

Fin whales are commonly observed in the Western Mediterranean Sea, mainly in summer in the Northern part of the basin. Sightings and observation efforts for the region were extensively recorded from 1993 to 2001, allowing to map their cumulative summer abundance in this area. Because of environmental spatial structure and data characteristics, a geostatistical approach was developed to estimate fin whale density. The distribution was modelled using a Poisson law, often used in independent random event count. Over the study period fin whale density maps obtained by Krigging indicate that fin whales were aggregated in patch within the North-Western Mediterranean sea. Available data about regional oceanographic parameters like bathymetry and measured from space like sea surface temperature, chlorophyll concentration, sea level and the associated gradients were used to investigate the statistical relationships between the climatalogy of the distribution of fin whales abundance index and the climatology of oceanographic factors over the Northern part of the western basin. Data were processed using multivariate geostatistical techniques. The occurrence of fin whales was found to be negatively related to SST and primary production gradient at a 80 km spherical scale, but positively related to primary production gradient , and negatively related to sea surface temperature gradient and sea level anomaly at a 160 km spherical scale. This distribution seems to reflect areas were sinking of dense water is taking place during winter and early spring, a process which stimulates primary production through water mixing.

Keywords

Fin whale, North Western Mediterranean sea, sea surface temperature, sea level, chlorophyll concentration, gradient, multivariate geostatistics, scale dependent process.

INTRODUCTION

The fin whale *Balaenoptera physalus* is the largest marine predator currently observed in the Mediterranean Sea with an abundance roughly estimated at about 3500 individuals, (Forcada *et al.*, 1996). Each summer about 900 individuals concentrate in the Northern part of the occidental basin (Gannier, 1997; Nortobartolo di sciara *et al.*, 2003) to feed on the zooplankter *Meganyctiphanes norvegica* (Orsi Relini and Giordano, 1992) and where they are exposed to shipping collisions a major threat for that species (Laist *et al.*, 2001). This is particularly true in the Mediterranean Sea where 30 % of the world's merchant shipping traffic is concentrated in only 0.8 % of the global ocean surface. Fin whales in the Mediterranean Sea are genetically distinct from the other North Atlantic populations (Bérubé *et al.*, 1998). However information on their year-round distribution is lacking and the question of possible geographic isolation between the Mediterranean Sea and the Atlantic Ocean had been debated for the last two centuries (see Nortobartolo di Sciara *et al.*, 2003 for review) but remains unanswered to date. The aim of this study was to investigate how the summer distribution of fin whales can be related to oceanographic features.

In marine ecosystems, the forcing of ocean dynamics (horizontal advection, upwelling and vertical mixing) and photosynthesis is able to impact on all the components of the trophic food web, from the plankton to apex predators (Croll, 1998). A wide range of predator ecology studies indicates that the variations in their distribution, abundance can be related to oceanographic features (Costa, 1993; Jaquet and Whitehead, 1996; Forcada *et al.*, 1996; Tynan, 1997; Guinet *et al.*, 2000). The connection between bio-physical parameters and marine predators in a given sector is likely to be achieved through biological enhancement (Hunt, 1991; Mehlum *et al.*, 1996). The underlying mechanisms are not yet thoroughly understood (Lutjeharms *et al.*, 1985), no more than the role played by zooplankton (Runge, 1988). It is however very likely that top predators respond, in abundance and spatial distribution, to the variations in the abundance and availability of their preys (Swartzman and Hunt, 2000). In the whale's case, associations between the distribution of whales and oceanographic features (Tynan, 1997) and chlorophyll concentrations (Jaquet and Whitehead, 1996) have shown change depending on which scale these relationships have been investigated.

The spatial description and simulation of spatial patterns can be investigated by using geostatistics (Wackermagel, 1995), which provides a set of statistical tools to analyse the relationships between variables that vary in space and to identify at which scale those relationships are taking place (Matheron, 1963).

METHODS

Observation effort and abundance index

The fin whales sightings database used in this study merges data coming from a variety of organizations (see acknowledgements). Available sightings data for the NW Mediterranean covered the period 1993 to 2001. The prospected area extends from 3°E to 11.5°E and from 41°N to 44.5°N. Only surveys for which observation effort could be quantified were used for this study. They were conducted either along random linear transects or onboard ferries along their regular lines between France and Corsica. Most generally, 1-3 dedicated observers were present onboard the vessels, continuously watching (naked-eye) over 180° ahead of the vessel and switching every 2 hours. Observations were only conducted under fine weather conditions (0 to 3 on the Beaufort scale). A GPS recorded the vessels tracks and any change in the observation conditions (effort interruption or change in sea conditions) was reported. The number of whales reported for a given sighting was considered as unreliable and we decided for the scope of this study to consider only sightings number.

For each year, July and August data were gathered to build a Summer Abundance Index (SAI) climatology which was computed from the number of fin whales sightings (SN) and observation effort (EF). For that, a regular grid of 0.1° x 0.1° cells was defined over the study area. In each cell, we computed SN. EF was defined as the time (hours) spent observing in a cell and was computed as so. Finally the grid was summed over the years, leading to a summer climatology of SN and EF. A Summer Abundance Index (SAI) was computed for each cell by dividing SN by EF, for each year and over the years, expressed in sighting-number-per-hour (Figure 1).

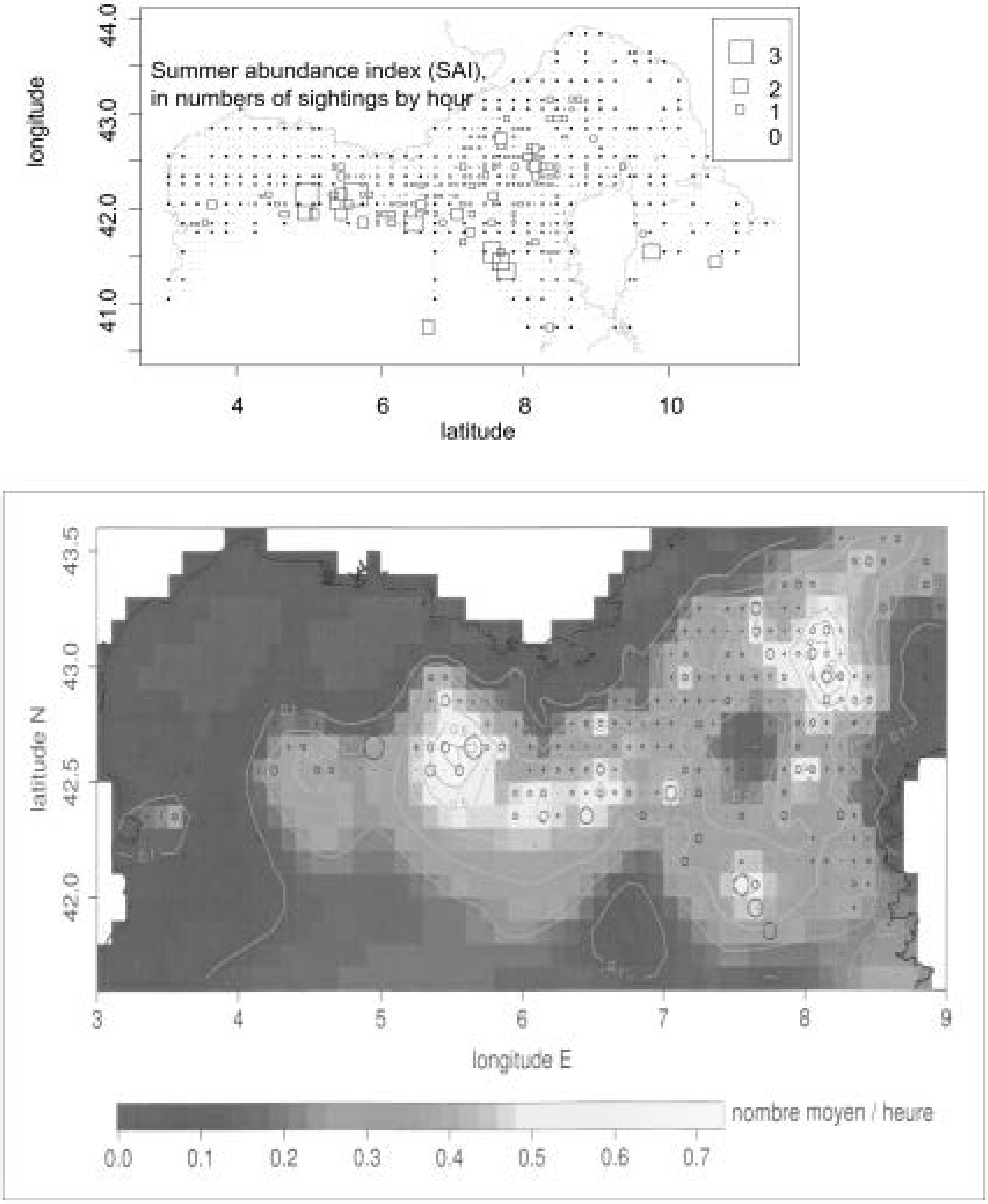

Fig. 1. Summer fin whales abundance index (SAI) (number of sightings per hour of observation); maps before (a) and after interpolation by Krigging (b).

Environmental variables

An *in situ* evaluation of the spatial distribution of fin whales foraging at the scale of a region is presently impossible. Satellite remote sensing, however, is able to provide measurements of relevant environmental parameters. Four environmental parameters could be documented: bathymetry (BAT), sea surface temperature (SST), chlorophyll-a concentration, and sea level (SL). We derived primary production (PROD) from chlorophyll-a concentration and calculated the gradient for each variable.

According to the summer climatology of the number of fin whales sightings, we computed the climatology of each variable in the same grid over the same period when the data were available.

All the characteristics: name, description, origin, resolution, unit, elaboration and reference of the variables used in that study are summarized in Table 1. Geographic extraction and averaging were operated with the Generic Mapping Tool software (Wessel and Smith, 1998), except for chlorophyll-a concentration where SeaDas software was used (SeaWIFs Data Analysis System, http://seadas.gsfc.nasa.gov/).

Table 1. Characteristics of the variables.

Name	**Description**	**Origin**	**Spatial Resolution**	**Unit**	**Climatology elaboration**	**Reference**
SAI	Summer abundance index	EPHE transect	GPS	nb of fin whales sightings by hour	July and August mean from 1993 to 2001	This article
BAT	Bathymetry	ETOPO2	1/3°	meters	–	Smith and Sandwell 1997
SST	Sea surface temperature	JPL *	0.1°	Celsius degrees	JPL Climatology	Casey and Cornillon, 1999
PROD	Primary production	Seawiff data derivated	0.1°	C by m^2 by day	July and August mean from 1997 to 2001	Morel and André, 1991
TP	Sea level anomaly	JPL *	0.25°	cm	July and August mean from 1993 to 2000	Halpern et al, 2000.
GRADIENTS	Second order derivative of environmental data	GMT calculation	same of the data	degrees	As the variable	Burrought and Mc Donnel, 1997

* www.podaac.jpl.nasa.gov

Data analyses

The aim of the statistical analysis is to find out what environmental parameters at which scale are critical in the control of the spatial distribution of fin whale abundance in summer. Oceanographic variables are also found to be generally spatially auto-correlated at different spatial scales. Autocorrelation is a very general property of set of ecological and environmental variables in space and may be defined as the property of random variables taking values, at pairs of locations a certain distance apart, that are more or less similar than expected for randomly associated pairs of observations (Legendre, 1993). Moreover in an aquatic environment, the fluids dynamics strongly structures the links between all parameters (Crépon, 1996). Consequently these values are not stochastically independent from one another and assumptions of classical parametric and non parametric statistics cannot be assumed. Nevertheless this property is at the root to the use of the geostatistics. Multivariate geostatistical techniques (Wackermagel, 1995) were used to synthesize the characteristics of the selected oceanographic variables and to investigate the spatial relationships between the fin whale abundance distribution and oceanographic variables. As the combined effect of different sources of variation is supposed to change from one spatial scale to another, factorial krigging analysis (FKA) was used to separate the sources of variation according to the spatial scale at which they operate. This method enables to distinguish between correlation structures encountered at different spatial scales. It involves multivariate variogram modelling, principal component analysis and cokrigging. Regarding the process acting in the ocean (vortex, gyre, current) , the LMC seems to be a truly adapted approach to analyses spatial link between environmental variables (variogram function).

RESULTS

Descriptive statistics for all the variables are reported in Table 2. Fin whales were sighted 490 times over 1221 pixels searched for 3695.5 hours of observations on 27 platforms in nine years. The distribution of the Sightings Abundance Index is presented in Figure 1.

Table 2.

Correlation between SAI and	**Pearson coefficient**	**Structural coefficient**	
		Sph 80 km	**Sph 180 km**
BAT	-0.34***	-0.66	-0.35
BATg	-0.05	-0.23	-0.49
SST	-0.11***	0.07	0.72
SSTg	0.13***	-0.20	-0.06
PROD	0	0.23	0.54
PRODg	-0.12***	0.18	0.23
SL	-0.08*	-0.66	0.39
SLg	0.15***	-0.23	-0.14

* significant for P<0.05; **, significant for P<0.01; *** significant for P < 0.001.
All other correlation coefficients are not significant.

Modelling the coregionalization of the variables

The experimental isotropic simple- and cross- variograms were calculated using distance classes of 10 km width. From the nine direct variograms, two main structures were identified and the nine experimental variograms could be mainly described as the sum two spherical structure at short (80 km) and medium (160 km) range. We used the linear and but also structural correlation coefficients to identify the environmental factors which correlate with the occurrence of fin whales at those scales. They are reported in Table 2.

The simple product-moment correlation coefficient did not reveal the real relationships among the variables, since it averages out distinct changes in the correlation structures occurring at different spatial scales. On the contrary, filtering the different components disclosed interesting correlations between the variables, changing as a function of spatial scale. In the focus of this study, we summarized the evolution of the structural correlation coefficient between SAI and all the environmental variables in Table 2. At short 80 km scale SAI and BAT and SL revealed strong negative correlations, whereas at medium spatial scale high positive correlations were between SAI and both SST and PROD.

DISCUSSION

Summer situation in the North-Western Mediterranean Sea

Abundance index computation

The climatology of fin whale distribution within the Ligurian Sea clearly indicates that fin whales were not homogeneously distributed but were more likely to be encountered over two main areas centred about 43° S, 8°10' E and 42° 40 S and 5° 30. Further analyses are requested to investigate possible inter-annual variation in the fin whale distribution within the study area.

Spatial scales

The methodology used in this study provides an objective way to identify spatial scale where relationships between the variables occurs. Three predominant and interacting scales were identified in the circulation in the Northern basin of the Mediterranean Sea : the basin scale, the sub-basin scale, and the mesoscale (Brankart and Brasseur, 1998). The two first structures at 80 and 160 km, both of them modelled by a spherical variogram, are linked with isotropic phenomenon. They are coherent with the scale of eddies and gyres in the western basin (Millot, 1999). Ayoub *et al.* (1998) gave some idea about the typical horizontal scales of variability. For the North-West basin, the basin scale circulation is characterized by the northern current, at a scale consistent with 180 km spherical range scale identified by our modelling. The mesoscale activity is composed of energetic signals, with scales from a few kilometers up to 100 km in the Mediterranean sea which correspond to off-shore eddies and instabilities of coastal currents (Millot, 1999). This estimation is coherent with the two ranges of the spherical variograms (80 and 160 km) found in the LMC.

Summer environmental parameters spatial heterogeneity

Examination of the summer climatology of the oceanographic variables suggests surface structures which are roughly located in the same areas from year to year. A description of the circulation in the western basin of the Mediterranean Sea was provided by Millot (1999). In the northern region, the surface circulation is dominated by a coastal current, the so-called Northern Current, with two branches flowing in a northward direction along the North western and eastern part of Corsica before merging and turning westward in the Gulf of Genoa and then flows westward from the Ligurian Sea towards the Balearic Sea. In summer this current is relatively wide and shallow, and it displays reduced mesoscale variability. The southern part of our study area is characterized by a very strong thermal front, the North Balearic Front between the relatively cooler water of the Liguro-Provençal of the North-West basin and the warmer water of the Balearic Sea. The bathymetry exercises a major constraint in the circulation of this area. The water which is encompassed between the north Balearic front, the Corsican branch of the Northern Current and the Ligurian-Provencal-Catalan part of the Northern Current is characterized by cooler waters and by a lower sea level.

Spatial environmental structures are likely to impact on plankton production and fate, from algae to foraging level. For example, swarming behaviour, diel vertical migrations, seasonal reproduction and recruitment are all influenced by environmental factors acting at different scales (Labat and Cuzin-Roudy, 1996). On a given summer foraging is distributed between *M. norvegica* young adults (born in winter of the same year) and those, born in winter of the previous year (Labat and Cusin-Roudy, 1996. The responses of SAI to BAT and BATg highlight the influence of the bathymetry in the foraging enhancement process. The responses of SAI to SL and SLg would therefore reflect the impact of dynamics on whale forage during the early or late recruitment phases and during its consumption phase (Orsi-Relini and Giordano, 1992b), at two scales identifying two clear oceanographic process. The medium range association between SAI and SST point up the impact of the temperature on the fin whales forage and consequently on the lower level of the trophic chain. The association between PROD/PRODg and SAI, with an expected positive correlation at two spatial level, is indicative of the level of the whale forage dynamics organized probably in a hierarchical patch system. Our results emphasize the different scales at which the relationships between oceanographic factors and fin whales occurrence are taking place.

