

Report of the Modelling Workshop on Cetacean-Fishery Competition

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The Workshop was held at the Southwest Fisheries Science Center, La Jolla, California, USA from 25-27 June 2002. A list of participants is given as Annex A.

1. INTRODUCTORY ITEMS

1.1 Welcoming remarks

Reilly welcomed the participants to the Southwest Fisheries Science Center on behalf of its Director. He outlined the facilities available to participants and apologised for the quality of the coffee!

On behalf of the IWC, Donovan thanked Reilly for the excellent facilities provided and in particular for stepping in at short notice to host the workshop that had originally been planned to be held in St Lucia on the same dates. He also apologised to the participants for this late change in venue and thanked them all for coming to the meeting.

He reminded participants of the Workshop's terms of reference. These had stemmed from discussions that had begun in response to a request from the Commission in 1999 and had since continued. The central question governing the Committee's deliberations is:

'How are changes in abundance of cetaceans likely to be linked (in the short term and the long term) to changes in fishery catches?'

It had originally been intended that the Committee should host a symposium and conference on competition between cetaceans and fisheries during 2001, but this had not occurred due to funding constraints. Given this, the Committee had agreed that it would begin its consideration of the topic by holding a small specialist workshop to consider modelling approaches that might be useful in addressing the primary question given above. Planning was undertaken by a Steering Group comprising Northridge, Donovan, Friday, Tamura and Walløe, who developed the terms of reference, draft agenda and list of potential participants (see IWC, 2002, pp.55-56; IWC, 2003, pp.53-54).

The terms of reference for the Workshop were as follows:

- (1) review existing modelling approaches that might be used to address the overall objective;
- (2) identify the constraints and data requirements in the existing models or modelling approaches that limit our ability to answer the above question;

- (3) describe the advantages and disadvantages of the various approaches, bearing in mind the areas for which they were developed; and
- (4) identify those approaches that seem most likely to be able to answer the above question, and provide guidelines as to when and where they might be used (e.g. depending on the likely level of data availability).

1.2 Election of Chair and appointment of rapporteurs

Northridge was elected Chair. Friday and Donovan agreed to act as rapporteurs. Authors of papers provided summaries for inclusion in the report.

1.3 Adoption of agenda

The adopted agenda is given as Annex B.

1.4 Available documents

The list of documents available to the workshop is given as Annex C.

2. OVERVIEW OF EXISTING MODELS

This item was intended to provide a brief overview of work to date to establish the framework for later discussions. Issues arising out of the presentation of SC/J02/FW4 are discussed under the relevant agenda items below.

SC/J02/FW4 reviewed the methods that have been used to model the competitive interactions between seals and fisheries. Such models have been classified in a number of different ways. For example, Whipple *et al.* (2000) distinguished between static-flow and dynamic models, and between empirical and process-based models. However, many of the examples in the marine mammal literature use different types of models for different trophic levels. Nevertheless, it is convenient to distinguish between models that focus on the interactions between a relatively small number of target fish species (often only one) and their major predators and prey, and those that attempt to model all, or most, trophic levels.

Surplus yield calculations model the effect of a single predator on its prey, and consider the effects of a reduction in predator numbers on the amount of prey that might be available to a fishery directed at that prey species. This ignores, amongst many things, the fact that other predators of that prey species will also respond to changes in prey abundance, although SC/J02/FW7 describes a method that may account for this. Where such surplus yields have been

¹ Presented to the meeting as SC/55/Rep1.

calculated, the uncertainties associated with the calculated values are not small (95% CLs $> \pm 40\%$), even for well-studied systems (e.g. Hammond and Fedak, 1994; McLaren *et al.*, 2002). However, they always indicate that there will be some increase in the amount of prey available to the fishery.

'Minimum realistic models' attempt to account for a large part (traditionally around 80%) of the predation mortality on a focal fish species. Indirect effects within these models can result in predictions that a reduction in the abundance of certain predators can actually result in a decrease in the amount of prey available to the fishery (e.g. Punt and Butterworth, 1995) through a phenomenon that has been called 'mesopredator release' (Courchamp *et al.*, 1999; Crooks and Soulé, 1999). MSVPA (see SC/J02/FW13) is an extension of this approach that considers all of the commercially important fish species in a system and their interactions with their predators and prey. Another extension of these minimum realistic models is to make them spatially explicit (see SC/J02/FW5 and FW6).

Finally, models such as ECOSIM (SC/J02/FW11 and FW12) and bioenergetic trophodynamics models (SC/J02/FW8) can be used to examine the way in which interactions between all trophic levels can affect the response of a particular prey species (and of fisheries on that prey) to changes in the abundance of one of its predators.

These models often differ in the way they address predators' responses to changes in the abundance of their prey (the functional response). Some models use a very specific form of functional response, whereas others consider a range of functional forms. It is clear that the form of this functional response can profoundly influence the effects of a change in predator abundance (e.g. Mohn and Bowen, 1996; SC/J02/FW10). So far, no one has attempted to estimate the precise form of the functional response for any marine mammal to a single prey species, let alone to all of its potential prey. Annex D provides a brief description of the kind of data that are required for this estimation process.

In discussion, it was noted that a working group established under the auspices of UNEP, has provided a list of the kind of information that is required for the scientific evaluation of proposals to reduce marine mammal numbers in order to benefit fisheries (Table 1, taken from UNEP, 1999). An important requirement is the need for a matrix of 'who eats whom' in the system under consideration.

SC/J02/FW4 examined four cases of interactions between seals and commercial fisheries in the context of the guidelines given in Table 1. The authors concluded that in each of these cases, despite relatively large datasets for some species, the UNEP criteria could not be met.

3. DATA REQUIREMENTS

The aim of discussions under this agenda item was to briefly review the types of data likely to be required for multi-species modelling exercises aimed at addressing the broad IWC objective, in the context of their limitations, likely availability, reliability and natural variability. It is neither an inventory of such data nor a catalogue of methods.

3.1 Cetacean population size and structure

An over-riding issue to any discussion of cetacean population size and structure is that of stock identity. This has been discussed extensively by the IWC Scientific Committee in the context of modelling populations for RMP

Table 1

Data required to evaluate proposals to cull marine mammals based on fishery impacts, from Table 2 of UNEP (1999).	
(i) Marine mammal	Abundance, distribution and migration. Per capita food/energy consumption. Diet composition, including methods of sampling and estimation. Demographic parameters.
(ii) Target fish species	Abundance, distribution and migration. Demographic parameters (weight at age, age at spawning, commercial catch per unit effort). Details of assessment models and results.
(iii) Other predators and prey of the target species	Abundance, amounts consumed, details of stock assessment if any.
(iv) Other components of the ecosystem	2-way matrix of 'who eats whom' with estimated or guessed annual consumptions. Estimated abundance by species.

and AWMP implementations (e.g. see IWC, 2001; 2002; 2003) and similar considerations are clearly important in any multi-species modelling exercises. It is not discussed further here but is implicit in the discussions below.

