WORKSHOP REPORT

MARINE MAMMALS:
FROM FEEDING BEHAVIOUR OR STOMACH CONTENTS TO ANNUAL CONSUMPTION – WHAT ARE THE MAIN UNCERTAINTIES?

Tromsø, 26 - 28 September, 2001

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CHAIRMAN'S SUMMARY

The main task of the workshop was to consider the methodological approaches to the calculation of consumption by marine mammals, making a detailed assessment of their relative merits. The overall goal was be to make concrete recommendations on what approaches should be emphasised, and to make recommendations for further research in this area.

Two different approaches can in theory be used to give a quantitative description of marine mammal diets: analyses of stomach contents in combination with estimates of stomach evacuation rates, and analyses of stomach or intestinal contents or faeces scaled to satisfy the estimated energy expenditure of the animals. For the latter method indirect evidence of the main prey species may be obtained from studies of feeding behaviour, e.g. by satellite-linked time-depth recorders, if samples of stomachs are difficult to obtain.

The stomach evacuation method is widely used in fishery studies, e.g. to determine the consumption of capelin by cod. In considering the applicability of stomach evacuation methods to marine mammals, the Working Group noted that evacuation must be determined experimentally under a wide variety of conditions, separately for each prey species and size, and that this was difficult for seals and dolphins and impossible for most whales. Such methods may only be applicable in areas and with species where a bolus-feeding pattern prevails, i.e. all food is eaten in one big meal per day, and this is not the case for many species in the northern North Atlantic. The level of assumptions required and general lack of data about evacuation rate for most marine mammals render these methods unsuitable for the calculation of consumption by North Atlantic marine mammals.

For the second method the diet composition and the energy expenditure may be estimated independently of each other:

Diet composition:
The Working Group concluded that the proportions of various prey items in the diet can be safely derived from undigested items in fresh stomach samples if such samples are available. Interpretation becomes increasingly more difficult as digestion proceeds. However, errors associated with identifying the prey eaten by seals from intestinal contents or faeces can be assessed using captive feeding experiments. Such captive feeding trials reveal which bones are most or least resistant to digestion. They also show the influence of fish size and total meal size on the likelihood of recovering bones of prey consumed. Identifying all hard parts to species increases the likelihood of identifying all prey consumed. This is particularly important for large species whose heads are not eaten.

A major difficulty for some species with the use of analyses of stomach or intestinal contents to determine diet composition is that samples are only easily available from a small part of the total distribution area of the animals and only from part of the year. Harp seals in the

Barents Sea illustrate this point as samples have as a rule been restricted to the areas along the ice edge in the spring and early summer. In discussion the Working Group observed that this example demonstrated the need for the collection of samples from the entire distribution range of the animal and at every time of the year, as diet may change greatly with changes in the distribution of prey species. Unfortunately sampling is all too often limited to the areas where samples can be collected easily. However, telemetry will be useful in defining the amount of overlap between marine mammal and fish distributions, provided the distribution of relevant fish species is available.

Data obtained by the remote monitoring of marine mammals, using either data loggers or satellite-linked time-depth recorders, may be used to evaluate the diet composition of the tagged species in the areas in which they operate. The approach is based on comparing data on the temporal and spatial distribution of the predator, including its 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. This approach is of particular interest when studying species such as harp and hooded seals, which, due to their pelagic migratory and dive behaviour, are not readily accessible for traditional diet composition studies based on collections of stomach/intestinal/faecal samples. The approach has obvious limitations, the most prominent ones being related to the often quite small sample size (due to the large costs associated with tagging) and the question of how to identify the likely prey in cases where more than one candidate exists. It was also emphasised that the approach depends heavily on the spatial and temporal resolution and quality of the fisheries resource data, which in most cases is much coarser than is the case for the distribution and dive behaviour data that may be collected from the predator. In discussion the Working Group noted that the co-occurrence of predators and prey in time and space is highly indicative of predation, but confirmatory observations by other means are always desirable. Extension of this work will require closer collaboration between marine mammal and fishery scientists at both national and international levels.

The Working Group also discussed the possibilities of obtaining information on diet composition from analyses of fatty acids and stable isotopes (from biopsy samples). It agreed that these methods are effective in detecting qualitative changes in feeding over the year or life history of the animal. They are also useful for obtaining some information on diet from areas and time periods from which information from traditional methods is not obtainable. However these methods have not as yet proven capable of providing detailed (e.g. species composition) quantitative information on the diet of individual animals, and some members were of the view that there was little hope that they ever would. They are therefore not in themselves adequate for use in estimating consumption.

Energy expenditure:

The energy expenditure (field metabolic rate) of free swimming minke whales has been determined from records of respiratory rate and lung capacity measurements. The Working Group agreed that although there are uncertainties with regard to oxygen extraction and the tidal volume fraction of the measured lung capacities, this estimate provides a useful value for the field metabolic rate of minke whales. Minke whales are amenable to this methodology because they breathe only once during each surfacing, the breathing frequency seems constant over large areas, and, like other whales, the tidal volume does not vary with physical activity. In order to calculate the total energy consumption of minke whales staying in the Northeastern Atlantic during summer time, one factor that has to be taken into account is the amount of energy stored in tissues, such as blubber or growth of a foetus. The calculations suggest that, on average, an additional 30% of daily energy expenditure is deposited per day as tissue energy (fat and foetus) during the summer period.