Summer fin whale abundance distribution related to the oceanographic environment

When looking at the fin whale summer abundance index it appears that fin whales were mostly observed in the deeper and cooler water of the North Western basin as previously described in other studies (Notarbartolo di Sciara *et al.*, 2003; Gannier, 2002; Forcada *et al.*, 1996). The analysis conducted here indicates that the spatial distribution of fin whales is scale-dependent and that different environmental factors are acting at different spatial scale. Jaquet and Whitehead (1996) have showed similar scale-dependent interaction between cetacean and environmental features (sea surface temperature and chlorophyll a). The scales found in the modelling of the linear coregionalization model may be interpreted with the structuring of the oceanographic phenomenon in the study area. The negative trend between sea level and fin whale abundance suggests that lower sea level anomalies at 80 km are favourable for fin whale forage abundance in the North-Western basin of Mediterranean Sea and consequently on fin whale abundance, and inversely at 180 km. This “Russian dolls” system is linked to the many scales identified in the circulation in the Northern part of the Western basin (Brankart and Brasseur, 1998).

As described by Millot (1999, and in this volume) the main oceanographic process taking place in the area is associated with the sinking of denser (i.e. saltier) surface water. The densification of the surface water is due to the strong evaporation enhanced by the cold and dry northerly wind blowing in winter and early spring over those areas. Water sinking induces the ascent of nutrient rich deep water and mixing over the whole water column, bringing nutrients into the euphotic zone and inducing intense spring bloom (Figure 2), which allows the development and growth of *M. norvegica* which in turn is likely to determine the distribution of the fin whale (their predator).

These areas of sinking dense waters also induce the creation of cyclonic gyres in locations roughly similar from year to year (Millot, 1999) and the summer distribution of fin whales probably mirror the spatial recurrence of these features.

The inter-annual changes in the amount and the location of sinking water during winter and early spring are likely to impact the amount and the spatial distribution of the primary production, and consequently the abundance of the newly recruited preys and possibly impact on the relative abundance of fin whales. This should be investigated in future studies. The Northern Current and the gyres could also play an active role in the transportation and in concentrating the preys in these areas of the North-Western basin which have been identified as the main summer feeding ground of fin whales by this study.

The 80 km-scale suggests that fin whales abundance is linked with gyres activities, probably associated with direct productive and concentrative process, while the 160 km-scale suggests an association to a lesser extent to the Liguro-Provençal part of the Northern Current.

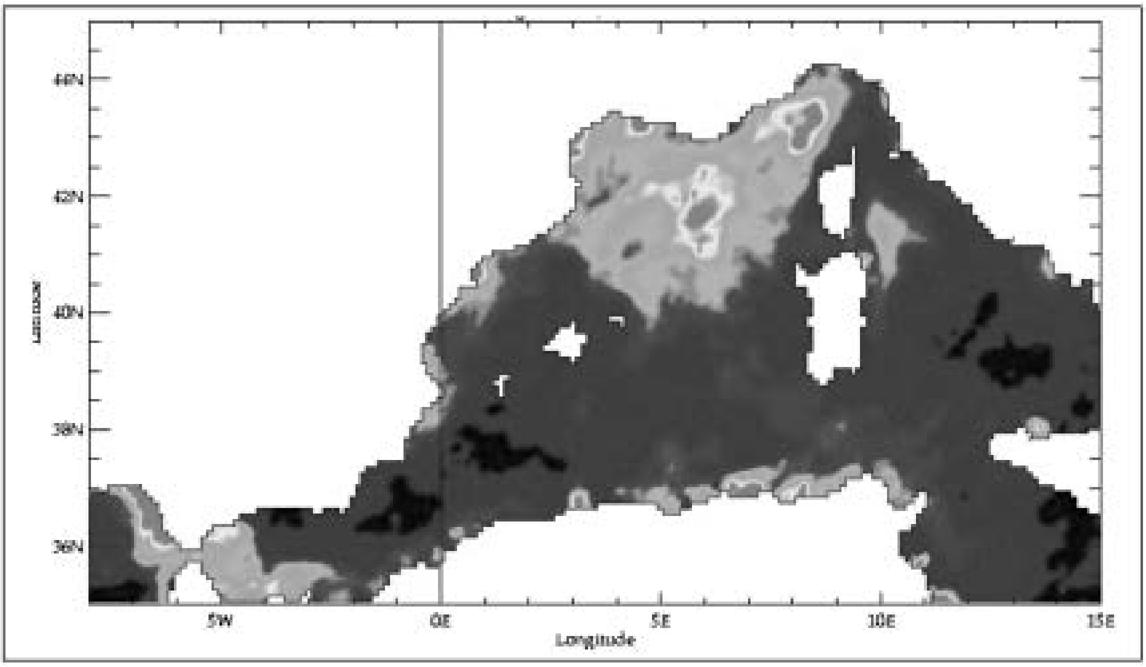

Fig. 2. Map of the relative mean primary production (in gC.m^2.day) in March 1998 calculated from a seaWIFF image. Areas of high production are indicated in red while areas of low production are indicated in blue. Two cells of off-shore active primary production are observed in the northern part of the western basin. The summer fin whale distribution appears to roughly match -in space and scale- the location of these events.

CONSERVATION IMPLICATION OF THE STUDY

This study showed that fin whales tend to concentrate over certain parts of the North- Western Mediterranean Sea which can be characterized according to the oceanographic processes taking place over those locations. Since shipping collision has been identified as the main threat for the species in the Mediterranean Sea a better understanding of their distribution and a precise description of their relatively fine scale distribution should help design mitigation measures to reduce the collision risk.

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Whales, Whaling and Ecosystem Change in the Antarctic and Eastern Bering Sea: Insights from Ecosystem Models

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The question of whether species assemblages are controlled by food availability or by predators is a fundamental ecological question that has implications for biological conservation, maintenance of biodiversity, development of marine protected areas, and management of economically and culturally important marine resources (Worm and Duffy, 2003). Increases in prey populations following the removal of predators by fisheries have been taken as proof that top-down processes control marine ecosystems (e.g., Worm and Myers, 2003). Similar arguments have been used to justify perceived benefits of whaling to fisheries (e.g., Tamura, 2003), or to account for large scale ecosystem changes noted in the northern and southern hemispheres following the cessation of whaling (e.g., Knox, 1994; Springer *et al.,* 2003).

There is considerable uncertainty about the role that whales play in the ecosystem. Many of the large-scale changes noted in marine ecosystems have been attributed to the effects of human activities, especially commercial whaling. One such example is the compelling and eloquently simple hypothesis proposed by Springer *et al*. (2003) to explain a cascading series of population declines that began in the late 1970s in the Gulf of Alaska, Aleutian Islands and Bering Sea. The core of their argument is that killer whales (*Orcinus orca*) were forced to eat smaller marine mammals after commercial whalers wiped out the fin, sei and sperm whales within 370 kilometers of the Alaskan coastline between 1949 and 1969. The end of whaling was soon followed by the crash of harbor seals, northern fur seals, and Steller sea lions through the late 1970s and 1980s (Pitcher, 1990; Trites, 1992; Trites and Larkin, 1996). This in turn was followed by the decline of sea otters in the 1990s (Estes *et al.,* 1998; Doroff *et al.,* 2003). Killer whales, it is theorized, had little choice but to eat their way through the top trophic levels of the North Pacific, leaving critically low populations in their wakes (Springer *et al.,* 2003).

An equally compelling hypothesis has been proposed to explain population dynamics at the opposite end of the world — the Southern Ocean (Knox, 1994; Berkman, 2002). Many Antarctic species were reduced by sealing in the late 1700s and early 1800s (Bonner, 1982; Knox, 1994), and by whaling in the first half of the 1900s (May, 1979; Berkman, 2002), and then by fishing in the mid 1900s (Kock, 1992). Numbers of some species have since increased (e.g., penguins and Antarctic fur seals; Bonner, 1976; Croxall, 1983; Williams, 1995; Boyd, 2002), but others such as the large whale species have not recovered (Kasamatsu and Joyce, 1995; Kasamatsu *et al.,* 2000). Increases in Antarctic fur seal populations through the 1950s–1990s may have been due to the removal of competitors by whaling during the first half of the 20th century, or by the finfish fishery in the late 1960s and early 1970s.

Evaluating the hypotheses concerning the effects of whaling on ecosystems is difficult given the lack of experimental controls or suitable ecological systems with which to compare them. However, it is possible to quantitatively evaluate the hypotheses using mathematical models that capture the essence and logic of their arguments. Ecosystem models are one means of synthesizing current understanding about food webs and interactions between species to determine whether the removal of species could have the expected outcome.

Two ecosystem models were recently constructed to test whether large whales played a significant role in structuring the dynamics of the Bering Sea and the Antarctic marine ecosystem (Trites *et al.,* 1999a; Bredesen, 2003). Both studies used Ecopath modeling software (Polovina, 1984; Christensen and Pauly, 1992), a widely employed program that provides a framework for describing food webs and tracking the flow of biomass through them. They also used Ecosim, a dynamic component of Ecopath that is capable of simulating ecosystem changes over time (Walters *et al.,* 1997). Ecopath and Ecosim represent all of the major components of the ecosystem and their feeding interactions, but are relatively simple. Ecopath estimates the trophic position of each species or group of species within an ecosystem, and provides a means of assessing the main effects that species such as cetaceans might have on the food web and the overall structure or composition of the ecosystem. These kinds of models readily lend themselves to exploring simple, ecosystem-wide questions about the dynamics and the response of the ecosystem to anthropogenic changes.

This paper reviews the findings of the recent Bering Sea and Antarctic ecosystem models to better understand the role that cetaceans play in marine ecosystems.

THE EASTERN BERING SEA

Ecopath models were constructed by Trites *et al*. (1999a) for the shelf and slope regions covered by the Alaska Fisheries Science Center's bottom trawl surveys (Figure 1). They encompassed two periods: (a) the '1950s' covering the years 1955 to 1960, before large-scale commercial fisheries were underway, and (b) the '1980s' covering the period 1979-1985, after many marine mammal populations had declined. Both were annual average models, which means that the biomass, together with the diets and species composition of summer and winter, were averaged to provide a year round 'annual average'. Biologically similar species were grouped into 'functional groups' (Figure 2), and input parameters were gathered from the literature, including biomass, rate of production, rate of consumption, and diet composition for the groups in the system (Trites *et al.,* 1999a and Coombs and Trites, unpubl. data). The seven marine mammal groups included: 1. baleen whales (fin, minke, blue, humpback, bowhead, northern right, gray)*;* 2. sperm whales; 3. toothed whales (beluga, killer, Dall's porpoise, harbour porpoise)*;* 4. beaked whales; 5. Pacific walrus and bearded seals; 6. Steller sea lions; and 7. seals (northern fur seal, harbour seal, spotted seal, ribbon seal, and ringed seal).

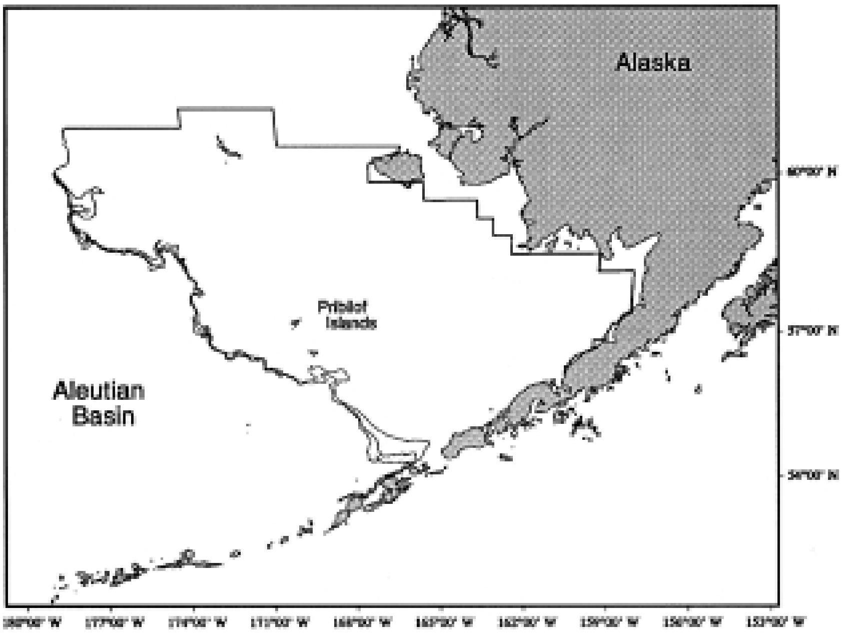

Fig. 1. The eastern Bering Sea as defined in the ecosystem model. Total area is approximately 500,000 km^2.

A flowchart showing trophic interactions and energy flow in the eastern Bering Sea during the 1980s is presented in Figure 2. The flow chart depicting the 1950s ecosystem is similar in layout to the 1980s flowchart, containing the same species at roughly the same trophic levels. Where the two systems differ is in the relative sizes of the boxes (i.e., in the biomass of the different functional groups). Large flows of energy in the Bering Sea emanated from three species at trophic level III – pelagic fishes in the 1950s and pollock and small flatfish in the 1980s. The major consumers (top predators—trophic level IV) included the marine mammals and birds, as well as large flatfish and deepwater fish.

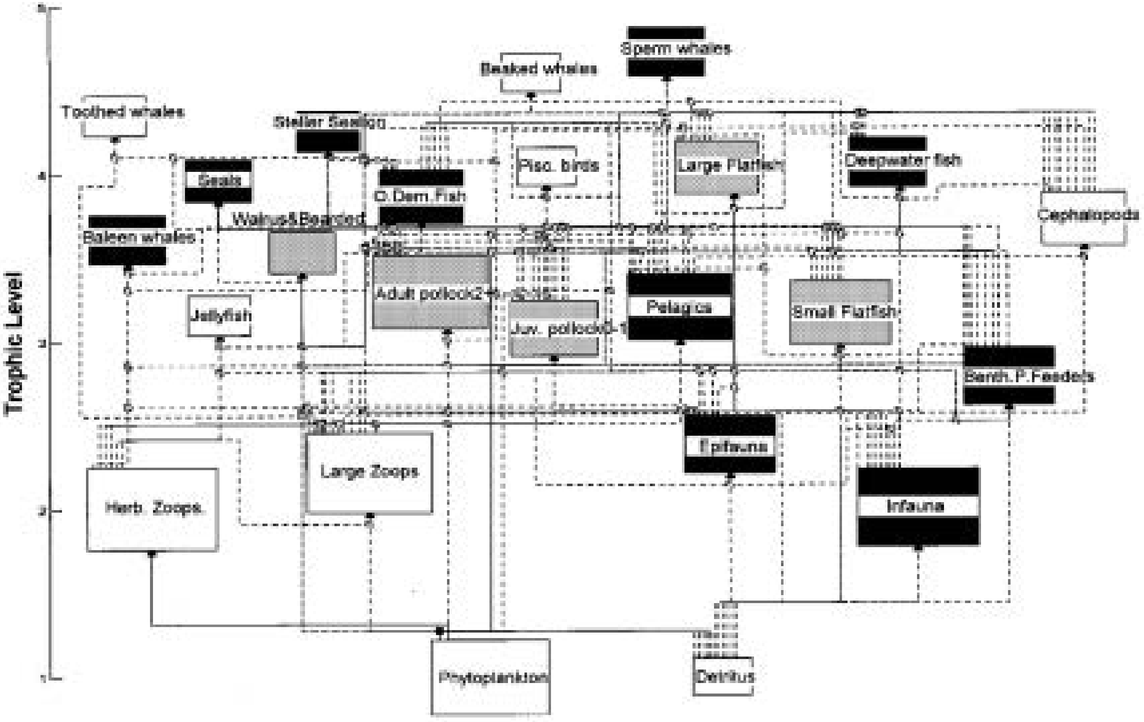

Fig. 2. Flowchart of trophic interactions in the eastern Bering Sea during the 1980s. The blackened boxes indicate which groups had lower estimated abundance in the 1980s than in the 1950s, and the shaded boxes show which species were estimated to have higher abundance in the 1980s than in the 1950s. Connecting lines show the major trophic flows of energy between functional groups (minor flows are omitted).

Niche overlaps were calculated between pollock, large flatfish and marine mammals in the 1980s model using two approaches. One determined the extent to which any two groups sought the same prey (referred to as prey overlap). The other approach determined to what extent they were subject to predation by the same predators (predator overlap).

In terms of which species sought the same prey in the Bering Sea, baleen whales and pollock (both adult and juvenile) had the greatest dietary overlaps (68-83%). There was also substantial overlap between seals and adult pollock, and between seals, sea lions and flatfish. Diets of toothed whales overlapped primarily with that of beaked whales and seals, while adult pollock shared a large proportion of their diet with juvenile pollock. The largest potential competitors of sea lions appeared to be seals, toothed whales and large flatfish.