3.1.1 Abundance and distribution

There are two classes of limitations to cetacean abundance data: the first are those associated with the available estimates and the second are those associated with the absence of any abundance data. With respect to the latter, it must be said that there are numerous species and populations of small cetaceans for which there are no abundance estimates available, and for which it seems unlikely that estimates will become available in the near future. Whilst the situation is better for large whales, there are still several species and areas for which estimates are lacking. In the case of the sperm whale (*Physeter macrocephalus*), methodological issues associated with obtaining reliable estimates of abundance remain; similar problems exist for beaked whales.

Methods for estimating absolute cetacean abundance have been summarised in a number of publications (e.g. Hiby and Hammond, 1989; Hammond *et al.*, 1990; Garner *et al.*, 1999; Buckland *et al.*, 2001). These methods can also be used to estimate distribution and there have been recent advances in spatial modelling (e.g. Hedley *et al.*, 1999). These can essentially be grouped into three types: the most common concern 'distance'-based methods where surveys are used to 'sample' an area and an abundance estimate is generated; on more limited occasions, it is possible to carry out a census of all animals in the population (e.g. bowhead and gray whales on the west coast of the USA); finally, mark-recapture estimates have been obtained using individually identifiable animals (e.g. humpback whales in the western North Atlantic). There are other methods being developed that show promise, particularly those using acoustic detections (e.g. harbour porpoises) although some problems remain in obtaining absolute rather than relative abundance.

It is clear that all methods are associated with uncertainty from a variety of sources. It is not appropriate here to detail these but it should be noted that CVs of abundance estimates can be up to 0.4 or more, although they can also be much smaller. Such uncertainty must be taken into account in any modelling exercises (see for example the approach used in the AWMP development process that takes into account bias and variance). In most cases estimates represent a 'snapshot' of the number of animals in a given area of ocean at a given

time. It is relatively rare that there are good time-series of data for a population: either annually or throughout the year. Information on both would be useful to assess food consumption for modelling purposes. Knowledge of the spatio-temporal distribution of cetaceans with respect to prey is also important in this regard. This is particularly important for migratory species.

3.1.2 Structure

Population structure is important in relation to assessing cetacean consumption and diet. In addition to the obvious link between the age/length² structure of the population and its biomass³, there are intraspecific examples of differences in diet by sex and age-class, as well as geographical and temporal segregation by age-class and sex. It is difficult if not impossible to distinguish the sex of most cetaceans at sea and age- and/or length-classes can only be distinguished at a crude level (unless photogrammetric surveys are undertaken – these are expensive and not universally applicable). Thus neither the age-length nor sex compositions of populations can be measured directly – they must be estimated through modelling (taking into account known, estimated or guesstimated direct⁴ and incidental⁵ removals) with all the associated uncertainty this entails.

3.2 Fisheries assessment data

Fishery catch and effort data are amongst those used to estimate both the magnitude of fishery removals and often the stock size in numbers at age or biomass. It might be assumed that information relating to fishery removals should be accurately known, but in reality fishery removals may be poorly quantified. Several issues were highlighted. While quantities of landed fish may be recorded, information on catches, and by inference therefore on discards, is often very poorly recorded. Monitoring of discards is now undertaken in many areas, but such monitoring is sensitive to the management regime in place, and to the availability and adequate placement of observers. Landings data may also be less than adequate where they are recorded by market category rather than by species, so that two or more species might be recorded under a single landings category. Landings data may not provide much information on the spatial structure of the fishery removals, and may also differ in their reliability among different fleets targeting the same fishery resource.

The size or age structure of the fish removed by fisheries is also sometimes poorly known, and again this is especially true of discards. One of the issues here is that sample sizes are often determined by the needs of commercial or stock assessment protocols that may be inadequate to address ecological questions.

Effort data are generally required to obtain some index of abundance for fished species and hence population size estimates, but the definition of units of effort is problematic, and the standardisations applied are sometimes inadequate. Effort can be particularly difficult to define in multi-species fisheries, or when fishery regulations change, thereby prompting some change in fleet behaviour. Depending on

the assessment model being used, gear selectivity or fish catchability for different gear types also needs to be addressed.

The basic outputs from fishery related data are the population size of targeted species, often described in an age or size structured manner, and/or population biomass.

3.3 Population size and structure of prey and competitor species

While some prey/competitor species populations can be assessed using fishery assessment techniques, other methods of population assessment are needed for many species which are either not fished commercially, or which are only fished incidentally to more commercially valuable species. Surveys are therefore required to provide at least indices of abundance. Not all relevant species will be adequately sampled by a single survey method, and it is therefore likely that several survey methods might be required to estimate the abundance of all the relevant prey or competitor species. Some of the typically used survey types are listed in Table 2, together with an indication of the types of species that might be sampled by each. It is clear that for any such surveys some definition or assessment of selectivity is required, as the assumption that all species and size classes are equally catchable under any single survey method will lead to biased assessments.

Table 2

Survey methods applicable to major species groups of interest. Prey species include smaller species or size classes, while competitor species of fish are large species or individuals.

Sampling method	Prey species					
	Commercially fished species		Non-commercial species		Competitor species	
	Fish	Invertebrates	Fish	Invertebrates	Fish	Birds
Trawls	x	x	x	x	x	
Acoustics	x	x	x	x	x	
Purse seine	x				x	
Long lines					x	
Video					x	
Plankton nets		x		x		
Benthic grabs, dredges			x	x		
LIDAR	x	x			x	
Visual surveys						x

3.4 Consumption rates by marine mammals

SC/J02/FW2 reviewed a number of studies that have used estimates of daily rates of prey consumption by cetaceans in ecosystem models. All of these studies scaled prey consumption rates to body mass of the predator using the general relationship $R = A M^B$, where R is the consumption rate, M is body mass, with A and B estimated from a number of different data sources. These data sources all relied on consideration of allometric relationships between energy requirements and body size rather than direct measurements of food consumed. For large whales, the value of B is the most influential but this is invariably derived from a regression with few data points for larger species. The studies considered fell into three categories, low values of B around 0.5-0.6, medium values of around 0.75-0.8, and the high value of 1 when consumption is just a straight

² Length is not a good proxy for age in most cetaceans apart from in the first year or two. Unless an individual has been identified in a longitudinal study, age has to be estimated from teeth or earplugs.

³ Issues relating to the estimation of cetacean biomass are discussed under Item 3.2.

⁴ e.g. hunting.

⁵ e.g. bycatches in fishing operations, ship strikes.

percentage of body mass. This range of values creates considerable uncertainty about the energy requirements of large whales. This uncertainty increases with body mass because of the non-linear relationship between body mass and consumption and the difficulties of studying metabolic rates in larger animals. For a forty tonne whale the estimates of daily food requirements considered differed by a factor of ten.