There is a range of methods available for measuring metabolic rate of seals in the field, but all have serious limitations. There was discussion of the use of heart rate as an indicator of metabolic rate since that could be measured over time periods of multiple months. While the Working Group recognised that there were potentially important limitations of this method, it appears currently to be the only candidate for development into a method for measuring field metabolic rate of species such as harp and hooded seals throughout the year. One alternative method of obtaining information on the energy consumption of wild seals is to use information on the level of food intake of captive animals fed food with known energy density. A study in which three four-year-old harp seals were kept under controlled conditions for a year was reported. The harp seals displayed seasonal changes in appetite, activity levels and fattening which correlates with information from wild populations. Also food intake, expressed as percent of body mass, varied between 1.5 and 5% depending on the season. The energy consumption estimated corresponds to a field metabolic rate (FMR) of about 2.7 times basal metabolic rate. Under certain assumptions such estimates of energy consumption can be used to calculate total food consumption of wild harp seal populations. The Working Group considered that the determination of FMR in captive animals was a valuable approach, but that some means was needed to correlate these observations with free-ranging animals. It has been shown through satellite tag deployments that harp seals spend 80 to 90% of their time diving, an activity that is not reproducible under conditions of captivity.

However, a main conclusion was that for all the relevant species of marine mammals in the North Atlantic the uncertainties in energy expenditure are small compared to the uncertainties in the estimates of abundance and compared to the uncertainties and lack of knowledge of the diet composition. As a first approximation it can be assumed that the marine mammals eat 3% of their body weight per day.

Research needs:
Previous recommendations to move beyond point estimates of consumption to address the range of uncertainties in these estimates are being pursued. It is important to take account of all sources of uncertainties in such computations, even if this requires subjective assessment of the range and probability distribution appropriate to factors which are poorly known.

The following were identified as the most important matters needing additional attention:

- Distribution of prey species in space and time;
- Spatial and temporal distribution of the diet composition of harp and hooded seals;
- Diet composition of dolphins (white-beaked and white-sided dolphins);
- Field metabolic rate of harp and hooded seals;
- Temporal changes in energy density of prey species;
- Diet of minke whales in Icelandic waters and further west;
- Consumption estimates synthesised within a modelling framework including full uncertainty evaluation;

Where do we go from here?

In a *next workshop* the main topic in my opinion should be the expected changes in the North Atlantic ecosystems if (or when) the abundance of one or more of the main fish or marine mammals species are changed abruptly or slowly. These problems can only be approached by ecosystem modelling. A number of different models are available for such studies, and new modelling tools are being developed in many countries. In the workshop the properties of the different models should be discussed and compared, as well as the desired spatial and temporal resolution that should be used for the simulation runs. Important input data to the model calculations will be what prey species the marine mammals choose when more than one prey species is available (diet preferences). Lack of knowledge of important input data to the model calculations should be identified.

Following this workshop, and if it is successful, I propose to contract out two or three tasks to suitable institutions or research groups: One task would be to collect from published literature and from discussions with the relevant scientists the necessary input data to the model calculations (and which have been identified in Workshop 1 and 2). An important point in this connection would be to present different alternatives in situations when direct relevant data are lacking. The other task would be to make one (or two) model(s) ready for simulation runs. The model(s) should have been chosen during Workshop 2. The task would include making a limited number of test runs. A possible third task would be for an economist to prepare the use of a simple econometric model to the output from the ecosystem model.

In a *third workshop* the main task would be to discuss and to chose a limited number of input data sets to the models, and to discuss the results as they will be calculated. This third workshop would of course also include sensitivity analysis of the most important input parameters and a full uncertainty analysis as discussed in the first workshop.

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1. OPENING REMARKS

Chairman Lars Walløe welcomed the members (Appendix 1) to the Workshop, and asked Grete Hovelsrud-Broda, General Secretary of NAMMCO, to give the background to the activities of NAMMCO in this area.

A 1996 Working Group (NAMMCO 1998) looked at the feeding ecology of minke whales, harp and hooded seals and found that there were many uncertainties involved in estimating consumption by these species. It also considered the use of multispecies models to assess species interactions in the Barents Sea and Central North Atlantic. The Scientific Committee, based on the results from the Working Group, concluded that minke whales, harp seals and hooded seals in the North Atlantic might have substantial direct and/or indirect effects on commercial fish stocks.

In 1997, the Council requested the Scientific Committee to pay special attention to studies related to competition and the economic aspects of marine mammal- fisheries interactions. The Scientific Committee, in response, convened a Working Group on the Economic Aspects of Marine Mammal - Fisheries Interactions (NAMMCO 1999). This Working Group considered bio-economic models of varying complexity and associated ecosystem models, and concluded that "many of the analyses were in a preliminary stage and should only be taken as first indications". They further concluded that, despite the preliminary nature of the results, the emerging cost benefit figures warranted serious consideration, as the overall costs to the fishing, whaling and sealing industries incurred by not whaling and/or not sealing could be quite considerable, and that the effects due to predation could be an important part of the overall picture.

At its 8th meeting in Oslo, September 1998, the NAMMCO Council tasked the Scientific Committee with providing advice on the following:

i) to identify the most important sources of uncertainty and gaps in knowledge with respect to the economic evaluation of harvesting marine mammals in different areas;
ii) to advise on research required to fill such gaps, both in terms of refinement of ecological and economic models, and collection of basic biological and economic data required as inputs for the models,
iii) to discuss specific areas where the present state of knowledge may allow quantification of the economic aspects of marine mammal-fisheries interaction;
    a) what could be the economic consequences of a total stop in harp seal exploitation, versus different levels of continued sustainable harvest?
    b) what could be the economic consequences of different levels of sustainable harvest vs. no exploitation of minke whales?