Removing baleen whales from the 1950s Bering Sea model increased the toothed whales, sperm whales, beaked whales, walrus, bearded seals, seals, sea lions and sea birds (Figure 3). Reducing baleen whales also increased zooplankton biomass (reduced predation) and increased their major competitors (pollock and cephalopods), which were consumed by other marine mammals. However, none of the increases were particularly large (i.e., most were <10%). Removing baleen whales had a positive effect on pollock and seals (northern fur seals, harbour seals, spotted seals, ribbon seals and ringed seals), but no discernable effect on pelagic fishes or sea lions.

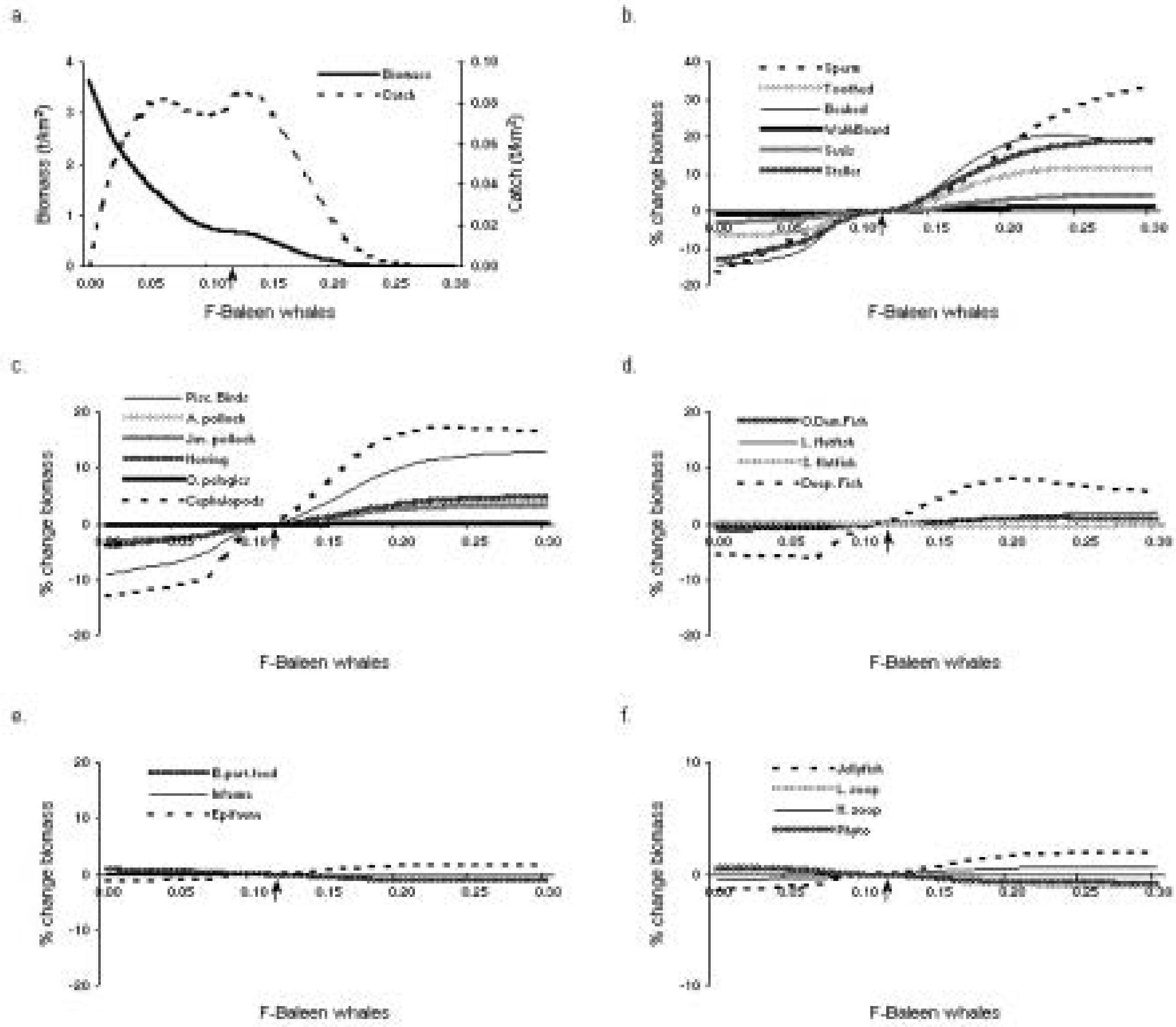

Fig. 3. Equilibrium biomass for Bering Sea species following changes to the fishing mortality of baleen whales in the 1950s model. Arrows mark the instantaneous rate of fishing (F‡year^{-1}) during the 1950s. The top left panel shows changes in the biomass and catch of baleen whales under different levels of F. The other five panels show the relative change (%) that could occur to other species in the ecosystem to compensate for changes in the abundance of baleen whales (at different levels of F shown in panel a).

The model predicted that increases of baleen whales in the eastern Bering Sea could reduce the abundance of pollock, cephalopods and deepwater fishes through direct competition for zooplankton. However, changes in the biomass of marine mammals appear to have little effect on the biomass of other groups in the Bering Sea (Figures 3 and 4). Removing baleen whales resulted in less than a 10% change in biomass of other groups after 100 years of simulation (Figure 4), with the exceptions of beaked whales (22% increase after 100 y), cephalopods (20%), Steller sea lions (16%), deepwater fish (12%), and toothed whales (11%). Overall, reductions in prey abundance can quickly reduce marine mammal populations, but marine mammals are unable to quickly recover when abundant food becomes available.

Commercial whaling and fishing activities had little effect on the simulated ecosystem. Fishing (i.e., killing whales and catching fish) failed to account for the large abundance of pollock and the decreased population sizes of seals and sea lions observed in the 1980s. It therefore seems unlikely that whaling could have unleashed the ecosystem-wide changes purported by Springer *et al*. (2003).

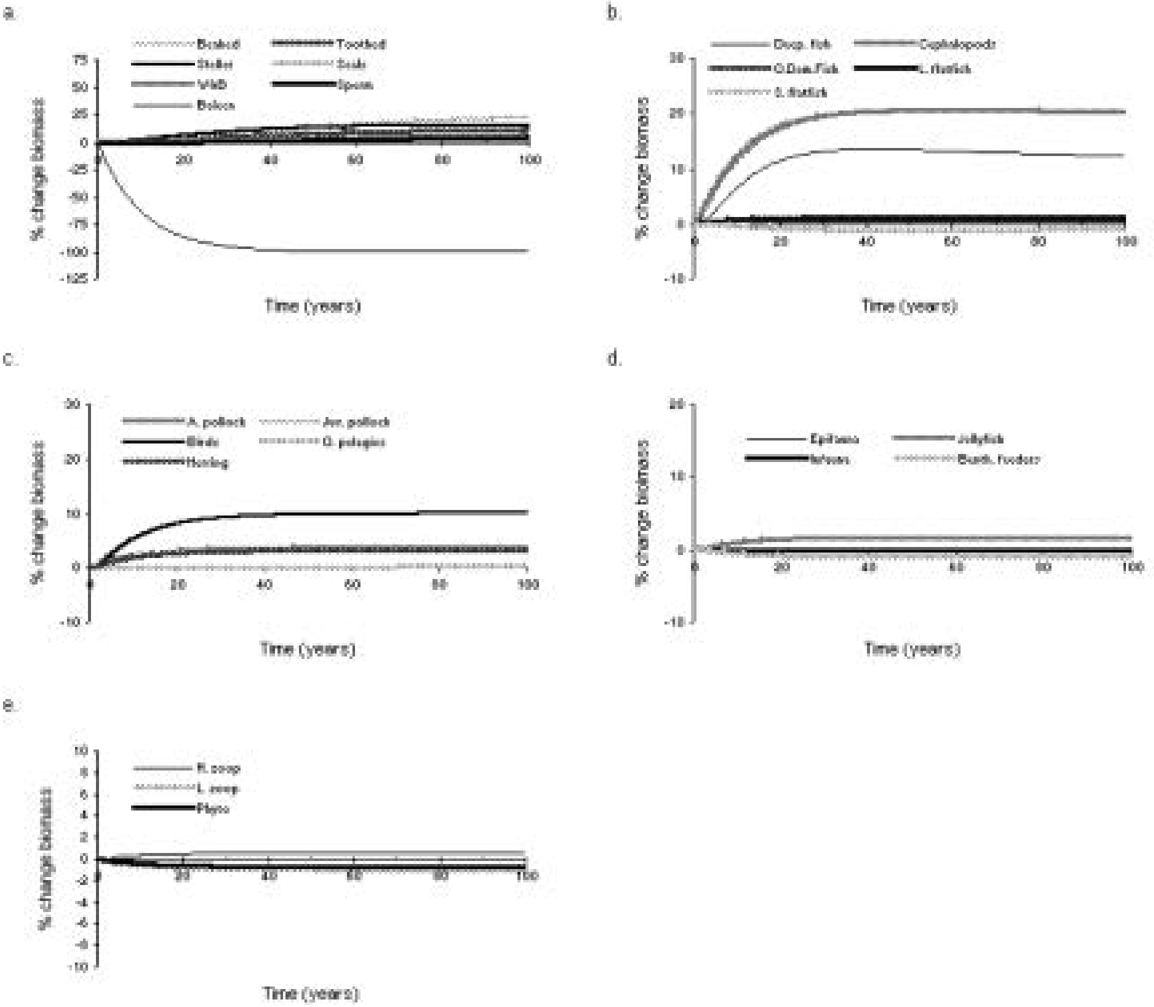

Fig. 4. Dynamic simulation of the effects of commercial fishing for 100 years starting in the 1950s. Note that some predators switched from eating pelagic fishes to eating pollock.

THE ANTARCTIC

The region of the Antarctic that was modeled included the South Orkney Islands and the Island of South Georgia (Figure 5). This South Orkneys/South Georgia region has been subjected to both historical and present-day exploitation, and supports large populations of top predators, including pinnipeds, seabirds, and baleen whales (Knox, 1994). Over 200 species of plankton, invertebrates, fish, birds, seals and whales feed and/or breed in the South Orkneys/South Georgia region. These organisms were classified into 29 functional groups. Detailed descriptions of the groups, data sources for all model parameters, and model outputs are contained in Bredesen (2003).

Two models were constructed to address questions concerning ecosystem interactions and the role of large whales. The first model represented the 1900s (i.e., after the extensive hunting of pinnipeds had ceased, but before whaling began), and was used to explore the effects of removing whales from the ecosystem. The second model, corresponding to the 1990s (i.e., present-day), was used to address the recovery of whale populations. Biomass during the 1990s was dominated by krill and other zooplankton, while whales, seals and birds contributed relatively little to the overall biomass of the ecosystem (Figure 6).

The whaling activities of the first half of the 20th century were simulated by removing 10% of the baleen whales from the 1900s model each year from 1900 to 1950. This was followed by 50

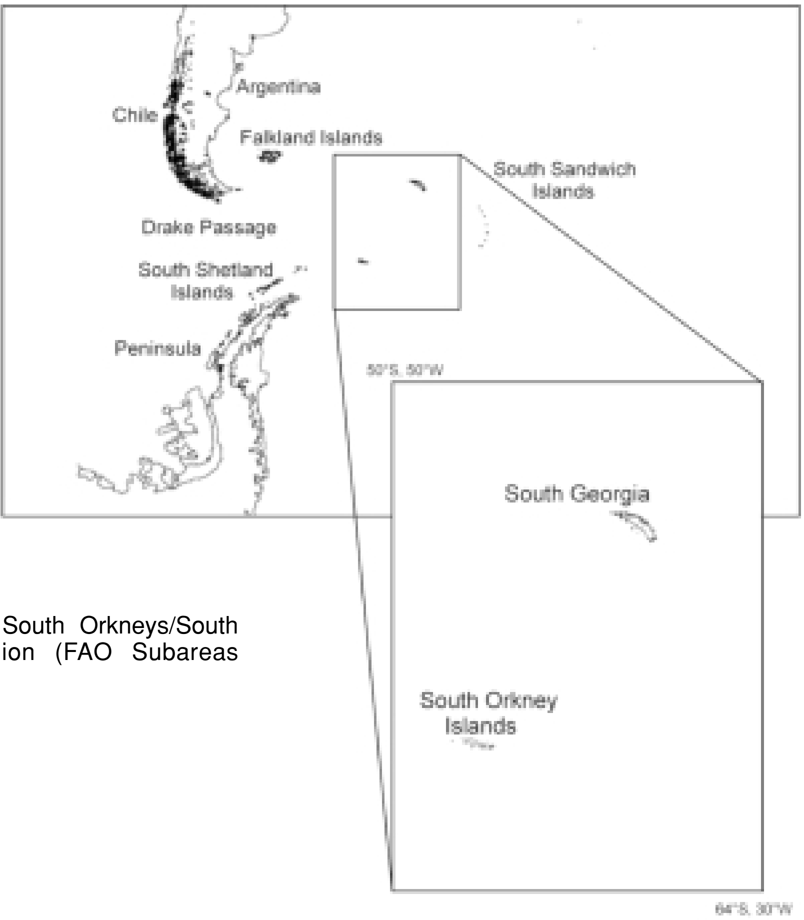

Fig. 5. The South Orkneys/South Georgia region (FAO Subareas 48.2, 48.3).

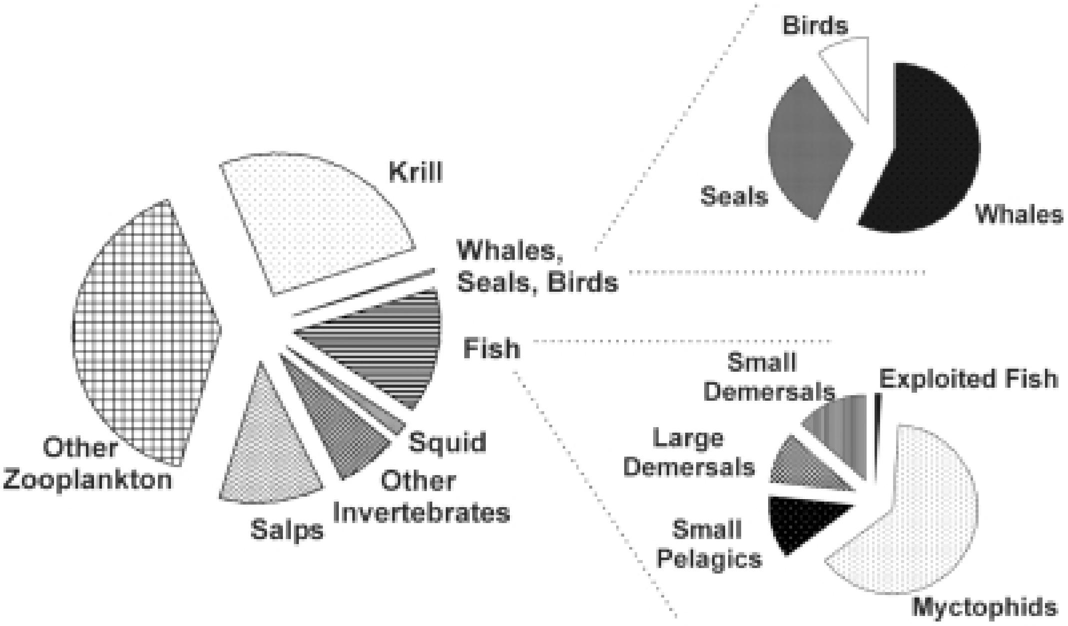

Fig. 6. The proportion of organisms (biomass) in the South Orkneys/South Georgia ecosystem in the 1990s. Exploited fish refers to the three main species that have experienced intense fishing pressure in the past (i.e., marbled rockcod, mackerel icefish and toothfish).

years of no whaling. This simulated hunt resulted in increases among some commercially important fish species (e.g., marbled rockcod, toothfish and mackerel icefish; Figure 7). However, the biomass of Antarctic fur seals did not increase, in contrast to the observed trend of Antarctic fur seal populations over the last century (Payne, 1977; Boveng *et al.,* 1998). Removing 10% of the baleen whale biomass each year reduced the biomass of the simulated whale population to about 5% of its original size in about 50 years. Cessation of whaling (after removing 10% for 50 years) resulted in whale biomass recovering to only about 10% of its original biomass at the end of 100 years of simulation.

Attempts to enhance the recovery of large whales were explored by 'culling' other species in the ecosystem. Running the 1990s model forward with a simulated cull of certain species (e.g., removing 10% of the biomass annually for the duration of a 100-year simulation) provided insights into the factors that influence whale abundance. Model results showed that culling Antarctic fur seals increased penguin and crabeater seal biomass, while culling both Antarctic fur seals and crabeater seals increased penguin biomass even more. A simulated cull of penguins resulted in a positive response in baleen whale populations — although even then, the model only indicated a 10% increase in overall whale biomass after 100 years of culling. The model suggested that the greatest increase in baleen whale biomass would result from a cull of myctophids, which would increase whale biomass by 40% over the 100-year time period. However, reducing myctophid biomass negatively affected other species, such as Weddell seals and king penguins.