Some alternative approaches to estimating consumption rates in large whales were also considered including direct measurement of intake from behavioural studies, estimates of intake based on analysis of stomach contents, and estimates of energy requirements based on utilisation of blubber stores. Estimates of maximum daily consumption based on feeding rates were considered for filter feeding whales based on measurements of plankton concentrations and estimates of the volume of water filtered. North Atlantic right whales were chosen as a case study and it appeared very unlikely that they could physically achieve the consumption estimates generated using the above equation with medium to high values of B . In addition, filter feeding whales suggest a theoretical basis for values of B of less than 0.67 otherwise larger whales would need to spend longer feeding, or swim faster. Estimates of energy requirements in fin whales based on measurements from whaling data of the amount of blubber stored by animals taken on the feeding grounds in the Southern Ocean and North Pacific fell below all the allometric predictions. Direct estimates from stomach contents for fin and sei whales were also lower than the allometric predictions, except for the lowest value of B of 0.52.

The studies reviewed indicated that neither theoretical considerations nor data support high values of B close to 1 and there is evidence for values of 0.67 or less.

The Workshop considered that although consumption rates may not be the greatest source of uncertainty from a modelling perspective, it is nevertheless important to understand the sensitivity of any model predictions to uncertainty in consumption rates. Hence, estimates of consumption based on low values of B should also be included within the range of input values for large whales.

3.5 Diet composition

SC/J02/FW1 gave a brief review of methods used to assess diet composition, with comments on their potential and limitations. Five approaches were presented. Only one of these, analyses of contents from stomachs, intestines and scats, had been developed specifically to address questions relating to predator diets. Four other approaches, fatty acid signatures, stable isotopes, genetics and remote monitoring were originally developed for other purposes, but have in recent years been adapted for use in marine mammal diet studies. Application of these new methods in cetacean diet studies has been particularly motivated by the need to develop non-lethal methodologies.

Studies of the diets of marine mammals based on analyses of either stomach, intestinal or scat (faeces) contents is based on the assumption that the relative frequencies of recovered undigested specimens, including otoliths, beaks, exoskeletons and other hard parts, reflect the frequencies of fish, cephalopods, crustaceans and other invertebrates in the diet in some known manner. The methodological problem with erosion of otoliths, which has been well studied in the context of seal diets, is less conspicuous in studies of whale diets. Most cetaceans have a multi-chambered stomach system, starting with the non-glandular fore-stomach where

otoliths and various other calcareous remains usually stay undigested. Certainly, differential passage and degradation rates of different fish and cephalopod types, and also the possible accumulation of some hard parts, represent methodological problems that have yet to be fully resolved in cetacean diet analyses.

The fatty acid composition of a prey is species specific and, as these compounds are assimilated through the diet and accumulated in the fatty tissues of predators (e.g. in blubber), they can be used as tracers of diet. In order to assess the diet of the predator, fatty acid signatures from its blubber are compared with fatty acid signatures from a variety of potential prey species using classification and regression tree analysis. The principle of the stable isotope method is that ratios of heavier vs lighter isotopes of particular elements (carbon, nitrogen, oxygen sulphur) in tissues of predators can be traced to those of their prey as they are assimilated in the diet. Both the fatty acid method and the stable isotope method require a prey library. Assuming that food web fatty acid and isotopic signatures are reflected in the tissues of organisms and that such signatures can vary spatially based on a variety of biogeochemical processes, both methods can be used to trace nutritional origin and migration in animals.

Genetic analyses of remains from scats or contents in the gastrointestinal tract may be used to identify prey species consumed. Originally the method was applied in combination with more traditional scat analyses, primarily to identify the individual predator or species for individual scats, assuming that epithelial cells from the colon wall, sloughed off and deposited in scats, are a reliable source of DNA to determine species of origin. A reference database for the genetic signature of actual prey species is needed.

Remote monitoring of marine mammals, using either data loggers or satellite-linked time-depth recorders, has been used to indicate potential prey or feeding areas. The approach is based on comparing data on temporal and spatial distribution of the predator, including the vertical movements (dive depths), with related data for potential prey species, in order to identify matches that may indicate the likely prey species of the predator. For co-occurrence of predators and prey in time and space to be indicative of predation, confirmatory observations by other means are always required.

Although identifying and measuring items in vomit, scats and gastrointestinal contents has several disadvantages and sources of errors, it still provides more information at considerably less cost than other new methods (such as fatty acid signatures, stable isotopes and genetics), and has not been replaced effectively by any other method at present. Advantages of the traditional methods over the new ones include that they:

- (1) provide information on meal size and relative composition of prey for each predator;
- (2) provide knowledge of size classes of prey;
- (3) allow for understanding of small scale spatial and temporal distribution of diets;
- (4) allow for small scale studies of predator-prey dynamics;
- (5) require samples that are easily obtainable from hunts, bycatch, culling or strandings;
- (6) require laboratory treatments of samples that are simple.

The main problem with several of the new methods is the very coarse spatial and temporal resolution that prevents quantitative descriptions of relative diet composition.

However, new methods based on fatty acid signatures and stable isotopes have some advantages over the traditional methods in that they:

- (1) integrate data over a longer period;
- (2) may detect shifts in diet;
- (3) may yield knowledge of distribution, migration and stock structure.

These methods also allow for the understanding of habitat utilisation and trophic relationships of the predators. All of the new methods will certainly be useful in studies of depleted, threatened and endangered species for which more direct sampling is problematic.

3.6 Linkages – inter/intra species predation

A discussion on predator-prey linkages and trophic complexity began with a brief presentation on these issues in relation to model structure and characterisation. Determining what predator-prey linkages should be included in a model depends on the types of questions being raised, the modelling approach and data availability. One key issue in modelling is whether there is an optimal level of realism, and hence complexity, in relation to model performance. Reducing complexity can be achieved by removing linkages or by aggregating linkages, both approaches resulting in a reduced number of weak links being represented in the model. Previous work on weak links has shown that they may have an important influence on model stability. The effects of model complexity, removal and aggregation of linkages, is an area of research that warrants further study. Current work by researchers at CEFAS (Centre for Environment, Fisheries and Aquaculture Sciences, Lowestoft, UK) addresses some of these issues with specific reference to models that include marine mammals. Other issues discussed were:

- (1) The effects of model ‘biases’ (marine mammal centric versus fish centric versus benthos centric model ‘designs’).
- (2) The inclusion of size/age structure (what level of complexity is necessary to consider ontogenetic changes in diets?).
- (3) Spatial and temporal heterogeneity in linkages: the way that available prey are defined (different approaches in models – vulnerability, suitability, spatial overlap).
- (4) Multispecies functional responses.

It was agreed that systematic and thorough investigations of trophic complexity in models relevant to whale-fishery interactions are needed in order to address the necessary levels of complexity needed in models posing questions about cetaceans and fishery competition.

3.7 Other issues

Two papers addressed the treatment of uncertainty and management constraints in modelling cetacean-fishery interactions. SC/J02/FW9 stressed the uncertainty in fisheries and other data used to parameterise models, as well as uncertainties in system function. SC/J02/FW10 showed that, if uncertainty and management constraints are ignored, coarse-scale ecological models of a ‘who-eats-what’ kind, such as ECOPATH, ECOSIM, MULTSPEC etc, inevitably predict that reductions of cetaceans will result in extra yields of each prey species to fisheries, by an amount exactly equal to the reduction in cetacean consumption, provided that

cetacean abundance and their consumption of each species are positively correlated, and provided that harvests of each species are adjusted so that the fisheries take an additional amount of each prey species equal to the reduction in cetacean consumption. Given perfect knowledge and complete control of the fisheries, such adjustments in the harvests would be possible in principle. Whether such adjustments are possible in practice depends on whether there is sufficient information available and sufficient means to control the fisheries. These questions have to date not been incorporated into the models considered,

SC/J02/FW10 provided an example of a simple case where whales and a fishery compete for the same fish stock, illustrating that when the ecological vulnerability of the fish stock to whale predation is low, the total consumption of fish by the whales, and the yield of the fishery, can be quite insensitive to the abundance of whales over a wide range. In such cases, reduction of whales over this range would not yield appreciable benefits to the fishery.

