I - Executive Summary

This synthesis was compiled by Giuseppe Notarbartolo di Sciara on the basis of significant inputs received during and after the workshop from Giovanni Bearzi, Robert L. Brownell, Christophe Guinet, John Harwood, Sidney Holt, Sascha Hooker, Mariano Koen-Alonso, Claude Millot, Graham Pierce, Kostas Stergiou, and Andrew Trites. Frédéric Briand took care of the final editing.

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)

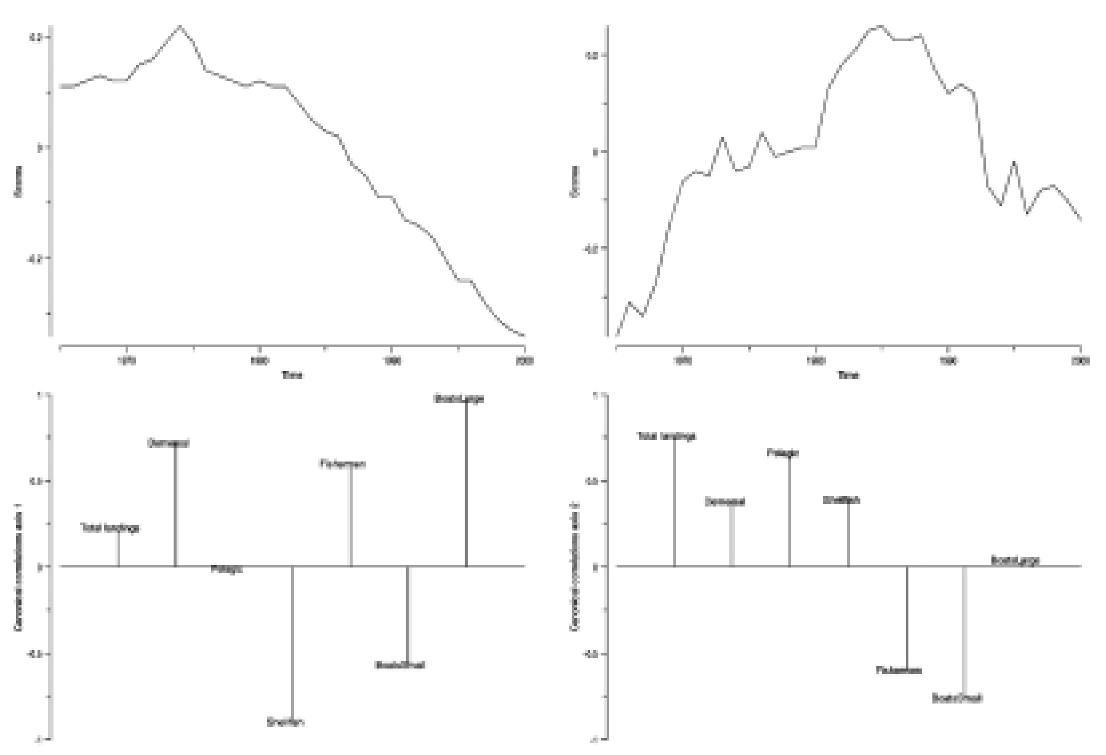

Fig. 1. Results of MAFA for fishing activity data for Scotland. Upper left graph: first MAF. Upper right graph: second MAF, lower left graph: canonical correlations for MAF 1, lower right graph: canonical correlations for MAF 2.

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).