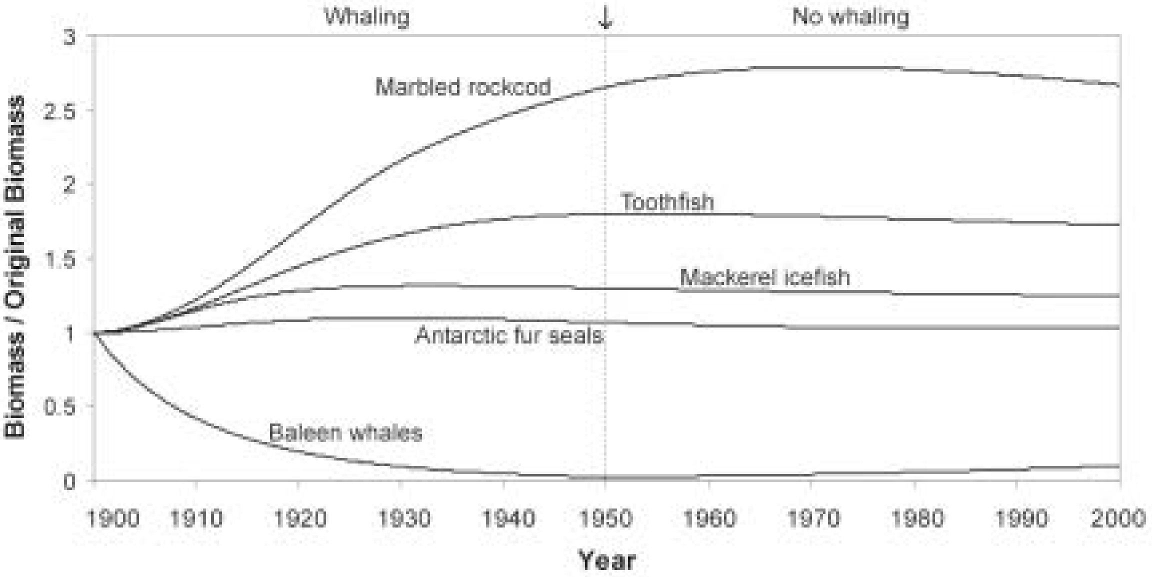

Fig. 7. Predicted biomass changes of several species in response to simulated whaling. Ten percent of baleen whales were removed from the modeled ecosystem each year from 1900 to 1950, followed by 50 years of no whaling.

CONCLUSIONS

The ecosystem models constructed for the Antarctic and the Bering Sea incorporate current understanding of biological interactions of species within the ecosystem (i.e., who eats whom and how much; Trites, 2003). Within the limitations that are inherent to simulations, both models suggest that removal of large whales had little measurable effect on lower trophic levels or on the dynamics of other species in their polar ecosystems.

Trophic interactions failed to explain the magnitude of changes in the biomass of the major species groups in the Antarctic and Bering Sea. Nor did fin-fisheries appear to have had a significant effect on the abundance of non-targeted species. This may mean that environmental effects (which were not modeled) play an important role in influencing the dynamics of marine ecosystems. Oceanographic factors such as changes in water temperature or ocean currents likely result in variations in ecosystem production and species recruitment patterns which are not captured by our Ecopath models (Trites *et al.*, 1999b).

The Ecopath modeling approach is a powerful means of synthesizing knowledge about ecosystems and the factors that influence ecosystem dynamics. They provide a straightforward means for estimating trophic levels and niche overlaps with other species to assess the potential for resource competition. While the models failed to support the hypotheses that large whales play a significant structural role in the Antarctic and Bering Sea ecosystems, they do support what most already know — i.e., that populations of large whales are easily reduced to low numbers, but take a long, long time to recover. They also help in recognizing the need to consider factors other than food web interactions when assessing the status of cetaceans, as well as highlighting the potential tradeoffs that can result when other species are removed from ecosystems.

Interactions between fishing activity and cetaceans that occur in the Southeastern Ligurian-Northern Tyrrhenian Sea

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The distribution, abundance and ecology of cetacean populations in the Mediterranean, and in particular in the Southeastern Ligurian-NorthernTyrrhenian Sea, is little known. Most of the information regarding life history of cetaceans, in particular on diet, reproduction, growth rates, etc. proceeds from the analysis of stranded individuals or from those incidentally caught by fishers. The area is characterised by a higher presence of cetaceans (Notarbartolo, 1994) and constitutes one of the richest Mediterranean area as regards this group. This is probably due to the particular dynamics of the water masses, which produces an increase in primary production and trigger processes that sustain a high biomass of organisms at the highest trophic levels (Orsi Relini and Giordano, 1992 ; Orsi Relini *et al.*, 1994b). The area knows, however, important seasonal changes in surface water temperature chlorophyll level as detailed elsewhere (Millot and Taupier-Letage, this volume).

Fishing activity is very intense, utilising different strategies. Artisanal fisheries are very important and constituted a traditional activity for several centuries. In the last 50 years semi-industrial fisheries have developed very fast and fishing capacity is now very high related to the available resources in the area. Game fishing is also well developed and its impact on several commercial resources cannot be neglected. Anyhow, the interaction cetaceans/fishermen mainly involves commercial fisheries. Some of the interactions between marine mammals and fishing activity can be considered as direct (or related with fisheries operational aspects that mainly imply incidental catches). Fishing activity, through the removal of individuals, is an additive (often not negligible) cause of population reduction beyond the natural mortality. It remains however very difficult to obtain reliable estimates of these incidental mortality rates.

Le Hydrological conditions show that in winter (left side of Figure 1) the Northern portion of the Elba island constitutes a front of interactions of two different water masses. The flux towards North of the Tyrrhenian current tends to orient from north to south the direction of both isotherms and isohalines. During summer (right side of Figure 1) the frontal structures are still present, but fractionated. They are often positioned transversally to the coast, and linked to the Ligurian waters intrusions. Tyrrhenian waters mostly remain at south of Elba island. The almost permanent presence of the frontal structures certainly enhancemes the dynamics of the biological activity in the area.

The semi-industrial fleet exploits both demersal and pelagic resources. The presence of marine mammals in the bottom trawlers by-catch can be considered negligible while some individuals are incidentally caught by midwater trawlers and purseiners targeting pelagic species such as sar-

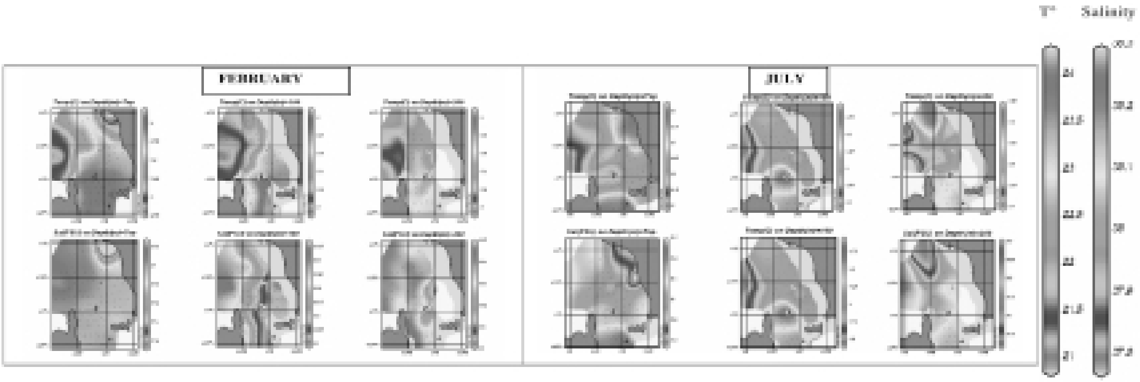

Fig. 1. Seasonal changes in temperature (top) and salinity (bottom) at different sea depths (from left to right: surface, 100 m, 200 m).

dines and anchovies. Unfortunately, only episodic information of marine mammal catches is available in the area (Magnaghi and Podestà, 1987). Cetaceans which constituted in the past an important by-catch of the swordfish fisheries with driftnets (Notarbartolo di Sciara, 1990) remain frequently entangled in fixed gears in the small scale fisheries (especially in gillnets). Long driftnets have been recently banned in national waters of the European countries but some illegal activity still remains.

Interactions have been better studied in fisheries occurring near shore, especially those related to artisanal fixed gear fisheries. Many marine mammals species are incidentally caught in fixed gears (trammel nets, gillnets, longlines). These species often feed on fish caught with the nets or with hooks and they become captured. Many times, marine mammals produce important damages to fishing gears. In some cases, the encounter with the gear is exclusively incidental. Cetaceans often compete with fishermen for shared resources. For example, the Risso's dolphin *Grampus griseus* and the Cuvier's beaked whale *Ziphias cavirostris* feed mainly on commercial cephalopods. In some cases, competition differs under a spatial point of view. For example, *G. griseus* compete with fishermen in the neritic zone while exploiting mainly non-commercial species offshore (Würtz and Marrale, 1993; Bello, 1992).

Even if marine mammals/fishery interactions have received more attention in the last years in the Mediterranean, the available information regarding the mentioned interactions with commercial fisheries is scarce and currently in the Southeastern Ligurian-Tyrrhenian area there are no research programs aimed at the improvement of the knowledge of this problem. In consequence, it has not been possible up to now to determine the full extent of incidental catches. There are objective difficulties for the quantification of this phenomenon. Limited monitoring efforts aimed at estimating the magnitude of by-catches (that may include cetaceans) by placing observers aboard commercial vessels were attempted. They are in general characterised by a very low efficiency, reflecting high costs and a high level of human resources. Alternative sources of information such as documentation of recovered stranded carcasses showing evidences of entanglement (impressions of net material, thin lacerations, etc.) have been used. Records of strandings, however, are of limited use to estimate the relative frequency of incidental catches. Quantifying the incidental fishing mortality experienced by each population of marine mammals present in the area is very important as regards the efforts aimed at the management and conservation of cetaceans. Fishermen liberate cetaceans incidentally caught (most of the times already dead) without providing any information to the port authorities or to the persons responsible for the monitoring of undesired catches. In some local instances where cetaceans flesh or dried meat is very appreciated as food, meat or entire specimens are illegally sold. In the Ligurian and Tuscany ports and landing sites that are monitored (especially with the goal to estimate landings of commercial species for both, industrial and artisanal fisheries) it is quite common that fishermen refer to incidental catches of dolphins. It is quite evident that this information is partial and the numbers of records represent a clear underestimate of the real phenomenon.

Obviously the higher contemporary presence of fishermen and cetaceans in a given area, the higher the probability of incidental catches (see Tregenza, 2000).

Incidental fishing is not the only source of mortality caused by human activities. Pollution, marine transport and sport activities, as offshore speedboat competitions and marine transportation, may also have important negative influence on the survival of cetaceans. Pollution threats on the Mediterranean striped dolphin *Stenella coeruleoalba* are discussed in Aguilar (1993). Collisions between ships and whales are discussed in Laist *et al.* (2001).

Another type of interactions between marine mammals and fishing activity is potential competition: when fishes targeted by fisheries are removed by a cetacean they cannot be removed by the fishery. Fabri and Lauriano (1992) and Bello (1992) discuss the potential competition for several marine resources, especially for cephalopods in the area. Viceversa, the removal by fisheries of individual fishes that are prey of certain marine mammal reduces the availability of food for the predator. This last phenomenon can trigger, in the years when food resources are scarce, adaptive behavioral mechanisms by cetaceans that more frequently try to eat entangled fish. These behavioural changes may consequently increase the frequency of incidental catches.

Fishing activity affects the abundance and demographic structure of target or by-catch species but also the characteristics of the ecosystems at which these species belong. In the Southeastern Ligurian-Northern Tyrrhenian, the excessive fishing pressure exerted on the continental shelf and slope has locally produced the almost total extinction of many species positioned at the top of the food webs, in particular selacians such as *Squalus spp*. and probably has also contributed to the depletion of stocks of small pelagics such as anchovy. It is likely that these changes have influenced (and modified) the ecological role of some cetacean species in the mentioned area.

DATA NEEDS

A priority is to perform a proper assessment of the status of the cetacean populations: this implies the knowledge of the species distribution, unit stocks, behaviour, population abundances, growth rates, causes of mortality, etc.

The analysis of the presence and relative abundance of the cetaceans in a given area constitutes the first step for a sound management of these resources. This is generally done through the utilisation of vessels, most of the times following parallel transects or zig-zags assumed to properly cover the studied area. Sightings are conducted by experienced persons aboard. A number of have been performed in the area (Notarbartolo *et al.*, 1993; Orsi Relini *et al.*, 2001; Zazzeta, 1998; Fabri and Lauriano,1992; Barale *et al.*, in press). Sampling increased in the last years, after the creation of the Liguro-Provencal international cetaceans sanctuary in 1999. Research cruises aimed at the quantification of abundance of cetacean species remain however time consuming very expensive and levels of uncertainty of the estimates, very high (Di Meglio, 1998).

The population dynamics of cetaceans in the Mediterranean, and in particular in the considered area is little known.

Growth rates have been studied for many species around the world, but scarce studies have been performed in the considered area. The growth performance aspect was analysed for *Stenella coeruleoalba* (Rostani *et al.*, 1997; Marini and Casini, 1999).

Behavioural aspects are very important for species conservation purposes. Even if the total avoidance of the risk for cetaceans to be captured with fixed gears is almost impossible, it is necessary to drastically reduce this undesired risk by the use of mitigation devices. Due to different and specific behavioural patterns, the methods of mitigation may be different for each single species. Another aspect of the same problem regards the desirable definition of allowable limits on the maximum number of marine mammals that could be taken within each specific fishery. This is particularly critical in the case of endangered species. The definition of such limits is however very. Moreover, it is also necessary to estimate, based on previous knowledge of the dynamics of the populations and through the utilisation of precautionary approaches, a limit of the proportion of the population that can be incidentally killed by the fisheries. This can be considered an acceptable (even if undesirable) compromise in order to allow the continuity of commercial fishing activity. Other important aspects related to the behaviour of the different species regards migrations, identification of reproduction and nursery areas.

The abundance, population and individual growth rates, survival rates, etc. depend on the biological (mainly trophic) interactions of this particular species with the other components of the ecosystem. Fishing activity may have (directly or indirectly) an important influence in these processes.

In recent years, many studies on ecosystems focused on the description of energy flows and measures of trophic interactions among groups in a system, as in Ecopath with Ecosim (Pauly *et al.*, 2000). Unfortunately, the majority of quantitative dietary studies of marine mammals derive from a relatively small number of samples, samples proceed from a small fraction of the species geographical distribution range, and many times, they do not apply to their entire distribution (Pauly *et al.*, 1998b). This fact makes difficult to define standardised diet composition for use in trophic modelling. Due to a restricted available information it is very difficult to obtain reliable estimates of dietary spectrum, quantification of food consumption, digestion rates, food conversion, etc. In the case of stranded cetaceans, it is likely that in many cases, they are individuals that arrive close to the coasts in bad health conditions, and gut data may not reflect the normal food habits of the species related with its size, age or region. Methodologies generally used in the analysis of predator diets (in the case of marine mammals) and its quantification are subject to high levels of errors and biases (Santos *et al.*, 2001a). Some recently developed methods as fatty acids analyses and stable isotope studies may help in the knowledge of the cetaceans' diets (G. Pierce in this volume).

Estimates of standing stocks biomasses are very difficult for several species, especially for those species that are not vulnerable to the main fishing gears operating in the area or for those without any commercial value (thus not reported in the statistics of the commercial landings). Mesopelagic species and high migratory tunas, sharks and swordfish may have very important roles in the Mediterranean pelagic ecosystems, but abundance and many aspects of their natural histories are not well known. Research on the trophic relationships of the marine communities in the Southern Ligurian-Northern Tyrrhenian area, with special attention to marine mammals is at the beginnings. It will utililise both available data derived from other previous studies and new collected data, that includes fisheries information, biological aspects, estimates of abundance of the main groups. In the area, in particular for demersal and semipelagic species, there is fairly good information about abundance, catch rates, growth, mortality, changes in space and time, thanks to the large amount of data derived from seasonal trawl-surveys and from monthly based catch assessment surveys initiated in 1985. Commercial data also concern the small pelagics. For many finfish species there is information regarding biomass, mortality and growth rates and in some cases on diet. At this moment, a data base gathering available information on all the pelagic groups (including cetaceans) is in force. Visual censuses will be performed in order to estimate the abundance of marine mammals. Based on the availability of information, the Ecopath with Ecosim model has been considered in this case a good candidate as the modelling approach.

Marine reserves, ecological theory and the role of higher predators in marine ecosystem management

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INTRODUCTION

Marine predators attract a great deal of attention in conservation planning, and are often used to promote various political goals. Here I ask whether, in addition to their value as campaign figureheads, they can play an ecological role in marine ecosystem management, with particular attention on is the ecological relationship between cetaceans and fisheries. Jackson *et al.* (2001) have stated that "ecological extinction caused by overfishing precedes all other pervasive human disturbance to coastal ecosystems", with such extinctions or reductions both of the harvested species (e.g., Myers *et al.*, 1997) or of bycaught species (e.g., Casey and Myers, 1998). Even parts of the ocean previously relatively untapped, such as the deep sea, are now facing potential increased exploitation (Roberts, 2002).