4. INDIVIDUAL MODEL STRUCTURES

4.1 Mass balance/energy system models

4.1.1 ECOPATH

ECOPATH is the mass-balance model component of the ‘ECOPATH-with-ECOSIM’ software package for examining predator/prey relationships and fisheries interactions. ECOPATH is a method of exploring and synthesizing data and offers a relatively straightforward and established method for constructing a food web. Bundy presented the basics of ECOPATH, gave some examples of results from the eastern Scotian Shelf, and discussed the limitations of the model. She also noted that ECOPATH provides the input data for the simulation model ECOSIM. It is thus critical that the ECOPATH model be well constructed, both for its own purposes and for use in simulation modelling. There is little point in undertaking ECOSIM modelling if the ECOPATH model on which it is based is poor.

The three methods of addressing uncertainty within ECOPATH are: (1) a pedigree routine; (2) a simple sensitivity analysis; and (3) the ECORANGER routine. The pedigree routine documents the degree of uncertainty in the input data. The simple sensitivity routine examines the effect on estimated parameters of varying all basic input parameters one by one in steps from –50% to +50%. The ECORANGER routine attempts to consider explicitly the uncertainty inherent in all input data by randomly drawing input variables from frequency distributions that are defined by range and mean/mode values for all basic parameters. Comments from the Workshop indicated that others also did not think that ECORANGER could provide more than an *ad-hoc* representation of parameter sensitivity, as issues of covariance and prior distributions are not formally incorporated into the routines. There was consensus that more rigorous methods of incorporating uncertainty into ECOPATH need to be developed.

Bundy presented results of two ECOPATH models for the eastern Scotian Shelf, Canada. Two time periods were modelled: 1980-1985 and 1995-2000, before and after the cod and haddock collapse. The nature of the cetacean data and the uncertainty associated with it were discussed. The sensitivity analyses indicated that the model was not highly sensitive to the cetacean input parameters (B, P/B and Q/B). A comparison of the predation mortality caused by cetaceans in the two time periods showed a general increase due to a

decrease in the biomass of many of the prey species, which are also commercial fish species (e.g. Atlantic cod). Predation mortality is estimated as the (consumption of prey(i) by cetaceans)/(biomass of prey(i)). In general, fishing mortality for each prey is greater than the predation mortality imposed by the cetaceans, with the notable exception of the transient mackerel and small pelagics in both models.

ECOPATH's mixed trophic impact procedure assesses the effect that changes in the biomass of a group will have on the biomass of the other groups in a system (Christensen *et al.*, 2000). This procedure is based on a method developed by Leontief (1951) to assess the direct and indirect interactions in the economy of the USA, and introduced to ecology by Hannon (1973) and Hannon and Joiris (1989). The routine in ECOPATH is based on a similar approach developed by Ulanowicz and Puccia (1990). To estimate the mixed trophic impact an $n \times n$ matrix of predators and prey is constructed, and each cell represents the interaction between impacting (i) and impacted (j) group as: $MTI_{i,j} = DC_{i,j} - FC_{j,i}$, where $DC_{i,j}$ is the fraction of prey (i) in the average diet of predator (j) and $FC_{j,i}$ is a 'host composition term giving the proportion of the predation on 'j' that is due to 'i' as a predator'. Essentially, the mixed trophic impact regime is a simple linear perturbation analysis. It differs from the sensitivity analysis because the latter looks at the response of all estimates to a change in one input parameter, whereas the trophic impact regime looks at how one functional group, as an entity (a composite of the biomass, P/B, Q/B and DC) affects the other functional groups, as entities.

For the eastern Scotian Shelf models, the groups most negatively impacted by cetaceans in both models are the transient mackerel, demersal piscivores and large demersals. Groups that positively respond include haddock, American plaice and flounders. The impact of an increase in other groups on the cetaceans was also discussed.

Advantages and disadvantages of using an ECOPATH approach were outlined. Advantages include placing cetaceans in an ecosystem context, estimating fluxes between groups and addressing questions of food availability, estimating consumption and mortality by cetaceans, exploring trophic impacts, and providing a starting point for trophodynamic simulation modelling. Disadvantages include a general uncertainty in the top and bottom of food webs that constrain the web, the lack of an adequate method of addressing uncertainty, and the requirement of data for the whole food web.

The Workshop noted that although ECOPATH has moved away from the equilibrium assumption with the introduction of the biomass accumulation term, it still relies on some equilibrium assumptions, such as $P/B = Z$. This assumption does not always hold true, such as when fishing mortality is too high on species 'x', causing the biomass of 'x' to decrease. In theory, this has been addressed with the introduction of the biomass accumulation (BA) term into the general ECOPATH equation. However, it is incorporated into the total mortality estimate ($Z = F + M + BA$) whereas BA occurs because either $P/B > Z$, or $Z = (F + M) > P/B$. In addition, the biomass accumulation term is unable to handle components of the food web that are cyclic.

Concern was raised by the Workshop about the apparent dual meaning of ECOPATH's Ecotrophic Efficiency (EE) parameter that seems to parameterise both the biological efficiency of a functional group and what is unknown about that group. Concern was also raised that building any food web model necessitates decisions about which species to include and whether and how to organise species into

functional groups. ECOPATH models attempt to model the entire food web in an ecosystem, but ecosystem complexity necessitates combining species into species groupings. Although guidelines are given, grouping species is a subjective process. In addition, some questions may require only specific linkages to be modelled rather than an entire food web.

The Workshop noted that ECOPATH is poorly equipped to deal with ecosystems that are not entirely closed. Although ECOPATH includes routines to include immigration and emigration in the model, these routines perform poorly. Many researchers scale species biomass by the time spent in the study area rather than using these routines. This lack of ability to deal with movement is of particular concern for highly migratory species, such as large whales, and is exacerbated by the fact that distribution changes between years as well as throughout the year.

4.1.2 ECOSIM

ECOSIM is the time-dynamic model component of the ECOPATH-with-ECOSIM software package. ECOSIM transforms the ECOPATH mass-balance model into a multispecies biomass dynamics (surplus production) model. Aydin presented the basics of ECOSIM and evaluated the predictive capabilities of ECOSIM models on three levels by examining in turn: (1) the advantages and disadvantages of this broad class of predictive models; (2) the ECOSIM-specific algorithms and assumptions; and (3) the current 'released' software version of the ECOSIM algorithms (EwE 4.0).