The Working Group on the Economic Aspects of Marine Mammal - Fisheries Interactions met in February 2000 to consider parts i) and ii) of the request. One of the conclusions of the Working Group was that significant uncertainties remain in the calculation of consumption by marine mammals, and this uncertainty was the most important factor hindering the development of models linking consumption with fishery economics (NAMMCO 2001). Considering this conclusion, the Scientific Committee decided to convene this workshop to further investigate the methodological and analytical problems in estimating consumption by marine mammals.

The Chairman emphasised that the main task of the current workshop would be to consider the methodological approaches to the calculation of consumption by marine mammals, making a detailed assessment of their relative merits. Although the estimation of marine mammal abundance is certainly also relevant to this topic, this will not be considered as it is the subject of another NAMMCO Working Group. The overall goal should be to make concrete recommendations on what approaches should be emphasised, and to make prioritised recommendations for further research in this area. The problems related to determining prey preference when more than one prey species is available, and the ecosystem responses to perturbations of the system by natural or anthropogenic causes (e.g. overfishing, culling of marine mammals) will not be discussed in the present workshop, but will probably be the main topic for a future NAMMCO workshop.

2. ADOPTION OF AGENDA

The draft agenda (Appendix 2) was adopted with minor changes.

3. APPOINTMENT OF RAPPORTEUR

Grete Hovelsrud-Broda, General Secretary, and Daniel Pike, Scientific Secretary of NAMMCO, were appointed as Rapporteurs for the meeting.

4. REVIEW OF AVAILABLE DOCUMENTS

The documents considered by the Working Group are listed in Appendix 3.

5. QUANTITATIVE DESCRIPTION OF MARINE MAMMAL DIETS

i. Stomach evacuation methods

Tjelmeland described the Norwegian program for determining the consumption of capelin by cod in the Barents Sea. This estimate is made annually and is used in the assessment of the capelin stock. The amount of capelin consumed by cod has a direct effect on the amount that can be taken by the fishery. The diet of cod is determined from a large sample (ca. 10,000) of cod stomachs collected throughout the distribution range and year. The stomach evacuation rate of cod is determined experimentally in the laboratory by prey species, prey size and temperature. Estimates of cod numbers by size class are available from an annual assessment. A model is used to estimate consumption based on these inputs.

Tamura reported that prey consumption by minke whales in the North Pacific has been estimated using a method based on stomach evacuation rate as estimated from the diurnal change in stomach content weight (SC/9/EC/8). It is assumed in this method that minke whales do not feed at night, and that all prey takes 8 hours to digest. Average daily consumption estimated using this method was between 63 and 113 kg, in general agreement with the 48 to 287 kg estimated using a method combining estimates of field metabolic rate with observed diet.

In considering the applicability of stomach evacuation methods to marine mammals, the Working Group noted that evacuation must be determined experimentally under a wide variety of conditions, separately for each prey species and size, and that this was difficult for pinnipeds and impossible for most cetaceans. Such methods may only be applicable in areas and with species where a bolus feeding pattern prevails, and this is not the case for many species in the northern North Atlantic. The level of assumptions required and general lack of data about evacuation rate for most marine mammals render these methods unsuitable for the calculation of consumption by North Atlantic marine mammals.

ii. Diet composition from analyses of stomachs, intestines or faeces

In presenting some aspects of SC/9/EC/9, Lindstrøm noted that there were limitations and assumptions inherent in all types of dietary analysis, particularly those involving reconstruction of digested contents. A major limitation for stomach and intestinal analysis is that the animal must be killed for sample collection, so that resampling of an individual is impossible. Faecal samples are easy to collect from some pinnipeds and have the advantage of being available from live animals, making it possible to study an animal's foraging behaviour over several foraging events. However their interpretation is difficult because only non-digestible prey items remain and this may lead to bias due to differences in the passage and digestion rates of different species and sizes of prey. Additionally, a meal may be deposited in more than one scat, leading to a risk of autocorrelation between samples. Moreover, there are large differences between the passage and digestion rates of different prey species and prey sizes, and this is likely to affect the reliability of the diet composition estimates. For example large prey are digested more slowly than small prey, and this is likely to lead to overrepresentation of large prey in stomach samples. Hard parts such as fish otoliths, which are commonly used to estimate the original fish weight, are subject to degradation and retention in stomachs. Although correction factors continue to be developed to compensate for digestion of otoliths, we should be cautious making quantitative inferences of animals feeding behaviour when using digested food to reconstruct the diet composition.

Trites reported that errors associated with identifying the prey eaten by pinnipeds can be assessed using simulation models and captive feeding experiments. Models can be used to determine appropriate sample sizes to minimise the error in identifying types and numbers of species consumed. Captive feeding trials reveal which bones are most or least resistant to digestion. They also show the influence of fish size and total meal size on the likelihood of recovering bones of prey consumed.