Traditionally, ecosystem management for fisheries has been species-based, taking the form of catch reduction (quotas), time-closures, or area closures. However, many of these attempts have not been as successful as anticipated, and many authors suggest that reserves, i.e. spatially explicit management areas, have greater potential to improve sustainability (Botsford *et al.*, 1997; Roberts, 1997). The modelling approaches detailed elsewhere in this volume (see summary by Harwood), highlight the difficulties inherent in measuring and predicting ecological complexity. Since reserves make no attempt to alter ecosystem function, but allow portions of the ecosystem to remain intact, they have great precautionary potential. This paper will focus on marine reserves in terms of the issue of marine predators and fisheries, asking (1) how can we use higher predators to inform conservation policy and (2) what aspects of ecological theory may be relevant to this?

MARINE RESERVES

A marine reserve is defined as a geographically delimited area designated for protection, which may include a broad area with limited management restrictions encompassing smaller zones which are closed to extraction (NRC, 2001). It is the spatial nature of these reserve areas which confer their benefits when compared to other management measures – focussing on the whole ecosystem, rather than providing a solution for one ecosystem component. In addition to the habitat protection aspects, the fisheries benefits of such reserves have been well demonstrated (Roberts, 1997). Fish within reserves live longer than those in fished areas. Combined with this, fish produce exponentially increasing numbers of eggs with their size, so there tend to be increases in both fish size and fish biomass following protection. Furthermore, these marine reserves often extend their benefits outside their delimited area by leakage or overflow from these areas into neighbouring areas that may be fished.

Threats to marine mammals are several (Hooker and Gerber, 2004). Many of these – particularly physical threats such as ship strikes or fisheries bycatch, competition with fisheries for prey resources, or acoustic impacts causing animals to abandon an area, become temporarily unable to forage, or even to sustain physical damage – can be mitigated by spatial protection. Marine reserves are therefore likely to benefit both marine mammals and their ecosystem.

Marine mammal critical habitats can be defined in terms of the ecological units required for successful breeding and foraging (Harwood, 2001; Hooker and Gerber, 2004). For baleen whales, seabirds and pinnipeds, these areas are often separated spatially, whereas for odontocetes these may occur in the same place. In the past, many conservation efforts for marine mammals have been based on protection of breeding habitat, such as the Ano Nuevo State Park which protects breeding northern elephant seal habitat, or the Hawaiian Islands National Marine Sanctuary which protects breeding grounds of humpback whales (Reeves, 2000; Hooker and Gerber, 2004). Part of this is due to the ability to encompass extremely high spatial aggregations of individuals in a small protected area. However, in many cases, these animals do not face their greatest threats during the breeding season. More attention needs to be directed at marine mammal foraging to establish how best to protect their access to food resources.

Although the optimal protected area would encompass the majority of a species distributional range (Reeves, 2000), I would argue that benefits will be observed from the establishment of much smaller protected areas. Many higher predators are relatively site-faithful over time-scales varying from daily (in the case of diurnal prey movements) to annual (in the case of migratory species), to decadal (in the case of species following El Nino events), such that boundaries can be established around hotspot-locations in which these animals are regularly found. Despite the fact that a predator might only use this protected area for a portion of its lifespan, this would reduce the frequency with which it would be exposed to certain impacts, and diminish the overall cumulative impact of other threats.

ECOSYSTEM CHARACTERISATION

Given that our aim is to provide protection to foraging grounds of marine predators, how do we define areas to protect? The goal of marine reserve establishment is to provide protection at the ecosystem level rather than simply single-species protection. However, our ability to quantify ecosystems and their trophic ecology is currently relatively poor. This is illustrated by the degree of variation that can reasonably be applied in the representation of any food web, which can range anywhere from the basic and simple to the incredibly complex (e.g., Yodzis, 1998).

That said, several studies have attempted to categorise the ecosystems around foraging marine mammals. Estimating food consumption is perhaps central to this, and has also been central to the debate and controversy over the impact of marine mammals on their prey and the consequent interactions with fisheries (Boyd, 2002). Many studies calculate the food or energetic requirements of particular populations, and our ability to do this has improved dramatically over recent years (e.g., Boyd, 2002; Winship *et al.*, 2002). Relatively simple estimates can be derived based on population size, trophic position, metabolic rate and assumed trophic transfer efficiency (Hooker *et al.*, 2002a; Kenney *et al.*, 1997). Such calculations have been used to estimate ecosystem size requiring protection by calculating the primary production that is required to support the known population size which uses that area (Figure 1; Hooker *et al.*, 2002a). By calculating the productivity required in a particular area to support the top predators there, and comparing this to known productivity measurements, it is possible to establish whether the size suggested for ecosystem protection is realistic. For northern bottlenose whales in the Gully, it appeared that there was a fairly substantial spatial subsidy into the region, allowing such a small area to support the abundance of higher predators found there (Figure 1; Hooker *et al.*, 2002a). Such an analysis resulted in recommendations to extend protection over a larger area to encompass the likely influx of resources.

More recently such calculations have become more refined, incorporating variations in metabolic rate with different life-history stages (Boyd, 2002; Winship *et al.*, 2002). However conclusions differ. Boyd (2002) found that population size was the most important determinant of prey requirements, but Winship *et al.* (2002) found that diet and bioenergetic parameters rather than population size had more influence on model predictions.

Although such studies have allowed broad calculations of prey consumption of marine predators, our ability to predict the consequences of changes in population size of marine predators remains poor. Ecosystem-level predictions are further compounded by multispecies effects. Predator-prey interactions, competition and mutualistic interactions can cause unanticipated changes in community structure and nontarget effects of management interventions. Of further cause for concern are the historical legacies which we see – the evidence that potentially irreparable ecosystem changes may be caused by competition for resources which can radically alter ecosystem structure, resulting in dramatic shifts in population demographics (May, 1979; Worm and Duffy, 2003). Trophic cascades have been found where removal of a top predator precipitates dramatic reductions in abundance of species at lower levels (Worm and Duffy, 2003).

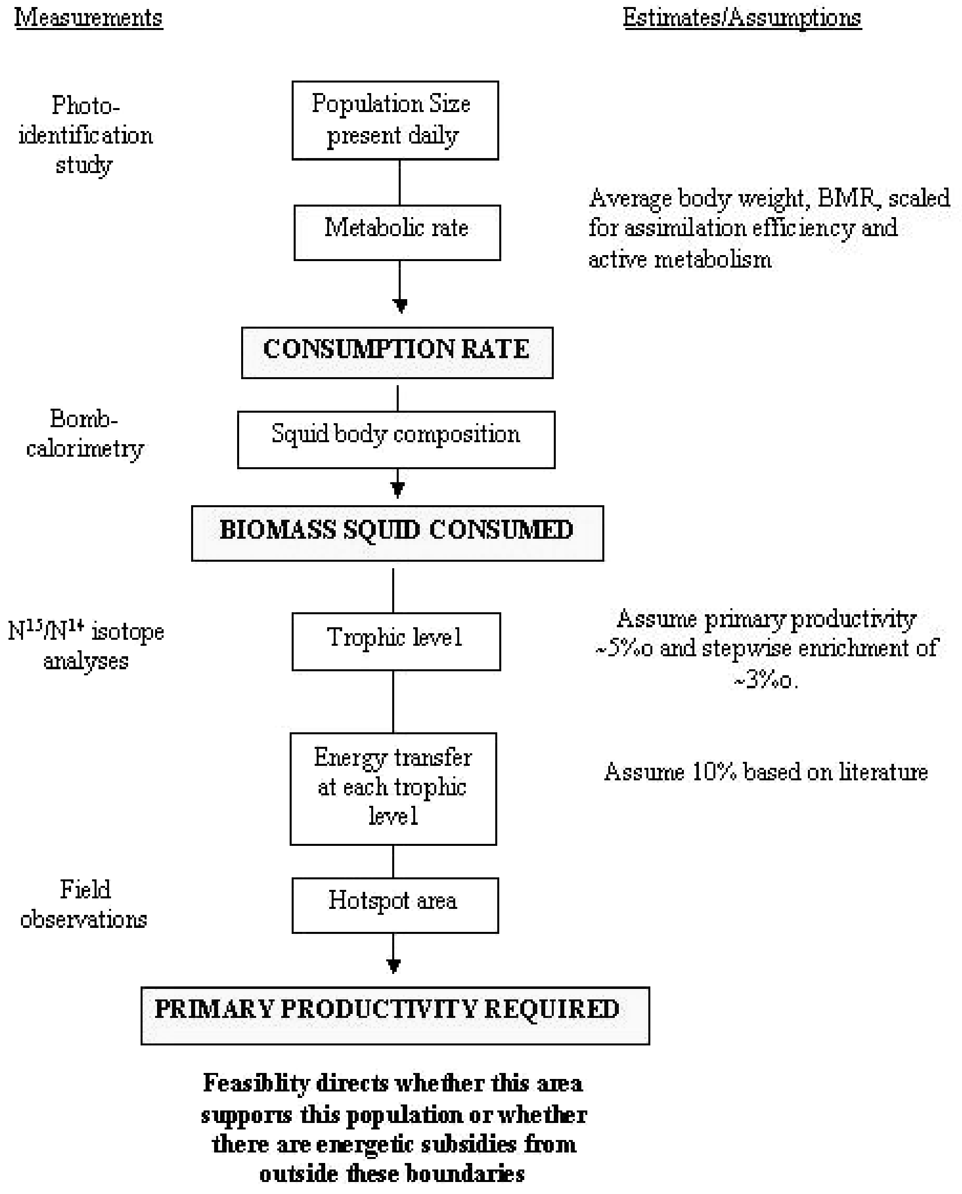

Fig. 1. Energetic calculations used by Hooker *et al.* (2002) to establish boundary for a pilot marine protected area based on northern bottlenose whale population in the Gully, Nova Scotia.

PREDATION, COMPETITION, MUTUALISM AND PARASITISM

In terms of these trophic interactions, can we consider fisheries as simply another competing higher predator? In fact, the interactions between marine mammals and fisheries can be relatively complex, encompassing several types of trophic interactions – potentially mutualism, parasitism and predation in addition to competition (Table 1). Conflicts between marine mammals and fisheries have previously been classified into operational conflicts and ecological conflicts (Lavigne, 2003), although many of the operational conflicts discussed by result in marine mammal death, and so could be considered as predation events, whereas ecological conflicts tend to primarily consider competition for the same fish stocks.

Table 1. Predation, competition and mutualism between fisheries and marine mammals.

Type	Description	References
Competition	For fish stocks	Lavigne, 2003
Predation	Marine mammals killed as bycatch	Perrin *et al.,* 1994
Parasitism	Marine mammals taking discards from fishing vessels, fish from lines.	Chilvers and Corkeron, 2001
Mutualism	Dolphins and humans receive mutual benefits from cooperative fishing	Pryor *et al.,* 1990

Competition is often assumed between marine mammals and fisheries when marine mammals are shown to take the same prey as fisheries at relatively high consumption levels (e.g., Croll and Tershy, 1998). However, rigorous detection of competition is problematic (Lavigne, 1996). In many cases, fisheries may take a broad range of size or classes of prey, whereas marine mammals may be quite specific. Even when dietary overlap is demonstrated, there may not actually be spatial overlap in prey capture and thus there may not be competition. Whether one predator will therefore have a measurable impact on another is not clear. In fact, even for species that would appear almost undoubtedly to be in competition, such as the Antarctic fur seal and macaroni penguin in South Georgia, competition cannot be conclusively established (Barlow *et al.*, 2002). These species forage on similar size ranges of Antarctic krill, dive to similar depths and are restricted in their foraging range during the breeding season, for which one species has shown local population increases while the other has shown population decreases. However, although their foraging ranges showed some overlap, the concentrations of their foraging activity were separated spatially. In addition, although the sizes of krill eaten were similar, over the last 12 years their diets have diverged.

If competitive ability between species was unequal, then we might expect to see evidence of competitive exclusion, known as the “ghost of competition past”. The relatively dichotomous distribution of sperm whales and northern bottlenose whales within the Gully submarine canyon off eastern Canada may be indicative of competitive exclusion (Hooker *et al.*, 1999), although again this is difficult to establish conclusively and it might equally reflect differences in prey choice or diving ability.

The deaths of marine mammals caused by fisheries can at times be quite extensive (Harwood, 1999; Perrin *et al.*, 1994). In general such catches are unintentional, although in some cases nets may be set around schools of dolphins in order to target tuna found in association with these schools. In general such bycatch is problematic for fishermen, causing damage to nets, and as such fishermen are keen to reduce this problem.

Parasitism of cetaceans on fisheries may take place if cetaceans obtain benefits from fisheries, such as taking fish caught on lines, or taking discards. Cases of whales taking fish from longlines are becoming increasingly common (e.g., Ashford *et al.*, 1996), and such behaviour is viewed by the fishing industry as harassment. In the case of rogue sealions at least, targetted culling of specific individuals and the use of acoustic alarms appears to have gone some way toward solving this problem. In some cases such parasitic interactions are not viewed negatively by the fishing industry, such as the case of bottlenose dolphins in Moreton Bay in which one group of dolphins forages in association with trawlers (Chilvers and Corkeron, 2001).

In some cases, there may be true mutualism between cetaceans and fisheries, in which both derive benefit from their association. This has previously occurred between dolphins and Brazilian fishermen. Dolphins would herd fish toward fishing nets set nearshore, and fishermen would throw the dolphins a portion of the catch (Pryor *et al.*, 1990).

Depending on the type of threat posed by any fishery, the establishment of reserves can mitigate many of their impacts. The threat of predation (bycatch) would be reduced, decreasing exposure at an individual level. Similarly, any competitive role between fisheries and marine mammals would be alleviated. Parasitic or mutualistic interactions are less of a threat to cetaceans but when they occur coincident with competitive or predation interactions, may unfortunately have the opposite effect to that desired, serving to encourage spatial interaction between the two. These may therefore to some extent negate the beneficial effects of reserve creation.

THE IDEAL FREE DISTRIBUTION

The distribution of animals will be determined by that of the resources that they require but also by the distribution of their competitors (Tregenza, 1995). Animals influence each other's success through various density dependent processes including exploitation competition in which the quantity of available resources is reduced, by interference reducing fitness by factors such as wasting time in interactions with other foragers or disturbing prey, and the influence of density on predation risk. Ideal free distribution models predict the distribution of competitors having some density dependent relationship between their numbers and their fitness in different prey patches. Fretwell and Lucas (1970) originally described the theoretical distribution of predators such that animals should distribute themselves so each obtains the same food intake. Thus the 'suitability' of a particular part of the environment will decrease with an increase in the density of competitors occurring there.

Although there is some disagreement about the empirical success of the model, in many situations the ideal free distribution appears to agree well with data given its simple assumptions (Tregenza, 1995). For example breeding populations of Antarctic fur seals also appear to segregate themselves during foraging (Boyd *et al.*, 2002). Similarly, the limited time spent by bottlenose whales in apparently profitable prey patches has been suggested as potentially due to the need to sample alternative patches (Hooker *et al.*, 2002b). In fact, even fisheries can be demonstrated to follow ideal free distributions to the extent possible given the information available to them (Whitehead and Hope, 1991).

The oceans are an extremely heterogeneous environment, consisting of prey patches of varying sizes and densities. These prey patches are often associated with oceanographic features, which could be used to identify foraging hotspots (Hooker and Gerber, 2004). If we assume that predators will distribute themselves in order to maximise their food intake rate, then, based on competitive interactions, the establishment of conservation areas within which fishing is prohibited should cause increased marine mammal densities within those areas and reduce their densities in areas in which competitive interactions with fisheries continue (outside reserve areas). In fact, this would present a test of whether competitive interactions exist between the two – whether the distribution of marine mammals is altered by the removal in some areas of potential competing fisheries.

HOTSPOTS AND ESTABLISHMENT OF PROTECTED AREAS

The identification of foraging hotspots for marine predators could be achieved via marine mammal survey work, associations with oceanographic features (see Dubroca *et al.*, and Millot, this volume), and through associations with fisheries. The Gully, a submarine canyon offshore of eastern Canada, appears to be a hotspot for cetaceans, which show elevated abundances in the vicinity of this feature compared with levels in surrounding regions (Hooker *et al.*, 1999). The distribution of cetaceans here is governed primarily by bathymetric features and so could be well defined by spatial boundaries. Three types of oceanic hotspots have been identified: (1) static systems, such as that in the Gully, determined by topographic features, (2) persistent hydrographic features, such as currents and frontal systems, and (3) ephemeral habitats, shaped by wind- or current-driven upwelling, eddies, and filiaments (Hyrenbach *et al.*, 2002). The last will be difficult to establish protection for, although over some time scale or over a large enough spatial scale, protection could be afforded to encompass the appearance of such features. For example, the upwelling to the south of Monterey Bay is variable in location interannually but could be encompassed over, for example, a ten-year timespan by extending boundaries over a larger spatial area. The overlaying of maps of different marine predators' (including the fisheries') foraging habits, together with a basic knowledge of their diet (e.g., piscivory or teuthophagy), broader ecosystems (e.g., upwelling dynamics), and habitat variability (e.g., persistence and spatial variation over annual and decadal cycles), should allow researchers to identify various hotspot features.

Assessment of socio-economic impacts in terms of fisheries overlap should then allow the optimal location of reserve areas in order to minimise management conflicts. In the southern Gulf of California, multiple levels of information on biodiversity, ecological processes, and socio-economic factors were used to establish a network of reserves that would cover a large proportion of habitat and reduce social conflict (Sala *et al.*, 2002).