Operationally ECOSIM can be classed broadly as a multispecies biomass dynamics (surplus production) model; in other words, a model that:

- (1) produces forward projections from initial conditions, by numerically integrating coupled differential equations that include non-linear functional responses between predators and prey;
- (2) uses biomass or abundance, but not both, as the state variables;
- (3) is deterministic if not forced by an external noise source;
- (4) possesses internal dynamics that are governed by multispecies interactions.

Fishing, climate, stochastic recruitment, etc. are applied as external manipulations and/or applied process errors.

Models of this class include 'classic' Lotka-Volterra models, models with single- or multispecies functional responses, and logistic models. They have a long history and are generally considered inadequate for single-species management (due to missing age-structure). Even so, single-species age-structured models also make necessary simplifications of constancy in species interactions (constant natural mortalities). Multispecies biomass dynamics models make a distinct trade-off: by fixing or eliminating age-structure, the models allow a basic re-evaluation of the constant natural-mortality assumption without an exponential increase in data requirements. However, this also leads to a decreased ability to statistically evaluate these models.

The disadvantages with this class of models include an inability to calibrate functional responses or select the 'appropriate' functional response, and the apparent ease of fitting to age-structure-free historical data without narrowing the parameter space sufficiently to provide confidence in

forward projections. Additionally, including age structure may be critical in investigating the differences between the relative impacts made by fisheries and marine mammal predators. In particular, cannibalism is an important dynamic in some fish species, which may require detailed age-structure to model adequately. ECOSIM does include an *ad-hoc* method for including recruitment dynamics.

The 'ECOSIM algorithms' include specific functional responses and numerical integration methods, which are modified to include a discrete-time age-structure model. One disadvantage of the specific functional response (the 'arena' functional response) is that its biological underpinnings are controversial and uncertain. Although the algorithms themselves are simple to program differently, independent of the package, most users accept the default 'arena' functional response, and many accept the default parameterisation of this functional response.

In addition to the 'arena' functional response, the 'ECOSIM' approach relies on fisheries management data in calibration and fitting and assumes that parameter space lies in a 'relatively controlled' world; in other words, the positive equilibrium is relatively stable and avoids chaos, bifurcations, stiffness, etc.

The software package itself, in building a set of parameters for ECOSIM from ECOPATH, provides a method for basic exploration and fitting. However, there are certain, specific weaknesses that must be addressed. An overwhelming problem is the transformation of ECOPATH's Ecotrophic Efficiency (EE) into a dynamic, equilibrium producing rate term (M_0). Recent work recognises that this transformation should be examined with respect to bioenergetics, available data, and the possibly inaccurate or dangerous assumptions that it introduces. This transformation is of particular concern given the dual utility of EE parameters as estimates of what is unknown about a species grouping as well as estimates of biological efficiency. Additionally, upper trophic level species, including cetaceans, tend to be among the least understood species in food web models and thus their EE values will tend to represent what is unknown rather than biological efficiency. Moreover, many undocumented numerical stabilisations have been introduced for the integration of the ECOSIM dynamics equations, and these may be inappropriate dampers of meaningful ecological cycles.

One of the main strengths of the software is that the fitting included in ECOSIM, although not statistically rigorous, allows comparison with many dimensions of fisheries data including catch, mortality, biomass, CPUE, and recruitment trends, although it is not possible to extract all relevant diagnostics. The issue of further implementation and reporting statistical uncertainty extends to the whole class of models: even with the best available data, it is worth asking what level of confidence, qualitative or quantitative, may be expected from a multispecies biomass dynamics model.

A parameterised ECOPATH and ECOSIM model of an ecosystem can aid in scientific discussion of the ecosystem (e.g. in a workshop setting) as long as the weaknesses of the model and modelling approach are understood. Their wide adoption provides a common language that has the advantage of being interpretable by, and allowing insights to be drawn from, data collectors, modellers, managers and ecologists. However, model building must make the maximum use of the 'human expertise' that exists for each individual ecosystem.

Ease of use and commonality of language is both a strength and a weakness of EwE, especially when these models are used in the public arena. It is easy to build a poor

model and produce poor results. Each given ECOPATH model must be subjected to rigorous review by those who best understand the particular ecosystem being modelled.

For dynamic projections, ECOSIM is a relatively cost-effective method for performing sensitivity analyses and determining the most important interactions. ECOSIM can be used effectively to determine or confirm what components are necessary and what components are unnecessary for producing a 'minimum realistic model'.

SC/J02/FW3 presented work that examined the effects of changing the assumptions of an ECOSIM model. In particular, interactions between cetacean predators, their prey and fisheries were evaluated for a simple system. Combinations of ECOSIM settings were formulated to represent six alternative hypotheses of feeding interactions between cetaceans and their main fish prey. The predicted response to simulated harvesting regimes for minke whales and their prey were used to evaluate the consequences of the alternative assumptions in terms of the dynamics of minke whale consumption rate, biomass, feeding time and mortality rate.

Regardless of the type of feeding relationship specified, intense fishing on the main fish prey of minke whales had a longer lasting negative impact on minke whales than when minke whale biomass was removed directly by harvesting. Consumption rate, biomass, feeding time and mortality of minke whales were all sensitive to the way in which feeding relationships were specified. Inclusion of handling time limited consumption of minke whales at high prey densities but also predicted higher consumption at low prey densities: features characteristic of a type II functional response curve. Predicted decline and recovery rates of minke whales were slower than when consumption rates were not limited. Addition of foraging time adjustments resulted in more conservative estimates of decline and recovery. However, when other mortality was linked to time spent foraging, exposure to higher mortality at low prey densities and reduced mortality at high prey densities, dramatic differences in predicted biomass trajectory resulted. Sensitivity to the 'other mortality' assumption is likely to be considerable for cetaceans when their predation mortality is a small proportion of total mortality specified in an ECOPATH model. Obvious differences in the feeding and biomass dynamics were also observed when prey availability to predators was represented by changes in prey vulnerability (v), confirming earlier reports that ECOSIM predictions are very sensitive to this parameter. Mackinson stated that, given that default settings and the capability of ECOSIM to characterise feeding relationships has changed over the course of the software's development, it is questionable whether reasonable comparisons can be drawn between 'apparently' similar studies.

The Workshop **agreed** that critical evaluation and comprehensive sensitivity analyses of ECOSIM predictions are needed.

4.2 Minimum realistic models

4.2.1 MULTSPEC and BORMICON

SC/J02/FW5 described the development and current status of the Barents Sea model MULTSPEC. MULTSPEC is a length, age and area structured multispecies simulator for the Barents Sea. The species modelled are cod, capelin, herring, polar cod, harp seals and minke whales. The details of the model are described by Bogstad *et al.* (1997).

MULTSPEC was designed initially to estimate the spawning biomass of capelin in connection with management of the capelin fishery, by quantifying the

predation of pre-spawning capelin by cod. The parameter estimates in the predation model are based on the calculated consumption of capelin using the joint Russian-Norwegian fish stomach content database and a model for the evacuation rate based on laboratory experiments.