Identifying all hard parts to species increases the likelihood of identifying all prey consumed. This is particularly important for large species whose heads are not eaten. Scats are thus a reliable means of identifying what species have been consumed. Furthermore, some recovered bones (such as otoliths) can be measured to estimate the size of fish consumed. Although research to date has concentrated on interpreting scat samples, analogous methods could be applied to stomach samples. However, differences in the relative digestibility of different species of prey, and the effects of pinniped activity and the presence of foreign objects in the stomach are not yet understood sufficiently to allow accurate estimates of numbers and sizes of prey consumed.

The Working Group concluded that the proportions of various prey items in the diet can be derived from undigested items in fresh stomach samples. Interpretation becomes increasingly more difficult as digestion proceeds. However it was noted that a proportional diet can be derived even from faecal samples if a large number of samples is available and the prey items are treated as presence/absence and of equal abundance. Table 1 presents a comparison of the advantages and disadvantages of various methods of determining diet composition.

Problems in determining the consumption of capelin by harp seals

In presenting SC/9/EC/7, Tjelmeland noted that modelling tools used in the assessment of commercial fish species in the Barents Sea are specific to species. Cod and herring stocks are assessed by calibrating simple population models to trends in time series data. The capelin assessment is founded on an annual acoustic survey conducted in September.

The mature part of the capelin stock will spawn about April 1 and there are no additional measurements of the spawning stock after September. The capelin dies after spawning. The capelin stock is managed using spawning stock-based biological reference points. At present, the consumption by harp seal on capelin during the period October to April is neglected. It would be important to quantify the mortality generated by consumption by harp seals during this period. However, the available stomach content data are inadequate for that purpose, because the samples have as a rule been restricted to the areas along the ice edge. Also, the understanding of the geographical overlap between capelin and harp seals in this period is poor.

The natural mortality of the immature capelin is estimated from data and consequently a quantification of the consumption by harp seal during April – September is less important.

Annual consumption of herring and cod by harp seal can be included as an additional catch in the current assessment procedures for cod and herring. However, the consumption should be dis-aggregated on prey age.

A co-operation between Fiskeriforskning (Tromsø), the Institute of Marine Research (Bergen) and the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Murmansk) has been started in order to improve the data basis for a quantification of the consumption of fish by harp seal.

In discussion the Working Group observed that this work demonstrated the need for the collection of samples from the entire distribution range of the animal and at every time of the year, as diet may change greatly with changes in the distribution of prey species. Unfortunately sampling is all too often limited to the areas where samples can be collected easily. However, telemetry will be useful in defining the amount of overlap between marine mammal and fish distributions, provided the distribution of relevant fish species is available.

Estimating diets of harp seals off Newfoundland, Canada.

SC/9/EC/5 described the diet of harp seals off the coast of Newfoundland as estimated from the stomach contents of seals collected since 1979. The reconstructed wet weights of ingested prey were estimated from a total of 5,567 prey-containing stomachs collected in 1982 and between 1986 –1998 using methods described in Lawson *et al*. (1995). Of these, 4,453 stomachs were from the east coast of Newfoundland and southern Labrador, Canada (NAFO Divisions 2J3KL). Samples were assigned to either a winter (Oct. – March) or spring (April – Sept.) season and divided into geographical areas based upon designated NAFO areas and distance from shore. The vast majority of samples (93.8%) were obtained from the nearshore area (defined as <25 km from headlands). More samples were obtained during the winter period (n=3,270) than during the spring (n=1,183) due to the seasonal migration of seals out of the area during the summer.

Prey lengths and weights were estimated from direct measurements of undigested prey or using hard parts using part length – total length and part length – and/or length – weight regression equations. If hard parts were too digested or eroded to measure accurately, an average value was calculated for that prey species based on measurable otoliths in the stomach or from samples taken from seals collected at the same area during the same year and season. The use of different regressions was found to result in different estimates of prey weights and lengths. Therefore, regressions based on fish collected in the local area were used as much as possible. Reconstructed wet weights were converted to energy densities using published energy values for each prey species.

To estimate uncertainty associated with diets, samples were grouped according to location and season of collection and simulated data sets of total energy consumed were created using a bootstrapping (i.e. resampling-with-replacement) technique. Each stomach was treated as a unit for resampling purposes. This process was repeated 1000 times to generate estimates of total mass and hence energy, from which proportions contributed by each prey group could be calculated. Visual examination of these distributions suggested that they were approximately normal. Although there is uncertainty associated with the use of regression equations to estimate prey weight, the additional contribution to the overall uncertainty is likely small and not included.

When samples from all years were pooled across years to estimate an average diet for the time period, the greatest proportion of energy in the winter nearshore diet came from Arctic cod (*Boreogadus saida*, 53.85%, SE=1.5), Atlantic herring (14.51%, SE=1.02) and capelin (9.08%, SE=0.55). Capelin (61.42%, SE=7.6) were the largest contributor in offshore areas although there was greater variation than in nearshore areas. American plaice (12.75%, SE=7.79), unidentified pleuronectidae (8.34%, SE=4.72) and shrimp (7.56%, SE=2.01) were also common contributors to the diet.

In discussion it was noted that the proportion of Atlantic cod in the nearshore diet of harp seals has not decreased since the 1980's, despite the near total collapse of the cod stock in the area. The offshore diet was based on relatively few samples as compared to the nearshore even though harp seals are known to spend the majority of their time feeding in offshore waters.