MONITORING SUCCESS

The establishment of marine reserves has shown widespread benefits to fisheries outside those reserves (Gell and Roberts, 2003). Much less is known about the ability of reserves to reduce conflicts between marine mammals and fisheries. Will such reserves provide a relatively pristine foraging ground for marine mammals within reserve boundaries, causing higher foraging densities within reserve areas, and reduced competition with fisheries outside reserves? Unfortunately such information on cetacean distribution prior to and since the establishment of fisheries does not exist. For most of the last century at least, fisheries have been relatively ubiquitous throughout most of the world's oceans. The test of such a hypothesis will therefore depend on the establishment of areas encompassing foraging hotspots which are then closed to fishing, and on the close monitoring of cetacean distribution resulting from this reserve implementation. In general, however, given the basic ecological theories described here, I would propose that in addition to general ecosystem benefits (e.g., Roberts, 1997), reserve designation is likely to help reduce fisheries and marine mammal conflicts.

Potential competition with fisheries? The case of sperm whales and beaked whales

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INTRODUCTION

Some have proposed that cetacean compete with marine fisheries and reduce the available yield. These types of arguments have been made for over 100 years. However, no real data have been provided to show that this is in fact the case. These ecosystems are very complex and numerous species within each system may be feeding on the same prey. Total annual catches by cetaceans have been estimated to exceed those of all world fisheries combined, with catches by cetaceans several hundred million metric tons compared to fisheries catches around 95 millions metric tons in 2000 (FAO, 2002). Nonetheless, it is not clear that cetaceans and humans are generally competing for the same species (see other contributions, this volume).

In some cases however marine fisheries and cetaceans compete for the same prey. In this paper, I will review possible future conflict of new marine fisheries and their impacts on over-exploited and endangered cetacean populations and other small local populations of non-endangered cetaceans. Two cases of different possible future conflicts will be examined: (1) endangered populations of sperm whales, and (2) local populations of beaked whales. To avoid these potential conflicts, it is recommended that experimental Marine Protected Areas (MPAs) be established in known hot spots for various populations of cetaceans when their resources are underutilized.

CASE STUDIES

Endangered Populations of Sperm Whales

Commercial used of sperm whales started in 1712 off New England and by 1820 they were being exploited on a global scale (Philbrick, 2000). Today most populations of sperm whales have been over-exploited throughout their range as a result of early Yankee whaling, commercial land stations around the world and worldwide pelagic whaling operations. Tens of thousands of sperm whales were taken in the 1960s and 1970s by illegal Japanese stations operations from Japan (Kasuya and Miyashita, 1988; and Kasuya, 1999) and illegal USSR pelagic operations worldwide (Zemsky *et al.,* 1995; Brownell *et al.*, 2000). The populations of sperm whales in two regions (Eastern Tropical Pacific [ETP] and western North Pacific) are examined in more detail below from the standpoint of their conservation status, feeding habits, and competing fisheries.

Sperm whales and squid off California, in the Gulf of California and off Peru and Chile

Over-exploitation has been documented in the eastern North Pacific (offshore from California) from Soviet pelagic whaling operations (Brownell *et al.*, 2000) and in the southern ETP from

Peruvian land station operations. Both operations greatly reduced the populations of sperm whales in these regions. Current population estimates in the California region (Eastern temperate eastern North Pacific) and ETP are 26,000 (Wade and Gerrodette, 1993) and 24,000 (Barlow and Taylor,1998) respectively. Some sperm whales, especially males, may move between these areas and the number of populations in each area is still unknown.

Sperm whales offshore of California mainly feed on Giant squid, *Dosidicus gigas* (Rice, 1963). Based on visual observations in the lower Gulf of California sperm whales there also feed on the *D. gigas* and sperm whales killed off Peru and Chile had been mainly feeding on *D. gigas* (Clarke *et al.*, 1988). However, during an El Nino period Smith and Whitehead (2000) found the 62% of the beaks from sperm whale fecal samples collected off the Galapagos Islands were from histioteuthids. These differences off South America are most probably related to sampling during El Nino and non El Nino years.

In both the southern Gulf of California, Mexico and off the coast of Peru large squid fisheries have developed in recent years. Giant squid have been exploited in the Southeastern Pacific since 1984 but the catches fluctuate by orders of magnitude between years. The low and high catch in metric tones in 1984 and 1994 is 16 and 192,831 respectively (Smith and Whitehead, 2001). In the Gulf of California, large-scale Japanese-Mexican joint ventures commenced fishing for giant squid in 1979. The small local fleet landed 300 tons in 1977. The catch increased to 22,000 tons in 1980 but then stabilized at below 500 tons since 1982 (Ehrhardt, 1991). Giant squid from these two regions are probably two separate populations (Clarke and Paliza, 2000). Without good information on the population dynamics of the squid taken in these fisheries, including population structure, it might to possible to reduce the squid populations to the point that the remaining biomass would be insufficient to allow the sperm whales to recover to their maximum potential.

Sperm whale and squid in the western North Pacific

Over-exploitation of sperm whales in the western North Pacific has occurred because of large catches in Japan and Soviet land stations operations. Almost 50 years ago, squid beaks were collected and identified for the first time from sperm whales in the western North Pacific, offshore from the Kuril Islands (Akimushkin, 1955; Betesheva and Akimushkin, 1955). However, in spite of the thousands of sperm whales killed by catcher vessels operating from the numerous lands stations in Japan and in the Kuril Islands by the USSR, no detailed account is available outlining what squid species are utilized by sperm whales in this area.

Species and Populations of Beaked Whales

The two best-known species of beaked whales are the northern bottlenose whale in the North Atlantic and the Baird's beaked whale in the North Pacific. A well-studied population of around 100 plus northern bottlenose whales appears to be resident in the "Gully". These bottlenose whales appear to feed mainly on a single species of squid. Baird's beaked whales off eastern Japan are migratory and number in the 1,000s (Miyashita). During the summer months when these whales are hunted offshore of central Japan their diet mainly consist of deep-sea fishes taken along the 1000 m deep curve.

MacLeod *et al.* (2003) reviewed the published data on the dietary preferences of beaked whales based on stomach contents analysis. Most of the available data is for only three of the six beaked whale genera (*Hyperoodon*, *Mesoplodon* and *Ziphius*). In general, some *Mesoplodon* spp. feed mainly on fish and some species only fish but both species of bottlenose whales and *Ziphius* feed on primarily on eighteen families of cephalopods and rarely had remains of fish in their stomachs. However, northern bottlenose whales taken off Labrador and Iceland commonly feed on fishes (Benjaminsen and Christensen, 1979).

Unfortunately, McLeod *et al.* (2003) were not able to include the results of our paper (Walker *et al.*, 2002) on the diet of *Berardius* in their analysis because ours was published just months before theirs. In the Pacific off central Japan, *Berardius* fed primarily on benthopelagic fishes (81.8%) and 18.0% cephalopods consisting of thirty species in 14 families. The main fishes consumed by *Berardius* in Japanese waters are from the families Moridae and Macrouridae and the most important squids were Gonatidae and Cranchiidae. Based on their wide range of food habits and the known migratory behavior, Baird's beaked whales may be the best generalists among the beaked whales.

DISCUSSION

Over a 1,000 living species of cephalopods are described but only around 650 of these species are currently recognized (Boyle, 1983). About 50-60 species of cephalopods in 28 families are known to be important in the diets of cetaceans (Clarke, 1996c). Some of these cephalopods like *D. gigas* form an important part of the diet of other top marine predators like swordfishes, striped marlins, and larger tunas (Nesis, 1983). As sperm whales are efficient hunters of squid, it is not surprising the a few new species of squid were based on specimens collected by sperm whales (Joubin, 1895; Robson, 1925). The role of cephalopods in the world's oceans was recently reviewed (Clarke, 1996b).

During the past 25 years, various rough estimates of the annual worldwide consumption of cephalopods by the world's sperm whale populations are in the range of 100 to 320 million metric tons (Clarke, 1977; Clarke, 1996; Whitehead, 2002). However, these estimates are too high because in all cases the number of sperm whales worldwide is grossly overestimated. Whitehead (2002) reviewed estimates and revised the current global sperm whale estimate down to 361,000 (CV = 0.36) whales. The previous total estimate was 1.9 million sperm whales. However, based the method described by Clarke (1996) with the smaller population estimate (361,000 sperm whales X 15 tones [mean weight] X 2 - 3 times [daily feeding rate %] X 365 days) between 39.5 and 59.3 mt of cephalopods are eaten annually by the sperm whales. This value is approximately half to two-thirds of the total annual catch of all fisheries by all countries combined. Even this downwardly revised estimate of cephalopod consumption by sperm whales may be too high. The daily feeding rate (per cent of body weight and the number of days spent feeding) on an annual basis is not well understood. However, the pre-exploitation global population of sperm whales probably exceeded one million whales and the magnitude of cephalopods eaten that time was about five times what sperm whale consume today. Did the massive reduction of sperm whales worldwide increase the available standing stock of cephalopod resources?

BEAKED WHALES

The 20 species of beaked whales in five genera (Dalebout *et al.*, 2002) represent the second most diverse group (ecologically and biogeographically) of cetaceans after the dolphins. Over 30 percent (7 species) of these 20 beaked whales were first described during the past one hundred years. The biology of beaked whale is poorly known but, based on available data, they exhibit very interesting biological traits, including reversed sexual dimorphism, higher mortality rates in females, small testes size in all species with data, and limited geographic distribution by species and sometimes small local populations. Some beaked whales also have apparently limited range of prey selection.

Beaked whales as a family are found over a wide geographic range but individual species have limited ranges with some being confined to single ocean basins like the Northern bottlenose whale in the North Atlantic and Baird's beaked whale in the North Pacific. Others are found in even smaller areas like the Pygmy beaked whale in the ETP. Only the Cuvier's beaked whale has a worldwide distribution and species, *M. densirostris*, is found worldwide in the tropics. Four other species, *B. arnuxii*, *Tasmacetus*, *M. layardii*, and *M. grayi* are found wide spread in the cooler waters of the Southern Hemisphere.

Whitehead *et al.* (2003) noted that differences in niche breadth in of the mesopelagic teuthivores might be closely related to their movement patterns. Both sperm whales and elephant seals have large ranges and as such should encounter the greatest variety of squid species but species with smaller total ranges like the northern bottlenose whales specialize in specific items like *Gonatus*. MacLeod *et al.* (2003) reported on evidence of niche separation and geographic segregation between three genera of beaked whales. Competition for food among the beaked whales is probably not a major issue because of the non-overlapping feeding areas (niche separation) and geographic segregation of the 20 beaked whales.

Important feeding areas and perhaps resting areas of beaked whales may have static features as the most important character of the areas. These areas include features like submarine canyons, like the gully off Nova Scotia, and seamounts. These are important places where prey of these cetaceans routinely concentrate.

NEED FOR NEW MPAS

New ideas are needed on how to conserve pelagic hot spots for top trophic predators like sperm whales and the numerous species of beaked whales. These hot spots are not homogenous and their resources are not limitless. Core protection areas may be needed primarily because of the increasing interest in underutilized marine resources.

Hooker and Gerber (2004) argued that the need for pelagic marine reserves is becoming increasingly apparent and that marine predators may be most effectively used as indicator species for the underlying prey distribution and ecosystem processes. Cetaceans will be the easiest of these top predators to monitor and determine their critical habitat needs. Cetaceans may also best serve as the “Flagship Species” to help establish MPAs.

CONCLUSIONS

- New ideas are needed on how to identify and conserve pelagic hot spots where cetaceans utilize squid and or deep sea fishes.
- A GIS process that plots available data including locations of cetacean sightings, fishing areas of the prey species taken by these cetaceans and depth information can to used to better identify possible hot spots.
- These potential hot spots could then need to be surveyed with sighting cruises to better define the main areas of abundance.
- Possible MPAs can then be proposed within countries EEZs or on the high seas local regions on the high seas like that established in the “Gully” for northern bottlenose whales south of Nova Scotia.
- Some new pelagic MPAs for certain cetacean populations may not have to be necessarily large and it may be sufficient to establish some new MPAs as small as the one in the “Gully” for northern bottlenose whales.
- Establishing MPAs within EEZs will not be as difficult as proposing MPAs on the High Seas. We know from the difficulties in establishing the UN driftnet moratorium in 1991, that creating pelagic MPAs on the High-Seas will be extremely difficult. Strong political will and public pressure will be needed to needed to establish pelagic MPAs.
- MPAs might first be established as moratorium on activities such as fishing for specific target species and naval operations (LFA)
- Pelagic MPAs will be of no value without management and enforcement. These protection measures will be of even more important as other marine resources are depleted.
- Mapping of hot spots, especially in static systems could also be important to protect beaked whales from Naval operations

The feasibility of establishing trial MPAs for beaked and or sperm whales (*Ziphius*, *M. densirostris* and *Physeter*) in the Mediterranean or in some other EEZ area should be studied.

The cetacean world as seen by physical and biological oceanographers

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1. INTRODUCTION

Since the dynamical and biological fields are at the basis of any food web study in oceanography, the major aim of our contribution is to present the up-to-date knowledge that may be useful to the elaboration of cetaceans-related programmes to be elaborated in the Mediterranean Sea. We suggest, in conclusion, a few directions for new sampling strategies.

Our disciplines (physics and biology) are the sole in oceanography to benefit from autonomous sensors, either deployed in situ or embarked on satellites., allowing collection of time series and a correct estimation of the space and time scales of the food web lower levels, and showing the complexity of the "cetacean world" (and that of human fisheries as well!). Can cetaceans estimate this complexity as well as fishermen do (or could do with the available technology)? Does this complexity constitute, for one and/or the other predator, a random parameter? These questions are some of those that we raise, as skeptics, in an annex.

2. THE FUNCTIONING OF THE MEDITERRANEAN SEA

Although the actual functioning of the sea is relatively complex, it can be thought as mainly resulting from a fundamental mechanism, the water deficit and its associated dense water formation process, and from two major phenomena driving the circulation, the Coriolis effect and the mesoscale activity.

The dense water formation process

The Mediterranean is a semi-enclosed sea that is characterised by an excess of evaporation over precipitation and river runoff in both the western and the eastern basins. The tendency for a difference in level between the Mediterranean and the Atlantic Ocean leads Atlantic Water (AW) encountered at the surface west of Gibraltar to flow into the sea at a rate of ~1 Sverdrup (1 Sv = 10^6 m^3/s, i.e. ~1000 times a major Mediterranean river flow). Typical values for AW at Gibraltar are T ~15-16 °C, S ~36-37 and σ ~26-27 (densities of 1.026-1.027). While progressing within the sea, the incoming AW forms a 100-200-m thick surface layer that is continuously modified, mainly due to interactions with the atmosphere and to mixing with resident waters. All along its course, AW is warmed (up to 20-25 °C in summer) or cooled (down to ~13°C, or locally less, in winter) but, overall, it becomes saltier (up to 38-39), hence denser (up to 28-29). In the fall, AW has thus been pre-conditioned (densified) but it is still at the surface; the euphotic zone is mainly nutrient-depleted, and a thin chlorophyll maximum is encountered at 80-120 m. In winter, cold and dry air masses entrained by relatively brief episodes of strong northerly winds induce a marked evaporation of AW (increase of salinity and loss of latent heat) and direct cooling (loss of sensible heat) which dramatically increase its density and make it sink.

Sinking occurs in specific zones located in the northern parts of both the western and the eastern basins according to two different processes. One process takes place on the continental shelves where waters are markedly cooled because the relatively shallow bathymetry does not represent a large reservoir of heat. However, since shelf waters are relatively fresh in general (due to river runoff), they cannot reach a density allowing them to sink deeper than a few 100 m. Such waters represent relatively small amounts, and are not directly important for pelagic species since the nutrients which they possibly transport at depth cannot be exploited directly. The other process occurs offshore in some subbasins, such as the Liguro-Provençal (subbasin). Fundamentally, densified AW sinking there mixes, sometimes over the whole depth (2000-3000 m), with denser water(s) lying underneath and thus forms new specific intermediate or deep Mediterranean Waters (MWs, T~13-14°C, S~38-39, $\sigma > 29$). Because the denser waters are nutrient-enriched after some stay at depth (remineralisation), mixing on the vertical brings nutrients into the euphotic layer and allows phytoplankton spring blooms as soon as the amount of light and stratification are sufficient. The zones of dense water formation are characterised all year long by a reduced stratification and a doming structure that has nothing to do with an upwelling process: the major process there on a yearly scale is a downwelling (of dense water). Note that the overall formation rate of the MWs is ~90% of the AW inflow at Gibraltar (10% being evaporated), among which ~3/4 is formed in the eastern basin.