Another application of MULTSPEC has been to investigate different scenarios for the interaction between fish and marine mammals. It was found that removing the marine mammals resulted in a predicted increase in yield from the cod fishery, but the effects on capelin and herring were critically dependent on the cod-capelin-herring dynamics. MULTSPEC is not currently being developed further due to lack of resources, but it was noted that MULTSPEC could be re-established for the Barents Sea using the BORMICON code (Stefansson and Pálsson, 1998).

BORMICON is another area-structured MRM, which is intended as an assessment tool rather than simply a simulator. Whereas MULTSPEC relied on single species VPA outputs to parameterise the cod population, BORMICON uses historic cod catch data to model the cod population directly.

It was noted in discussion that the marine mammal (whale and seal) dynamics are independent of prey dynamics, and that MULTSPEC as currently formulated would not be able to address the question as to how fisheries might impact on whale populations. Although this could be addressed within the same overall modelling framework, major modifications of the model would be required. It was also noted that the suitability coefficients used to parameterise marine mammal predation are taken from observed predation rates over a period of time, but it was questioned whether this approach could then safely be used to examine major perturbations outside the range of the observed time period. The issue of uncertainty was also considered and, as with most of the other modelling attempts, it was noted that this is not addressed in MULTSPEC.

4.2.2 SEASTAR

SC/J02/FW6 described ongoing modelling work to incorporate minke whale predation into fish stock assessments in the Barents Sea. The herring assessment model SEASTAR generates predation mortalities for the Norwegian spring spawning herring stock based on assumed total food consumption by minke whales during 1950-2002 (a constant level in the current application). Minke whale consumption is partitioned among herring, capelin and krill and the parameters are adjusted so that the consumption in the Barents Sea in 1992-1994 was roughly equal to the consumption calculated from a bioenergetics model and the diet data.

Model runs produced an appreciable increase in estimates of herring spawning stock biomass in 2002 once minke whale predation was explicitly included. Standard medium-term probabilistic projections showed that the herring is only affected to a small degree when the predation from minke whales is removed, but when predation was tripled these projections were appreciably affected.

The medium-term projections in the present implementation did not take account of the herring-capelin interactions. Increasing the herring stock size in the model leads to very small capelin stocks, resulting in increased minke whale predation of herring. However, such interactions might be addressed in future by combining SEASTAR with the capelin assessment model BIFROST, in order to make medium-term stock projections for both stocks.

The present work is very preliminary and the input parameters need to be revised and minke whale stock dynamics also need to be incorporated. The approach itself is similar to the one that has been taken in models of the interactions between seals and cod in Canada (Mohn and Bowen, 1996). There is no attempt to model the predator (minke whale) population through time, though there is age-structured predation mortality on herring. The approach does not include any second order interactions, so that any reduction in whale numbers is bound to result in an increased herring yield.

4.2.3 *Multispecies VPA and MSFOR*

SC/J02/FW13 described the basic working of multispecies VPAs and MSFOR, as implemented by ICES for the North Sea. MSVPA is an extension of single species VPA for the estimation of inter- and intra-species predation. A similar approach has also been used in several other shelf areas including the Gulf of Maine and the Baltic, Bering and Barents Seas. Food suitability coefficients are calculated from observed stomach contents, or in the case of seals, from scat analyses. Mortality rate estimates for each prey-predator age class interaction are calculated iteratively, but residual mortality rates, not attributable to predation, are also allowed.

MSFOR is a means of forecasting stock numbers at age, using as input the output from MSVPA, as well as a stock recruitment relation, fishing mortality and predicted ratios for each of the various predator groups. The MSVPA model assumptions lead to a Type 2 functional response, and the system is modelled as a top-down system, with no food limitations. There are no marine mammal (which in the case of the North Sea implementation means just seals) stock dynamics. This means that at present it cannot address the question of how changes in fishing might affect marine mammals. No environmental processes (such as those governing recruitment) are included in the model, and no migration in or out of the area is considered. It is also a deterministic model that does not address errors in the input data. As with other models therefore there is little attention paid to the uncertainties inherent in the model, though a stochastic multispecies model is being developed.

The model is conceptually simple, and is closely focused on the commercial fish species. It uses many of the same input parameters as are used for stock assessments. It is however, over-parameterised and requires a huge amount of data to generate inputs. It may therefore be useful only in contexts of well-studied and heavily fished areas like the North Sea, where a time-series of catch at age and fishing effort data are available to develop MSVPAs. On the other hand, MSFOR can be used to predict forwards, as long as some data are available to specify the initial conditions of the model.

4.3 Food web models

4.3.1 *Bioenergetic trophodynamics*

SC/J02/FW8 described an approach to multispecies biomass dynamics that extends the predator-prey models of Yodzis and Innes (1992) to multispecies systems. In this approach, population dynamics are deduced from bioenergetics. Allometric relationships based on body size are used to estimate some parameters, and to sufficiently explicate the biological meaning of others so that reasonable bounds can be placed on them. Both age and spatial structure can be incorporated, although both increase the data requirements.

The models are systems of coupled differential equations, similar to those of ECOSIM. However, bioenergetic trophodynamics has not been packaged with a simple user interface; using it requires access to computer programming skills. This has the disadvantage of limiting the potential user circle, and the advantage of flexibility and transparency.

The form of the functional response in a multispecies model has a profound influence on the behaviour of the model, yet little is known about it empirically. Therefore, in bioenergetic trophodynamics particular care is taken to avoid prejudging the form of the functional response. Two examples were presented to demonstrate how this is done.

The first example (Koen Alonso and Yodzis, 2004) involved a simplified model of the Patagonian shelf, where squid, anchovy, hake and sea lions interact. The approach taken here to functional response is to apply a range of functional responses (a generalised Holling family, a frequency-dependent predation family, a family of responses with prey refugia and the ECOSIM arena response) to the system. The Workshop was shown results for the generalised Holling family of functional responses. Solutions to the system of equations were fitted to observed time series of fish stock parameters using a newly discovered global optimisation algorithm, termed self-cooled simulated annealing (SCAA). Different assumptions about the basal species were tested and the best fit was found by allowing competition for zooplankton between anchovy and squid. The model accurately predicted observed increases in squid harvest and biomass with increased harvesting rates of hake.

The second example was of a more abstract nature. In a study of the Benguela ecosystem (Yodzis, 1998), the issue was the response of fisheries to a relatively small removal of Cape fur seals in a system that had been conservatively managed for some years. The available data included a 29-species food web, but few time series. Under these circumstances, a model linearised around a putative equilibrium is appropriate for the entire food web of 29 species. Then only the first derivatives of the functional responses need to be specified, and biologically sensible bounds can be given for these – one is investigating the set of all biologically sensible functional responses. Assigning a uniform probability distribution within its bounds to each derivative produces a statistical universe of models, from which it is possible to calculate probability distributions for the answer to any question involving relatively small changes to the system. The conclusion reached was that a cull of fur seals is more likely to be detrimental to the total yield from all exploited stocks than it is to be beneficial.

Typically, food web data are available for more species than are time series data. A prudent modelling approach could combine a local model like the Benguela example with global models like the Patagonian example for subsystems. This would give a range of possible behaviours, which could be narrowed in targeted studies.