There was general concern that hard parts such as otoliths may underrepresent a prey item in a stomach sample if only part of the prey is eaten. This has been observed among harp seals. This is an area where the supplementary techniques described under 5.iii. may prove particularly useful in determining if hard parts provide an accurate estimation of the representation of the prey item in the diet.

iii. Diet composition from fatty acids, isotopes and proteins

Although the Working Group had no papers that dealt directly with this topic, published papers have shown that the methods are useful for some purposes. In general they give an integrated view of feeding over large spatial and temporal scales. They are effective in detecting qualitative changes in feeding over the year or life history of the animal. They are also useful for obtaining information on diet from areas and time periods from which information from traditional methods is not obtainable. However these methods have not as yet proven capable of providing detailed (e.g. species composition) quantitative information on the diet of individual animals, and some members were of the view that there was little hope that they ever would. They must therefore be supplemented with traditional methods of diet determination and are not in themselves adequate for use in estimating consumption.

iv. Diet composition from feeding behaviour

Data loggers and telemetry

Folkow presented information on how data obtained by the remote monitoring of marine mammals, using either data loggers or satellite-linked time-depth recorders, may be used to evaluate the diet composition of the tagged species in the areas in which they operate. The approach is based on comparing data on the temporal and spatial distribution of the predator, including its 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. This approach is of particular interest when studying species such as harp and hooded seals, which, due to their pelagic migratory and dive behaviour, are not readily accessible for traditional diet composition studies based on collections of stomach/intestinal/faecal samples.

Data from recent satellite-telemetry studies of harp seals from both the Greenland Sea and Barents Sea populations, as performed by representatives of the Department of Arctic Biology, University of Tromsø, were presented to exemplify the type of data that may be provided by use of this approach. This includes data on the geographical area in which the tagged animals operate at different times of the year, their diving behaviour (dive depths) within these areas, which, when related to bathymetry, may indicate whether they were feeding on benthic or pelagic prey. Moreover, potential temporal (diurnal) changes in diving depths within an area may indicate whether the prey performed diurnal vertical migrations or not, which may represent yet another cue as to what type of prey the predator was feeding on. The approach has obvious limitations, the most prominent ones being related to the often quite small sample size (due to the large costs associated with tagging) and the question of how to identify the likely prey in cases where more than one candidate exists. It was also emphasised that the approach depends heavily on the spatial and temporal resolution and quality of the fisheries resource data, which in most cases is much coarser than is the case for the distribution and dive behaviour data that may be collected from the predator.

Boyd presented information on animal-mounted video cameras, which are beginning to be used to examine the foraging behaviour of pinnipeds. This method has been restricted to use on animals that can be recaptured and is therefore presently not useful for most North Atlantic marine mammals. However the method has some potential to provide additional information about diet.

In discussion the Working Group noted that the co-occurrence of predators and prey in time and space is highly indicative of predation, but confirmatory observations by other means are always required. The difference in spatial and temporal scales between fisheries surveys and telemetric tracking data is problematic, but additional information can be gained by monitoring fishing activities in the area as well. Extension of this work will require closer collaboration between marine mammal and fishery scientists at both national and international levels.

General discussion

It is apparent that valuable information on diet can come from a variety of sources, and that some methods are suitable for some species, times and areas, but impossible or of limited use for others. The advantages and disadvantages of various methods are summarised in Table 1, and their applicability to various species is described in Table 2.

The challenge remains to integrate information from a variety of sources to get a better quantitative picture of diet, along with the uncertainty associated with its estimation. To do this will require the process of diet determination to be dis-aggregated into its component parts, including components related to spatial and temporal distribution, and the age, sex and reproductive status of the predator, and the energy density of the prey. Data from different sources, along with estimates of precision, can then be entered into the appropriate part of the framework. If no data exists, appropriate "guestimates" can be used. Uncertainty in the estimation of diet can then be estimated by resampling techniques. The Working Group developed an example of such a framework, described in Annex 1.

6. ESTIMATING ENERGY CONSUMPTION

i. Baleen whales

Determination of field metabolic rate from energy expenditure

Blix explained how the energy expenditure (field metabolic rate) of free swimming minke whales has been determined from records of respiratory rate and lung capacity measurements, as described in Blix and Folkow (1995). From this effort a value of 80 kJ. kg^{-1} day^{-1} was obtained for a 4000 kg animal.

The working group agreed that although there are uncertainties with regard to oxygen extraction and the tidal volume fraction of the measured lung capacities, this estimate provides a useful value for the field metabolic rate of minke whales, which is 2.2 times the basal metabolic rate as estimated by Folkow and Blix (1992). Minke whales are amenable to this methodology because they breathe only once during each surfacing, the breathing frequency seems constant over large areas, and like other whales, the tidal volume does not vary with physical activity.

Estimating energy use for tissue deposition

In order to calculate the total energy consumption of minke whales staying in the Northeastern Atlantic during summer time, one factor that has to be taken into account is the amount of energy stored in tissues, such as blubber or growth of a foetus. Nordøy presented information gathered during the Norwegian scientific minke whaling programme when a number of minke whales caught early in the summer season (average catch date: mid-May) and late in the summer season (average catch date: mid-September) were dissected and the amount of muscle mass, blubber mass and visceral fat determined (Nordøy *et al.* 1995). The energy density of samples of the different tissues were determined by bomb calorimetry and the total amount of energy stored into blubber, muscle mass, visceral fat and growth of foetus determined for an assumed stay of 180 days in Northeast Atlantic waters. The calculations suggest that, on average, about 150,000 kJ is deposited per day as tissue energy during this period in an adult (6,000 kg) whale. This amounts to 30% of daily energy expenditure. It can moreover be calculated that this amount of stored energy can only cover about one third of the energy expenditure during the 180 days when the whales are supposed to be in other waters. The energy consumption for different age classes and sex of minke whales was determined by combining the above data with data on energy expenditure and urinary and faecal energy loss.