The Mediterranean Sea is thus a machine that transforms AW into MWs. As dense water formation is a dynamical process that is essentially seasonal, the offshore zones of sinking are characterised by a marked biological signal at seasonal scale. Although dense water is formed in winter, the phytoplankton must, for a while, remain in the euphotic layer (i.e. surface waters must have re-stratified) and receive enough light, both conditions occurring only in early spring. This is evidenced in the Liguro-Provençal by the monthly composites of satellite ocean colour (chlorophyll integrated over a few 10 m) images (not well reproduced here in grey tones, but available in colour on http://www.me.sai.jrc.it) in Figure 1 (see also Bosc *et al.*, 2004). Although deep mixing occurs over a relatively wide area, the distribution of the phytoplankton bloom is by no means homogeneous spatially, as seen on Figure 2, due to mesoscale phenomena (see also Morel and André, 1991, and Levy *et al.*, 1999). Note that this zone is the one where cetaceans in the western basin are generally thought to be concentrated (e.g. Guinet *et al.*, this volume). Nowhere else, do the dynamical processes themselves display such a dramatic seasonality, and biology there is modulated on a seasonal scale mainly by light availability and stratification. For instance, in the Alboran, although the upwelling associated with the AW inflow along the Spanish coasts is quite permanent (nutrients are always available in the euphotic layer), the most intense primary production occurs in early spring too. It must be emphasised that, on a yearly average, primary production in the Alboran is higher[1] than in the Liguro-Provençal (Bosc *et al.*, 2004).

The circulation

We shall focus on the AW circulation that is of major concern for cetaceans.

To describe (intuitively!) the overall circulation of AW in the sea, let us consider the monthly composite[2] infrared image of January 1998 (Figure 3) that is representative of all winter months for what concerns the temperature values. Temperatures range from ~18°C along the coast in the eastern basin to 15-16 °C west of Gibraltar, ~13°C in the dense water formation zones of the Liguro-Provençal and ~10°C or less for the rivers outflows in the Adriatic and for the whole

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[1] High values permanently associated with the major rivers outflows on these images are partly due to suspended mater, while those around the Kerkennah islands (Tunisia) are due to the few-metre depths there (the signal comes from the bottom).

[2] A monthly composite image has the advantage of giving an overview of the surface temperature in the whole sea with the same colour table and without any cloud. It has the disadvantage of giving a blurred vision of moving mesoscale features.

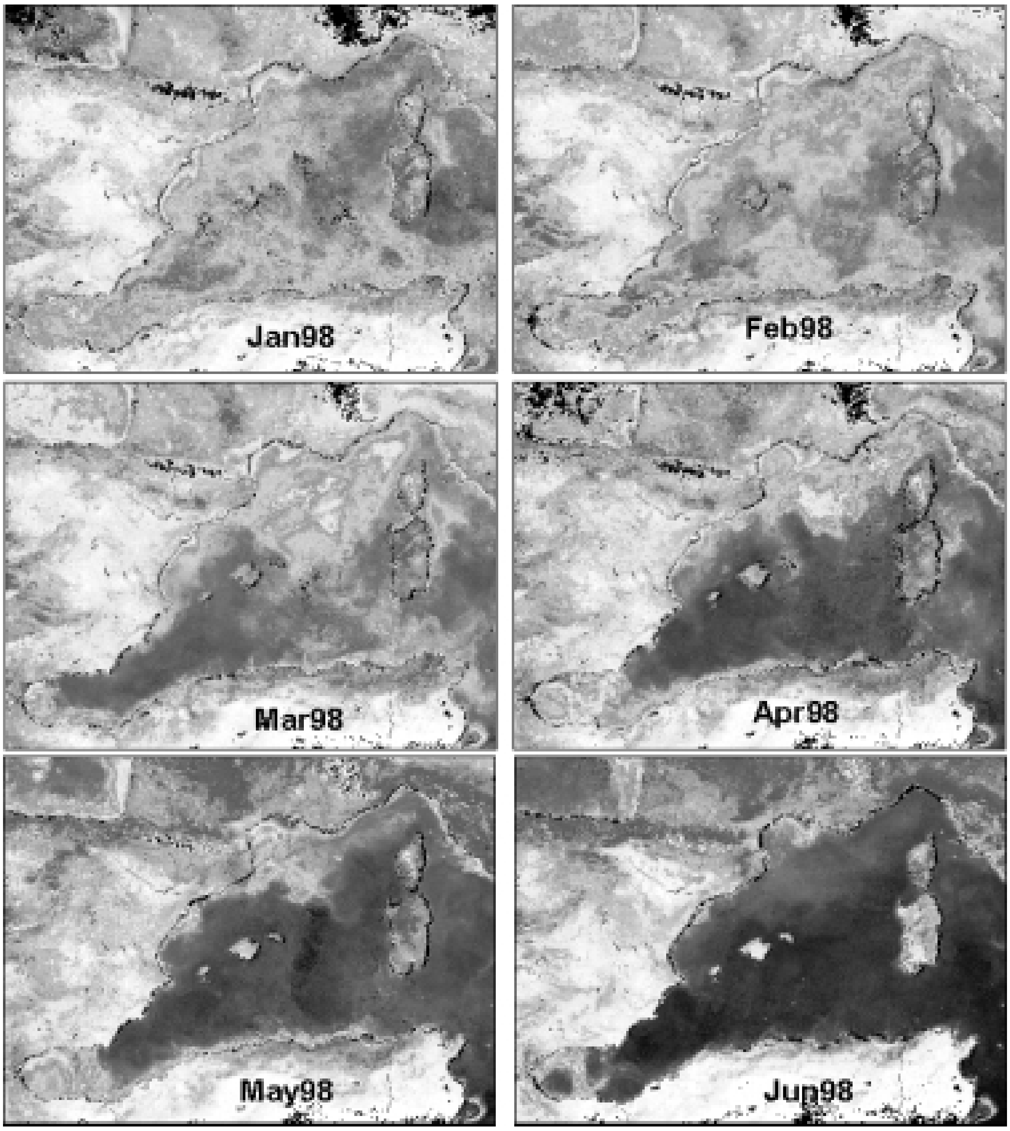

Fig. 1. Monthly composites of the chlorophyll concentration distribution from January to June 1998 (SeaWiFS images processed by the JRC).

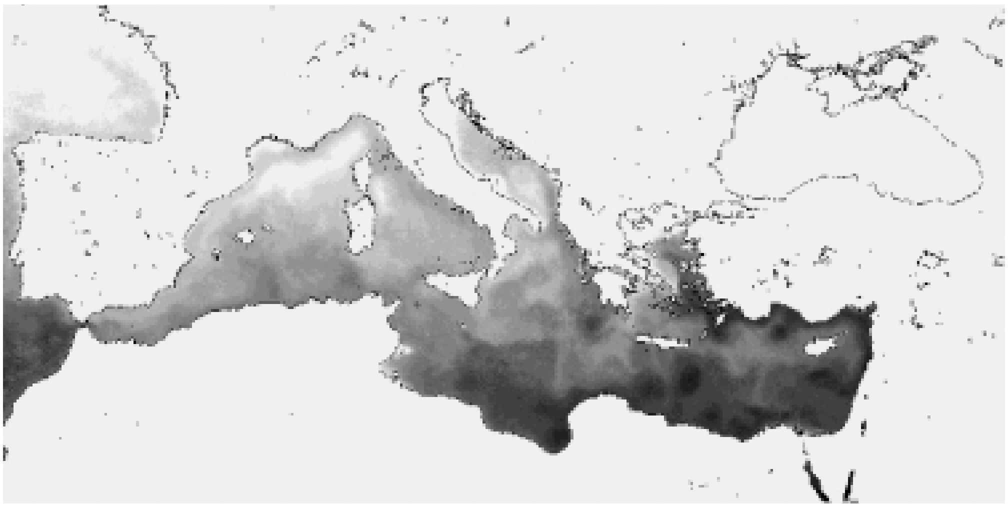

Fig. 2. Chlorophyll concentration distribution on 26 February1998 (SeaWiFS images processed by the JRC).

Black Sea. This image is also representative of all months and years for what concerns most of the overall AW circulation features, since most of them do not vary seasonally in a significant way.

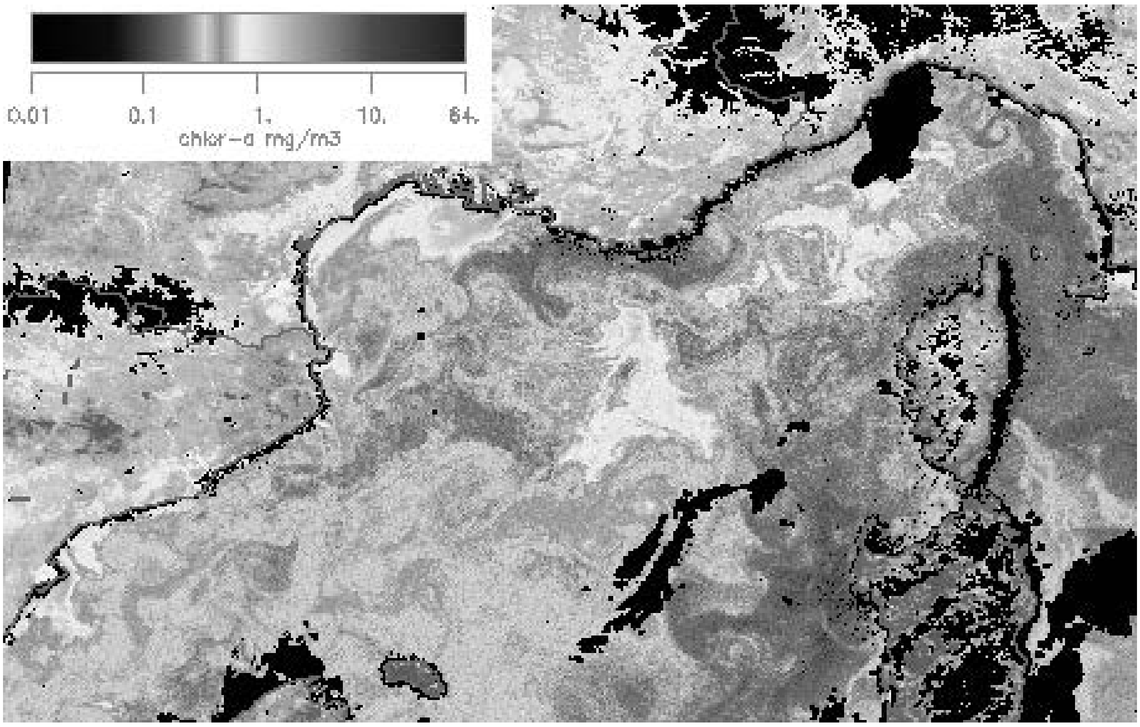

Fig. 3. Distribution of the sea surface temperature (SST), monthly composite of January 1998 (NOAA/AVHRR image processed by the DLR). The temperature increases from light to dark grey.

Overall, and due to the Coriolis effect, all waters that are forced to circulate at basin scale tend to follow, in the counter-clockwise sense, the isobaths at their own level. Therefore, the flow of AW tends to form almost permanent basin-wide “gyres” a few 10 km wide along the upper continental slope. This simple diagram is complicated by the fact that the flow of AW in the south of the basins is unstable in some specific zones (there, we identify the flow with the Algerian Current and the Libyo-Egyptian Current), generating mesoscale features that are mainly “eddies”. These eddies reach diameters of 100-200 km, sometimes up to ~250 km, they propagate at up to a few km/day and some have lifetimes up to ~3 years at least. They sometimes extend down to the bottom (several 1000 m), hence following the deeper isobaths and finally separating from their parent current (where the direction of these deeper isobaths diverges from that of the upper continental slope). Together with wind-induced eddies having similar characteristics (such as Ierapetra and Pelops) they entrain AW and MWs towards the central part of the basins.

The schematic diagram in Figure 4 is from Millot and Taupier-Letage (2004). It summarises the diagrams proposed by Millot (1999) for the western basin and by Hamad *et al.* (2004) for the eastern one. The permanent currents that flow alongslope and are relatively stable (in the northern parts of the basin mainly) represent the clearest portions of the basin-wide gyres. They are a few 10 km wide, transport ~1 Sv each, and are a few 100 m thick, the maximum velocity in their core being of ~1 knot. These currents skirt north of the zones of dense water formation, thus leading to the doming structure previously mentioned. These zones are relatively quiet in summer and turbulent in winter (down to the bottom, horizontal scale of a few 10 km, velocities of a few 10 cm/s). Their biological impact has been mentioned in the previous section. Transports within the largest mesoscale eddies in the southern part of the basins can be all year long of several Sv, furthermore when they extend down to the bottom, with maximum velocities still reaching ~1 knot. Such eddies are relatively intense in the zones specified by ΣA_E, ΣL_W and ΣL_E where they tend to accumulate and to induce a marked biological variability. First, the similarity between the thermal (dynamical) and visible (biological) signatures of such eddies (Figure 5) shows that, at mesoscale, the dynamics drives the biological response (at least at the phytoplankton level). Second, similar images show that such eddies induce a significant biological response at scales up to seasonal and even interannual (see also Taupier-Letage *et al.*, 2003).

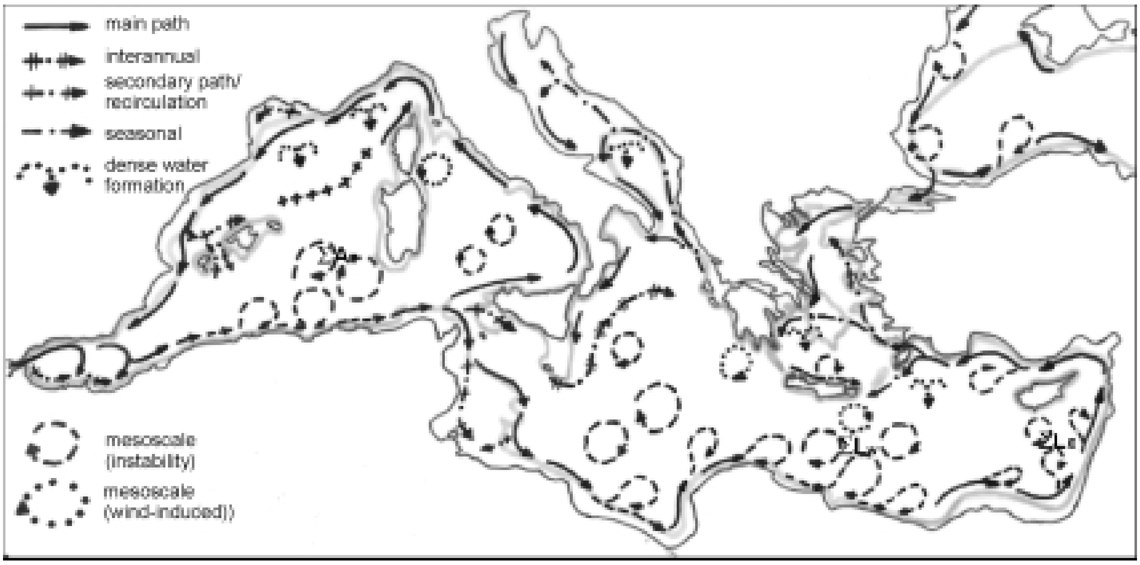

Fig. 4. The surface circulation (of AW, mainly along the 200-m isobath) in the Mediterranean (from Millot and Taupier-Letage, 2004).

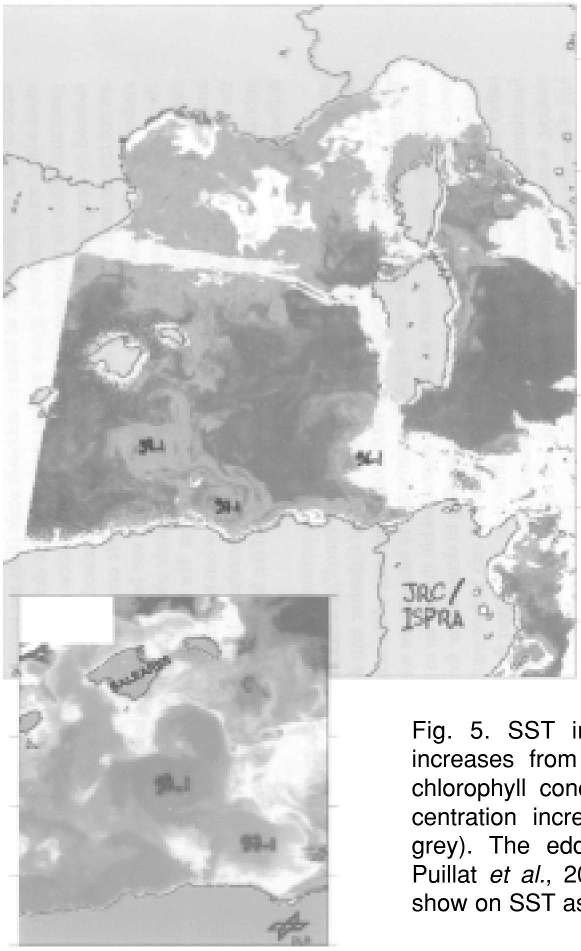

Fig. 5. SST image (top; temperature increases from light to dark grey) and chlorophyll concentrations (bottom; concentration increases from dark to light grey). The eddies are identified as in Puillat *et al.*, 2003 (eddy 96-1 does not show on SST as clouds cover the area).