4.3.2 Index of predator influence

SC/J02/FW7 presented a summary of published predator-prey models arising from work in CCAMLR and extensions of recent work aimed at evaluating whether or not culling of predators might improve fisheries. Although the Antarctic marine ecosystem is relatively simple compared to other parts of the world, data are of much poorer quality and/or absent than for many other regions, and this makes it unsuitable for detailed multi-species modelling. The context in which models have been developed for CCAMLR has been directly related to managing the effects of fisheries for krill on predators of krill. In particular, these models have been directed towards how to make robust decisions to meet the ecosystem objectives of CCAMLR.

Three published modelling approaches have been presented to CCAMLR, from Butterworth and Thompson (1995, extended in Thomson *et al.*, 2000), Mangel and Switzer (1998) and Constable (2001). The characteristics of the models are summarised in Table 3.

A difference in considering the effects of fishing on predators and the effects of predators on fishing is that they look at different parts of the food web, changing the focus from one prey-many predators to many prey-many predators (with additional predators). The potential for unforeseen outcomes external to the focus on predators of fished species is thereby increased. It was noted that there are a number of difficulties in considering the effects of predators on target prey species because of limitations of 'surplus yield' models and the difficulties in erecting models for data-poor food webs. There are many uncertainties to account for including the dynamic nature of systems, model structure, parameter estimates, natural variation and potential for extreme events.

These uncertainties need to be addressed in order to provide advice on the management questions. A key question is whether or not the intensive investigations associated with the issue of predator-prey-fisheries relationships would be worth undertaking. SC/J02/FW7 introduced an Index of Surplus Production, which evaluates the strength of influence that a predator might have on controlling the available production of prey (Index of Predator Influence: consumption relative to production of

Table 3
Antarctic ecosystem modelling approaches: characteristics of three models.

	BT95	MS98	C01
Effect direction	Prey on predator (potential to examine predator on prey)	Prey on predator	Prey on predator (potential to examine predator on prey)
Prey	Krill	Krill	Potential for many
Predators	Many individual predators not interacting	Adelie	Potential for many predators with competition
Predator dynamics	Age structured population	Autecological energetic model	Age structured population
Prey dynamics	Age structured population	Biomass	Biomass Physical forcing of prey dynamics
Data used	Some fitting of models, estimated parameters	Estimated parameters	Estimated parameters to be used
Spatial scale	None	Colony	None
Temporal scale	Years	Seasons	Years
Predator limits	Carrying capacity	Food density	Carrying capacity
Prey limits	Population stochastic model	Maximum density	Carrying capacity
Effects on predators	Population numbers	Mortality, reproduction	Productivity, biomass, population numbers, reproduction

prey species) and whether this might be caught by the fishery. It can be developed to take account of age, space and time relationships between predators and prey and natural variation in the abundance of target prey. It uses Monte Carlo simulations to integrate across the uncertainties of all the parameters to estimate probabilities for a proportion of target prey production that might remain if the subject predator was removed from the food web and all other relationships remained unchanged. While it is a static measure, it could be used to evaluate whether a fishery might be capable of supplanting a predator in the system. It was suggested that the lower percentiles of the index would best be used as measures to judge whether or not further development of food web models to address these questions would be warranted.

5. SYNTHESIS

5.1 Modelling approaches

The Workshop noted that despite recent advances, most multispecies models are still at developmental stages. It **agreed** that no single approach could be recommended at this stage to provide reliable information of value to consideration of cetacean dynamics in an ecosystem context. However, this does not necessarily rule out the possibility of inferences that could be drawn if a number of different approaches yield qualitatively similar results.

In all cases considerable further work is needed to fully incorporate uncertainty, both in terms of model uncertainty (including concepts surrounding functional response curves and choices of these) and 'data' uncertainty (both absence of data and uncertainty in available data). The Workshop **agreed** that for all current models, perhaps the most important weaknesses concerned the issue of functional responses. Given this fundamental importance and the lack of time to address it here, the Workshop **recommends** that consideration is given towards organising a separate workshop on this one issue.

Considerable work is also needed to develop methods to examine whether models can be 'validated' – both in the context of their ability to explain past 'knowns' and to provide reliable future predictions. This is a difficult and complex task and a number of issues will need to be addressed in this context, including:

- (1) How well does an individual model explain past information?
- (2) Can other alternative models fit past data equally well?
- (3) Do models from (1) and (2) above provide similar future predictions?
- (4) If not, how would one distinguish amongst them?
- (5) Is it possible to develop realistic simulation frameworks to test models (cf RMP/AWMP development work)?
- (6) Is it possible to establish 'diagnostic' short-term predicted changes that can be measured in the real world to provide an indication of whether the predicted longer-term changes are likely to occur?

Clearly, the ability to address such questions is a fundamental part of determining the value of such models in a management context.

A feature of the modelling approaches considered is that in many models/studies, cetaceans (and indeed all top predators) have not been given high priority. The Workshop **agreed** that given this, the IWC is probably not the best forum to focus developmental work. A more productive approach would be to work in cooperation with other bodies, for example ICES, to ensure that cetaceans are included (and

in an appropriate manner). In particular, specific features of cetacean feeding behaviour need to be taken into account (e.g. the potential importance of patch density as opposed to overall density) in any modelling exercises.

The Workshop also **draws attention** to the fact that cetaceans form just one part of the system that needs to be modelled in order to try to answer the IWC question posed in the terms of reference of this Workshop. It is also extremely important that modelling exercises include an ability to take into account environmental variability in the short-term and the long-term.

5.2 Data

It is not possible to generalise about data requirements other than to note that these will be case-specific. Given the discussion above, it is clear that there will be very considerable data requirements (preferably time series not just a single 'snapshot') for all levels in the system, even with 'minimal' approaches. This again points to the need for cooperation with other organisations to discover: (1) the nature of the data available; (2) the quality of the data available; and (3) the likelihood of obtaining sufficient quality data for any identified gaps.

5.3 Conclusion

The reality is that for no system at present are we in a position, in terms of data availability and model development, to be able to provide quantitatively predictive management advice on the impact of cetaceans on fisheries or fisheries on cetaceans. To reach such a position will require a considerable investment in time and resources.

Given this, the Workshop **agreed** that it would be best to concentrate effort on those areas/systems where there is the most likely chance of success based on a number of factors, including:

- (1) simplicity of the system;
- (2) availability of data;
- (3) ability to collect data in the future;
- (4) likelihood that any predictions can be tested in some way.

The Workshop suggested that the most feasible areas/systems for modelling could be identified according to certain key characteristics summarised in Table 4.

Table 4
System characteristics in relation to modelling feasibility.

System property	More feasible to model	Less feasible to model
Data availability	High or reasonable	Low or non-existent
Food web properties		
No. of species	Relatively low	Moderate or high
No. of species interactions (i.e. complexity of the food web)	Low	High
Species interaction strength	Strong	Weak or diffuse
Habitat properties		
System openness	Relatively closed	Wide open
System boundaries	Tight and obvious	Loose or merging
Depth	Shallow or moderate depth	Deep
Physics (e.g. environmental forcing)	Low - or else obvious	High or else unclear

The Workshop also **agreed** that simulation studies will be required to test the sensitivity of predictions to uncertainty in the data (and model assumptions) and the ability of field techniques to detect the reliability of predictions. The iterative link between modelling and data requirements requires further investigation. The experience of the

Scientific Committee in such work might represent a valuable IWC contribution to cooperative studies, in addition to providing cetacean data and expertise.

6. CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE WORK

The Workshop **agreed** that consideration of ecosystem interactions between fish stocks and cetaceans is a potentially important research topic. At present, considerable further work is required at a variety of levels before the Committee can provide unequivocal answers to the Commission's questions for any system. Even with a large investment of time and money both with respect to modelling and data issues, there is no guarantee that in the medium term, it will be possible to provide the Commission with satisfactory advice. However, if the Commission wishes to pursue this further, the Workshop **draws attention** to the following important issues (it did not have time to discuss these in detail and they represent a synthesis of ideas suggested in the final session):

- (1) All of the modelling approaches available thus far (and developed in the future) must explicitly allow for uncertainty in all aspects of their use including model specification and assumptions.
- (2) Existing models should be used to determine data requirements in terms of quality and quantity.
- (3) The simulation approaches in terms of accounting for uncertainty used in RMP/AWMP development should be considered.
- (4) Modelling approaches should include consideration of how they might be validated.
- (5) Consideration should be given to the possibility of establishing a relatively complex 'virtual' ecosystem for testing approaches.
- (6) Modelling approaches should try taking into account the effects of short-, medium- and long-term ecosystem changes.
- (7) Models must be flexible/expanded to take into account the nature of competition, functional responses etc.
- (8) Fisheries must be modelled realistically, particularly taking into account uncertainty in data; the level of detail and realism required for reasonable single species management may be insufficient for multispecies analyses.
- (9) Further work on field methodology is required to improve data quality and availability for all aspects of systems, including abundance/production of species that are not fishery targets etc; links between models and data requirements should be followed up in terms of sensitivity, power analysis etc.
- (10) Attention should be focused on specific areas/systems where there is most chance of success.

The Workshop **agreed** that the Scientific Committee should try and establish cooperative links with other long-term ecosystem studies (e.g. with ICES), particularly those that include top-predator dynamics as an integral part.

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Annex B

Agenda

1. Introductory items
 - 1.1 Welcoming remarks
 - 1.2 Election of Chair and appointment of rapporteurs
 - 1.3 Adoption of agenda
 - 1.4 Available documents
 2. Overview of existing models
 3. Data requirements
 - 3.1 Cetacean population size and structure
 - 3.1.1 Abundance and distribution
 - 3.1.2 Structure
 - 3.2 Fisheries assessment data
 - 3.3 Population size and structure of prey and competitor species
 - 3.4 Consumption rates by marine mammals
 - 3.5 Diet composition
 - 3.6 Linkages – inter/intra species predation
 - 3.7 Other issues
 4. Individual model structures
 - 4.1 Mass balance/energy system models
 - 4.1.1 ECOPATH
 - 4.1.2 ECOSIM
 - 4.2 Minimum realistic models
 - 4.2.1 MULTSPEC and BORMICON
 - 4.2.2 SEASTAR
 - 4.2.3 Multi-species VPA and MSFOR
 - 4.3 Food web models
 - 4.3.1 Bioenergetic trophodynamics
 - 4.3.2 Index of predator influence.
 5. Synthesis
 - 5.1 Modelling approaches
 - 5.2 Data
 - 5.3 Conclusion
 6. Conclusions and recommendations for future work
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Annex C

List of Documents

SC/J02/FW

- 1 HAUG, T. and LINDSTRØM, U. Diet studies and cetaceans – methodological aspects.
- 2 LEAPER, R. and LAVIGNE, D. Scaling prey consumption to body mass in cetaceans.
- 3 MACKINSON, S., BLANCHARD, J.L, PINNEGAR, J.K. and SCOTT, R. Consequences of alternative functional response formulations in models exploring whale-fishery interactions.
- 4 HARWOOD, J. and McLAREN, I. Modelling interactions between seals and fisheries: model structures, assumptions and data requirements.
- 5 TJELMELAND, S. Is MULTSPEC applicable for assessing cetaceans – fish competition?
- 6 LINDSTRØM, U., TJELMELAND, S. and HAUG, T. Implementing predation by marine mammals in fish stock assessments – minke whales and Norwegian spring spawning herring as a case study.
- 7 CONSTABLE, A.J. and GALES, N. Evaluating the strength of interaction between predators and prey species in food webs: an index of predator influence (IPI) on controlling production of prey.
- 8 YODZIS, P. Bioenergetic trophodynamics.
- 9 MEISENHEIMER, P. Uncertainty in models of predator-fisheries interactions.
- 10 COOKE, J.G. Some aspects of the modelling of the effects of changing cetacean abundance on fishery yields.
- 11 AYDIN, K. ‘Bottom up’ ECOSIM.
- 12 BUNDY, A. ‘Top down’ ECOSIM.
- 13 VINTHER, M. Multispecies VPA.

Annex D

Data Required to Parameterise a Functional Response

J. Harwood

A typical form of the functional response of a predator to changes in the abundance of all of the prey species that it may consume is:

$$F_{i,j} = \frac{a_j N_{i,j}^{m_j}}{1 + \sum_j a_j t_j N_{i,j}^{m_j}}$$

were F_{ij} is the quantity of prey species j consumed by predator i , and N_j is the abundance of prey species j . a_j is often termed the encounter rate with prey species j . A mechanistic interpretation of the functional response is that t_j is the length of time it takes for the predator to handle a single item of prey j . A more empirical interpretation is that it defines an asymptotic value for the number or biomass of prey that an individual predator can consume per unit time.

In order to estimate the parameters of such a functional response, information is required on the number or biomass of each prey species consumed by individual predators over a range of prey abundances, and quantitative information on prey abundance or density in the area over which the predator had been foraging. The relevant diet data can sometimes be reconstructed from stomach contents, provided these are not too digested. However, for species,

like baleen whales, which feed on highly aggregated prey, estimates of diet which use individual stomachs as the sampling unit will probably have a high variance. For many other species, which consume a small number of large prey items per day, many sampled animals will have empty stomachs. Faecal (scat) analysis can provide information on the proportion of different prey that are consumed. The analysis of fatty acid profiles may also be able to provide the same information, although the methodology for this analysis has yet to be published. These proportions can be rescaled to provide estimates of the quantity of prey consumed using estimates of the daily energy requirements of the predator, at least for situations where the total abundance of all prey species is sufficient to meet those requirements.

Estimates of prey abundance are required for all of the prey species known to be consumed by the predator in the area where it has been foraging. These estimates do not have to be unbiased (although the bias should be consistent across prey densities), because the a_j parameters can compensate for this. In general, predators forage on a finer scale than the scale on which data on prey abundance is usually collected, for example in fisheries surveys. Use of prey abundance data that has been collected at an inappropriate scale will reduce the reliability of the estimates of the parameters of the functional response.