The residence time of 180 days for minke whales in the Northeast Atlantic is an important assumption in the model. Very few whales are detected in early spring, at a time when there is good enough light to see them if they were there. It is possible that some minke whales stay during the dark winters, but observations of migratory patterns suggest that most whales leave the area during winter. Nothing is known about the whereabouts of juveniles, but it is thought that new-borns could not survive in the cold winter water. The body condition of the minke whales in spring suggests that they do not feed as much in winter, because most of the blubber has disappeared by then.

ii. Seals

Free ranging animals

Boyd presented a range of methods available for measuring metabolic rate in the field. These mainly include indirect respirometry and include the use of single- and double-labelled water, and heart rate. All methods have limitations. A relatively small total number of individuals are usually included within studies and these usually include a narrow range of size, age and sex classes. Since information is mainly restricted to a narrow range of age, size and sex classes from a narrow range of species, it is necessary to extrapolate among age, size and sex classes and also among species.

There is a requirement to develop a method that will allow the estimation of metabolic rate of seals that range over large distances and that cannot be recaptured. There was discussion of the use of heart rate as an indicator of metabolic rate that could be measured over time periods of multiple months. While the Working Group recognised that there were potentially important limitations of this method, it appears currently to be the only candidate for development into a method for measuring field metabolic rate of species such as harp and hooded seals throughout the year. This will require further validation of heart rate and the development of instrumentation to allow the transmission of data to a satellite.

Captive animals

One alternative method of obtaining information on the energy consumption of wild seals is to use information on the level of food intake of captive animals fed food with known energy density. The relatively small body size of the harp seals compared to baleen whales, like minke whales, makes it feasible to obtain long-term measurements of food intake on a number of captive animals. Nordøy reported on a study in which three four year old harp seals were kept under controlled conditions for a year and the exact daily food intake was monitored. The experimental photoperiod simulated the outdoor photoperiod at 70°N, while water temperature was close to natural. Body condition was monitored by labelled water techniques, while the activity pattern was recorded through wave movements. The harp seals displayed seasonal changes in appetite, activity levels and fattening which correlates with information from wild populations. Also food intake, expressed as percent of body mass, varied between 1.5 and 5% depending on the season. On average, the energy consumption or Gross Energy Intake was about 26,000 kJ/day for an average body mass of about 81 kg, which when corrected for loss of energy through faeces and urine, corresponds to a field metabolic rate (FMR) of about 2.7 times basal metabolic rate (Kleiber). Under certain assumptions such estimates of energy consumption can be used to calculate total food consumption of wild harp seal populations.

The Working Group considered that the determination of FMR in captive animals was a valuable approach, but that some means was needed to correlate these observations with free-ranging animals. It has been shown through satellite tag deployments that harp seals spend 80 to 90% of their time diving, an activity that is not reproducible under conditions of captivity. It is possible that the FMR of free ranging animals may actually be lower than that of captive animals in some cases.

7. METHODS FOR INTEGRATING CONSUMPTION, ABUNDANCE AND DISTRIBUTION INFORMATION

Trites presented three different approaches to estimating the amount of food consumed by marine mammals.

The first is a multispecies or ecosystem approach, which estimates the amount of energy flowing to marine mammals from their prey. Ecopath is a software package that uses mass balance principles to model ecosystem dynamics. Six parameters are required for each species or group of species in the ecosystem. They include biomass (total weight of all age classes), diet composition (the fraction of different species consumed), consumption (the amount consumed per year), production (accumulated and lost biomass), ecotrophic efficiency (the fraction of production passed up the food web) and export (what leaves the ecosystem). This approach is informative about the relative amounts of prey consumed by different species within the ecosystem, but estimates may not be particularly precise.

A second approach to modelling consumption by marine mammals applies the following framework

$$Q_i = \sum_s N_{is} W_{is} R_{is}$$

where Q_i is consumption by species i, N is the number of individuals by sex s of species i, W is the mean individual weight by sex and species; and R is the daily ration for an individual of weight W. This simple model can be applied to species of marine mammals about which little is known.

A third approach for modelling gross energy requirements (*GER*) uses the following framework:

$$GER = \frac{P + (A \times BM)}{E_{HIF} \times E_{f+u}}$$

where *P* is production or energy deposition, *A* is an activity metabolic multiplier, *BM* is basal metabolism, E_{HIF} is the efficiency of utilisation of metabolizable energy (or 1 – heat increment of feeding as a proportion of metabolizable energy), and E_{f+u} is fecal and urinary digestive efficiency (metabolizable energy as a proportion of gross energy). This detailed approach can be used to estimate the energy requirements for each age, sex, reproductive status (immature, mature, pregnant), and day of the year.

Working paper SC/9/EC/6 used this detailed approach to estimate the energy requirements of Steller sea lions. Most model parameters (means and standard errors) were derived from captive experiments and field observations of sea lions. Some parameters were drawn from studies of other pinnipeds. Parameters were selected at random (from their estimated distributions), and the model was run 1,000 times to yield a mean estimate (plus standard deviation) of gross energy requirements. A sensitivity analysis indicates that most of the uncertainty in model estimates for Steller sea lions can be attributed to uncertainty in basal metabolism and the activity multiplier (*A BM*), and suggests directions for future research.