Inertial currents

When the seasonal stratification (mixed layer and associated thermocline) develops, the wind temporal variability (mainly) creates oscillatory currents of a few 10 cm/s at the Coriolis period, i.e. ~17h30' at 43°N and ~20 h at 36°N. These currents are sometimes associated with vertical oscillations of a few 10 m at the thermocline level that propagate from the coast. They induce of a few km loops that are superimposed on any other current, and hence increase the difficulty of interpreting a current measurement (i.e. what is it composed of?). Of course, the inertial currents drive the trajectory of any drifting object or animal swimming or not (i.e. plankton and nekton). This is demonstrated by the trajectories of drifting buoys (see Figure 13 of Taupier-Letage and Millot, 1986), and by those of whales for instance. The trajectory of a whale tagged with an ARGOS emitter and located at the maximum frequency, i.e. several times per day, describes loops at the Coriolis period (Mouillot and Viale, 2001) that, although actual, are not perceived by the animal. When positions are not acquired with a frequency allowing the filtering out of these oscillations (i.e. at once or twice a day only), they induce noise (i.e. an incomprehensible signal) in the data set and generally lead inexperienced authors to assume that the strange resulting pattern results from erroneous positions (i.e. they reject more positions than we do).

3. Discussion

There are indubitable facts about the displacements of animals at seasonal and ocean/basin (100s-1000s km) scales, i.e. migrations. While the causes of animal migrations are generally well accepted, how do animals navigate to accomplish their migrations? In case animals have sensors that we are unable (yet) to imagine and/or reproduce, can we assume that they use these sensors to navigate rationally (i.e. not randomly) to find food at mesoscale (several 100 km) in the open sea/ocean? Are the data sets already collected about these displacements correctly analysed, or at least could they be analysed in a different way? Do we assess adequate data sets about the links between the behaviour of the animals and their physical environment?

Part of the misunderstanding might be due to the frequent "anthropomorphic" formulation of the observations. This is the case for instance when papers say that an animal is "*taking advantage of the current*" to accomplish its migration. In the open sea, without any visual help from the bottom or the coastline, the animal has no way to detect and "*know the current*"[3]: we only observe that the animal is drifting in the current, just as a coconut would do.

To provide examples about how a given data set can be analysed in quasi-opposed ways, let us consider two papers dealing with loggerhead and green sea turtles shown, from a set of ARGOS positions, to move westward, respectively in the central South Atlantic (Luschi *et al.*, 1998) and in the central North Pacific (Polovina *et al.*, 2000). Routes followed by several turtles equipped at Ascension Island that are similar and "*show an impressive coincidence with the current direction*" are interpreted by the authors as deliberate "*migrations taking benefit of the current and remaining downstream from the island*" towards a common target that is said to be the shortest course for reaching the Brazilian coast. Noting that turtles have "speeds" of the order of the speed of the current (when expressed in similar units!), we rather consider that the turtles drift, at least for most of their displacement, with the current (passively, as that they cannot "feel" it), and finally reach the Brazilian coast ... just because this is the main path of the current! Why not then build a drifting buoy having the density of a turtle, release it together with turtles and compare the various trajectories? In addition, why not try to specify from where the turtles found at Ascension are coming, and/or why not equip turtles in Brazil to evidence backwards migrations toward Ascension, a much difficult "target", if any? In the second example, turtles are said to swim against the current (but how can they feel it?), modifying their route according to the current intensity (could it rather be that the variations observed are due to the combination of the variations of the current intensity plus those of the swimming activity of the turtle? i.e. the turtle would be more or less entrained by the current), and to concentrate wilfully close to temperature fronts.

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[3] In the same way, a person walking in a train at night and without any visual clue does not experience more difficulties in walking "upstream" than "downstream". Provided the train maintains a constant speed, it is even impossible for that person to tell in which direction the train is heading; and that person perceives a deceleration in one direction exactly as an acceleration in the other direction!

Why not assume that turtles are entrained by converging processes towards these fronts and that they will tend to remain there either passively (as any drifting material or plankton), or actively because their food is concentrated there?

Actually, stating that the animals are located where the food is the most abundant, or that a given animal is preferentially found close to thermal or ocean colour fronts, or any other environmental feature can be misleading.It implies that there is an active strategy to find the adequate feature; but how can animals proceed, not having any information about the spatial distribution, such as that provided by satellites? Determining gradients is not an easy task (see annex), and to establish that there is more strategy than luck in the location of an animal in its preferred environment will require numerous tracking with a very high temporal and spatial interval.

Indeed, significant improvement will come from tracking at high temporal resolution for any displacement where animal sight is invoked, as it will provide information on potential differences in trajectories or behaviour between day and night, and between clear and cloudy days as well, provided the cloud cover can be monitored finely enough. This will require many analyses of individual tracks, simultaneously with that of environmental parameters. Although there are definite improvements, as with CTDs carried by sea lions, we think that there is still a long way to go.

If we take the specific example of fin whale distribution in the Mediterranean, specialists agree that fin whales aggregate offshore during summer in the northwestern Mediterranean (e.g. Nortobartolo di Sciara *et al.*, 2003; Littaye *et al.*, 2003; Guinet *et al.*, this volume). But do we have the adequate data sets to establish that fin whales do migrate in winter? And where? As nearly all efforts to look for them have been carried out only in this part of the basin and only in summer, a complete and reliable picture of their distribution is still lacking[4]. In addition, satellite imagery shows that the Liguro-Provençal is not the most productive place (in terms of primary production, see Figure 2; and Bosc *et al.*, 2004) of the Mediterranean. The Alboran is the most productive place, and regularly so (due to a quasi-permanent upwelling), but then why whales do not concentrate there, if they were able to "guess" or use a strategy to find richer zones? It is hard to conceive that they can know/guess where better trophic conditions are, when considering the tremendous spatial and temporal variability at mesoscale evidenced on satellite images. We rather imagine a simple lucky-unlucky foraging search.

As a final illustration of the lack of adequate data sets about Mediterranean cetaceans, we note that a few species have been only observed in the Mediterranean … once stranded.

4. SUGGESTED DATA COLLECTING STRATEGIES

It is clear that the migrations of cetaceans in the global ocean are driven by feeding and breeding needs, and are mainly directed poleward-equatorward. Such migrations can be triggered by environmental parameters (water temperature optimum vs. food availability), and the navigation based just on the sun observation and/or on the direct perception of the temperature (additional hints such as magnetic field not excluded). We think that the high population densities of cetaceans in the Mediterranean result from the fact that the place is convenient for both feeding (sufficiently rich) and breeding (sufficiently warm).

Now, with the help of numerical simulations (which allow predicting primary production and hence prey abundance), and of satellite localisations, We can start testing many hypotheses about cetacean's ecology.

We should continue to locate the animals using well-tested visual surveying techniques. An objective sampling strategy using this technique is i) to look for cetaceans everywhere, i.e. not only in places predicted as favourable, and over a period as long as possible (a full year at least) and then ii) to confront these observations with the satellite contemporaneous observations. Such a strategy could be deployed in two feasible steps.

The first step is related to the issue of the fin whale distribution during winter and their alleged

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[4] Facing the same uncertainties about the distribution of dolphins (*Tursiops truncatus*) during wintertime, acoustic surveys carried by F. Dhermain (GECEM) showed that, most probably, there was no seasonal change in the population density.

capacity of migrating rationally to find most convenient places for feeding. In the western basin for instance, the phytoplankton bloom occurs earlier in the south (it begins in November – December, e.g. the January and February images on Figure 1), and is especially strong within Algerian eddies (Figure 5, Taupier-Letage *et al.*, 2003). Meanwhile, the north is relatively poor (the bloom begins offshore in March –April). According to the hypothesis that whales in the western basin migrate to find more convenient places that they should be aware of -or be capable of- finding, they might be more numerous in the south during winter. Given the appropriate tracking of eddies that can be done, a fast and efficient cruise could be designed to estimate the abundance of fin whales in such eddies and compare it between late fall - early winter and late winter - early spring.

The second step would be to conduct a more objective experiment and make regular observations on a regular route during a sufficiently long period. We are currently elaborating a CIESM project aiming to install a thermosalinometer and a fluorometer (plus a meteorological station) on a Trans-Mediterranean ferry, which would provide an excellent platform for a cetacean observational program. Weekly routes from Marseilles to Algiers and from Marseilles to Tunis are scheduled, and arrangements could be discussed with the ferry company to host observers.

Finally, in order to obtain objective and regular monitoring, why not set hydrophones, fitted with adequate filtering and recording software and devices, on top of dedicated mooring lines? The recorded time series might allow identifying and counting several species of cetaceans, and would provide months to years long observations, whatever the meteorological conditions. It would be especially efficient in relatively small areas such as Gibraltar, allowing monitoring the passages between the Mediterranean and the Atlantic Ocean, and indicate in the end whether the animals are migrating or not. It would also be efficient in places where moorings are continuously maintained and regularly operated, such as in the Ligurian, or in places where operations are scheduled for a limited period, such as in Egyptian waters in the forthcoming years.

ANNEX

We list here some of the questions we have about migrations processes and mechanisms. These are just “naïve” questions, raised by the fact that we probably have an apprehension of the physical environment different from that of the other participants in the workshop, and surely by the fact that, mostly unaware of the “incredible abilities” of the animals, we always tend to look first for the simpler explanation. The goal of this annex would be reached if it contributed to induce some elements of doubt.

Migration in the ocean

Let us first consider the fish said to migrate across an ocean back and forth such as salmon (back to their own river after a trip several hundred km long in the open ocean), eel (to and from the Sargasso Sea) and tuna fish (various trips worldwide). We focused on the most recent papers dealing with salmon which are the most numerous since i) several sensors and mechanisms have been invoked for salmon, ii) it can be captured for tagging and recaptured in rivers, and iii) it has been grown in farms and hence studied for a while. In addition, the “alleged” migration of eel is more difficult to document since it involves a larval stage, and it seems less and less plausible (for Mediterranean eel, catches in the Strait of Gibraltar are would be tremendous!); tuna fish seemingly has not been tagged a lot, probably because easily wounded or preferably kept after catch.

Let us specify that these so-called “migrations” are not directed north-south, so that the sun does not has to be involved when looking for “explanations”, although “data support the hypothesis that chum salmon utilize orientation clues associated with the sun during open sea migration” according to Friedland *et al.* (2001). Pelagic fishes, contrary to birds, do not have any terrestrial referential that they can see. Hence, and although “processes underlying open-ocean migrations by salmon have been debated for years but little evidence exists regarding the sensory mechanisms and clues used in these migrations” (Dittman and Quinn, 1996), “knowledge of the migrations and geographic distribution of post-smolts of Atlantic salmon in oceanic waters is sparse” (Holm *et al.*, 2000), and “there is still no definite answer to migration of salmon” according to L. Hansen (pers. com. late 2003). How could such fish navigate accurately towards a waypoint?

Could fish use astronomical navigation as invoked for birds? This hypothesis seems no longer accepted in general, maybe just because the stars and planets are continuously moving and have a relatively small dimension while the fish vision might not be adequate.

Using olfactory sense (e.g. Hasler and Scholz, 1983) just allows smelling a particle that comes into your nose. Assuming one is able to memorise the "odour of his/her birth place", and if, by an extraordinary chance, a particle from that place enters your nose when several 100 km away, how could this help you in telling where (even in which direction) is your birth place? Similarly, sharks are attracted by the smell of blood only if blood particles come into their nose, obviously. Considering that such particles emitted by an injured animal drifting with the current or by any animal without any current will not diffuse a lot around the animal and that, more generally, diffusion will only occur downstream from a fixed source, such a source cannot be smelled from even a few metres upstream. Why not consider then that sharks can efficiently use (i.e. as a predator) their olfactory sense for blood only if they can perceive the current, i.e. if they see the bottom, in order to swim upstream? (in any case, it would be more efficient for them to listen and use acoustic (directional) waves).

Dead reckoning, i.e. integrating speed and heading, allows accurate navigation … provided the speed is measured in a fixed referential (not with respect to the water, which is the sole speed easily measured). Since humans cannot do this without any sophisticated instrumentation, how could animals proceed?

The specific case of the (migrating) cetaceans

In line with the context of this monograph, we shall now focus on marine mammals, first on their migrations and second on their displacements at smaller scale. Dynamics evidently drives the primary (at least) production. For instance, in the western tropical zones of the Atlantic and the Pacific, the trade winds and the Coriolis effect both combine to upwell nutrient-rich deep waters into the euphotic layer, hence triggering productive food webs that, although permanent, encounter seasonal latitudinal displacements. Dynamics also drives the primary production and the whole food web at higher latitudes, more or less mixing the surface of the ocean and seasonally bringing nutrients into the euphotic layer. Unfortunately for fishermen, the high latitudes zones, which are richer than those at latitudes, are also characterised by more severe meteorological conditions.

Simultaneously, cetaceans are reported to migrate seasonally, at least in some coastal zones of the world Ocean, most probably triggered by environmental factors. Could these migrations be driven, at least partly, by the environmental conditions becoming too harsh, e.g. the water temperature becoming too low, or the surface too icy for breathing normally? Alternatively, is it widely accepted that cetaceans, as other animals, have to migrate between feeding and breeding grounds. It is assumed that cetaceans migrate towards the equator for breeding in relatively poor but warmer waters and towards the poles for feeding (as shown by Mate *et al.*, 1998, at least during a part of what is expected to be a poleward route; in fact, many other bearings have now been observed according to Mate, pers. com.), remaining there as long as environmental conditions are convenient and as long as they do not have to breed (Mate *et al.*, 2000). Now, some populations that used to migrate have been observed to settle definitely (at least for some years) in places where environmental conditions allow feeding and breeding in the same environment (usually in places where the winter is no longer too harsh). Could this be a hint on the triggering mechanism and the hierarchy of the (numerous?) processes that enter into the migratory pattern? What if the climatological conditions become too severe again? Are there any observations of migrations that resumed after an interruption of several-years?

Is there any scientific evidence of migrations other than north-south (poleward-equatorward) in the open ocean or back and forth along a roughly north-south coastline (as documented, although without any solid conclusion, by Mate *et al.*, 2000)? To be explained, do these migrations have to take into account physical processes and features not directly related to breeding (in warmer waters located equatorwards) and feeding (in richer waters located polewards)? In other words, are migrations between a warmer-poorer place systematically polewards and a cooler-richer place systematically equatorwards?

In any case, we can make some additional remarks and ask some additional questions. Could it be considered that the actual migrations of cetacean and fisheries (fishermen migrate according to fish –as did whalers with cetaceans!- migrations, or at least according to what they think that fish migrations are) are motivated by the same reasons (i.e. feeding vs. giving birth or simply living for fishermen!)? Could it be that the north-south orientation of these coastal zones is fortuitously convenient for some navigation simply based on the sun direction, in particular for the cetaceans?

When trying to understand the roles of cetaceans -and that of human activity as well- in the marine ecosystem, sea-going oceanographers (who are not specialists of cetaceans!) first try to consider themselves as cetaceans or fishermen equipped with the most sophisticated sensors. They realise that, although they can measure locally with the utmost accuracy any kind of state parameter (for instance the temperature or concentration of chlorophyll, etc.), they cannot measure it remotely (at any distance, even a few metres away). In case they want to find a place with a different value of that parameter (for instance to find warmer or more productive waters) they can sail / swim either towards a "known better place" or look for such a place. In the second case, they can sail / swim randomly, and maybe fail, or they can proceed with some strategy and try to estimate some specific gradient. To do so, they have to swim in a given direction (to be estimated and memorised) for a given distance (several 100 m to filter out the small-scale turbulence, i.e. a distance larger than the cetacean dimension). Then, they have to estimate the change in the parameter they track and decide to continue in the same direction or swim in another one. Finally, they have to summarise all the observations and specify the gradient. Is such a strategic attitude possible / realistic? Alternatively, is the search for a place with better conditions more erratic and random?

For sure, cetaceans and fishermen have more or less efficient hydrophones, so that they can passively listen to the noise emitted nearby. Similarly, they have more or less efficient sonars, so that they are able to echolocate suspended particles (zooplankton mainly) or fish shoals. However, is the dimension of the sphere which they can prospect in such a manner relatively large (i.e. as large as 10 km to 100 km)? Are these sensors able to provide significant information for migrations (over 10 km to100 km) or are they only efficient at a more local (100 to1000 m) level? In addition, is the fact that cetacean songs can be heard over relatively long distances (whatever they are) indicative that the eventual message could concern food (i.e. "Come here, the food is abundant!")?

Another parameter of interest for both cetaceans and fishermen is the current. Fishermen may have some instruments allowing them to know the current while sailing on their ship; however, this requires such a high level technology, especially in deep and open waters, that they do not get accurate measurements of the current. For a physical oceanographer in the open sea (away from any terrestrial referential), it is necessary to have a DGPS and a current profiler (ADCP), or what are called XCP probes. Without such instruments, human beings are unable to feel any current, whatever its intensity and direction. Then how could cetacean or fish "feel" the current, and possibly use / avoid favourable / adverse ones?

Finally, a major feature conditioning the attitude of naive classical oceanographers is that, being faced with accurate, detailed and numerous data sets collected either remotely or in situ, they have now realised that the "cetacean world" is extremely complex. Do both the cetaceans and fishermen actually feel an environment changing so rapidly in both time and space at all scales? Are they able to efficiently use their actual (i.e. not subjective) senses? In other words, has the natural variability to be considered as significantly felt by cetacean and fishermen or more or less as a random parameter?