All three approaches to modelling bioenergetics offer different, but complementary insights into the amounts of prey consumed by marine mammals.

In discussion the Working Group expressed some surprise at the high consumption estimated for juvenile animals in SC/9/EC/6, up to 13% of body weight per day. Some members felt that this was unrealistically high; this might relate to concerns about the formulation of the equation for GER above. The Working Group also noted that in other areas, population parameters have been among the largest contributors to the variance of the consumption estimate, whereas in this case uncertainty about metabolic rate was the major factor. This is presumably dependent on the precision of the available estimates of population size, age structure, etc., which are quite low for most populations. However there is some subjectivity in the estimation of precision, because for some components of the model precision is not known and best guesses must be substituted.

Estimates of precision are not presently implemented into Ecopath models so the results may be misleading. However they do provide an excellent framework for incorporating data from a variety of sources and gaining a better understanding of the role of the predator in the ecosystem.

Estimating the consumption by NW Atlantic harp seals

In SC/9/EC/5, consumption of prey by harp seals in NAFO divisions 2J3KL was estimated using a bioenergetics model that integrates information on the numbers at age, age-specific energy requirements, seasonal distribution and diet of the predator. Abundance was estimated using a population model integrating pup production, annual estimates of reproductive rates and data on age-specific removals. Energy requirements were estimated using age specific body mass. The proportion of energy obtained off Newfoundland was considered proportional to the residency time of seals in the area based on results of satellite telemetry and traditional tagging studies. The diet of harp seals in nearshore and offshore waters during winter and spring was determined by reconstructing the wet weight of stomachs collected in 1982 and 1986-1998. Uncertainty in the consumption estimates were approximated by incorporating the variance in the numbers at ages, diets and seasonal distribution into the model using resampling procedures. Capelin and Arctic cod were the primary prey consumed while Atlantic cod was a relatively small component of the individual diets. Based on their average diet, harp seals consumed an estimated 893,000 (95% CI: 682,000-1,100,000) tonnes of capelin, 185,000 (95% CI: 58,000-457,000) tonnes of Arctic cod and 37,000 (95% CI: 14,000-62,000) tonnes of Atlantic cod in 2000. Improvements in estimates of consumption can be achieved by further diet sampling in offshore areas and increased information on residency of seals of all ages in the area. However, estimates will likely remain quite variable owing to the strong temporal and spatial changes in diet composition.

Rosing-Asvid pointed out some factors that might influence the outcome of the consumption model presented in SC/9/EC/5. The distribution of the harp seals found by telemetry is based on animals released around Newfoundland in late May-June. By this time the number of adult harp seals in Greenland is already peaking and these early –migrating animals are therefore not included in the seasonal distribution used in the model. The migration pattern is likely to be influenced by the time by which the animals start to migrate, because the optimal foraging strategy may be different for an animals that starts to migrate in late April compared to an animal that starts to migrate in mid June. It is therefore important to distribute the transmitters so the early migrants and all age and sex groups are included.

Data was presented indicating that harp seals start to leave Greenland not as one unit, but with fat seals leaving first, and it was argued that weight increases in one area might be caused by the influx of fat animals and not necessarily fat gained in the area. In order to derive a model that takes care of these kinds of energy transfers when calculating consumption in particular areas, the mean weight and energy content of the stomachs from that area should be incorporated.

In discussion the Working Group noted the observation that it appears that Northwest Atlantic harp seals hardly ever leave shallow waters, just as in the Barents Sea. Seals off the coast of East Canada are not usually found in waters deeper than 400-500 meters. Seals were observed to stay mainly on the shelf and move quickly between shelf edges.

8. RESEARCH NEEDS

Background

Previous recommendations (NAMMCO 2001) to move beyond point estimates of consumption to address the range of uncertainties in these estimates are being pursued (e.g. SC/9/EC/4, 5 and 6)). It is important to take account of all sources of uncertainties in such computations, even if this requires subjective assessment of the range and probability distribution appropriate to factors which are poorly known (see also Annex 1).

Such exercises also provide guidance on research priorities, as they quantify the proportions of the overall uncertainty in consumption estimates that is attributable to each of the component factors. Priority should then be given to research aimed at improving knowledge on those factors which contribute most to the overall uncertainty. There is little point in investing resources in a factor that contributes little to the overall uncertainty, if improvements are not first possible for other more influential factors.

In discussion, the question was raised as to how to account for "uncertainties about uncertainties" when dealing with factors for which probability distributions need to be specified in a more subjective manner. It was suggested that computations be repeated for each of the different specifications of such distributions by a number of scientists involved in the research concerned. What is important is the ranking of factors as regards their impact on the overall uncertainty in a consumption estimate. It was suggested that consumption estimate exercises for the marine mammals and regions of interest be conducted on this basis, i.e. incorporating full evaluation of all uncertainties.

It was further suggested that attention would need to be given as to what aspects of consumption estimates were most influential as regards conclusions concerning the possible impact of marine mammals on fishery catches. While estimates of consumption would be important, it could be that estimating the extent to which such consumption and its components by species change in response to changes in prey species abundance will prove even more important. This may affect research priorities.

Specific Research Recommendations

The following were identified as the most important matters needing additional attention:

- Distribution of prey species in space and time;
- Spatial and temporal distribution of the diet composition of harp and hooded seals;
- Diet composition of dolphins (white-beaked and white-sided dolphins);
- Field metabolic rate of harp and hooded seals;
- Temporal changes in energy density of prey species;
- Diet of minke whales in Icelandic waters and further west;

- Consumption estimates synthesised within a modelling framework including full uncertainty evaluation;

The next workshop should *inter alia* consider which aspects of consumption estimates are likely to be most influential for calculating the possible impact of marine mammals on fishery catches

9. ADOPTION OF REPORT

The Report was adopted by the Working Group on September 28, 2001 at 1615. The Working Group expressed its thanks to Professor Blix and the Department of Arctic Biology for hosting the Workshop at The University of Tromsø, NAMMCO for the practical arrangements and Walløe for his chairmanship.

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Table 1. Relative merits of various methods of determining the diet composition of marine mammals.

Method	Advantages	Disadvantages
Stomach	i) Information on meal size and composition; ii) Information tied to an individual; iii) Easy to obtain samples from a hunt, bycatch or cull;	i) Resampling of individuals impossible; ii) Sampling not possible in small, localised populations iii) Sample size small relative to total population; iv) Sampling may be biased with respect to space, time, age/size/class structure of the population ; v) Potential correlation between samples
Intestine	i) Potentially integrates across several meals; ii) Information tied to an individual; iii) Easy to obtain samples from a hunt, bycatch or cull;	i) Resampling of individuals impossible; ii) Sampling not possible in small, localised populations iii) Sample size small relative to total population; iv) Sampling may be biased with respect to space, time, age/size/class structure of the population v) Loss of resolution of prey composition vi) Potential correlation between samples
Scat- Hard Parts	i) Potentially integrates across several meals; ii) Relatively easy to obtain samples for some species; iii) Non-lethal and non-invasive; iv) With appropriate spatial and temporal stratification could provide an accurate indication of diet in species that haul-out regularly v) Sampling of small/localised populations is possible vi) In some species, unlimited sample size.	i) Not applicable to species that rarely haul-out; ii) Resampling of individuals is difficult; iii) Samples may not be independent; iv) Potential for bias when there is spatial and temporal heterogeneity in diet; v) Substantial loss of resolution of diet composition vi) Information tied to an individual if accompanied by molecular genetics, and this is costly.

Method	Advantages	Disadvantages
Scats - Proteins or DNA	i) Potentially integrates across several meals; ii) Relatively easy to obtain samples; iii) Non-lethal and non-invasive; iv) With appropriate spatial and temporal stratification could provide an accurate indication of diet in species that haul-out regularly v) Sampling of small/localised populations is possible vi) In some species, unlimited sample size.	i) Does not work in all circumstances? ii) Requires large amount of data about proteins in prey species; iii) Information tied to an individual only if accompanied by molecular genetics, and this is costly; iv) Potential for bias when there is spatial and temporal heterogeneity in diet;
Fatty acid signature analysis	i) Integrates over long time scales; ii) Samples relatively easy to obtain from lethal or non-lethal sampling; iii) Relatively non-invasive; iv) Resampling of individuals may be possible;	i) Require large amount of information about prey fatty acids; ii) Coarse resolution; iii) High cost; iv) Potential for bias when there is spatial and temporal heterogeneity in diet; v) Heterogeneity of distribution in tissues. vi) Quantitative description of diet not currently possible.
Stable isotopes	i) Integrates over very long time scales; ii) Samples relatively easy to obtain from lethal or non-lethal sampling; iii) Relatively non-invasive; iv) Resampling of individuals may be possible; v) Historical sampling is possible;	i) Very coarse resolution; ii) Requires large amount of information about isotopic levels in prey. iii) High cost; iv) Potential for bias when there is spatial and temporal heterogeneity in diet; v) Heterogeneity of distribution in tissues. vi) Quantitative description of diet not currently possible
Satelite Linked Time Depth Recorder/Time Depth Recorder	i) Longitudinal information for individuals; ii) Sampling over large spatial and temporal scales; iii) Information is spatially and temporally explicit iv) Linked to specific individuals	i) Lack of ground-truthing ii) Not easily applied to large cetaceans; iii) Costly, implying small sample size of individuals; iv) Depends on the availability of fishery data. v) Relatively indirect.
Camera	i) Highly detailed information about prey encountered; ii) Linkage to specific behaviour and locations; iii) Linked to specific individuals	i) Recovery of data is difficult in most circumstances; ii) Small sample size; iii) Not easily applicable to all species; iv) Short record duration, i.e. sampling over small spatial and temporal scales; v) Prey encountered may not equal prey ingested

Method	Advantages	Disadvantages
Direct Observation	i) Detailed information about location and timing; ii) Possible prey identification; iii) Linkage to individuals in some species;	i) Applies to a narrow range of species and situations; ii) Possible sampling bias, including observer effects; iii) Small sample size

Table 2. Scientific applicability of methods of diet determination to some North Atlantic taxa of marine mammals. If no *, method is not applicable; if ***, method is very applicable.

	Stomach[1]	Intestine[1]	Scat - Hard Parts	Scat - Protein/ DNA	Fatty Acid Signature Analysis	Stable Isotope	Time Depth Recorders[2]	Camera	Direct Obser-vations
Minke	***	**			*	*	*		*
Dolphins	***	**			*	*	*		*
Harp	**	**			*	*	**		
Hooded seal	**	**			*	*	**		
Grey seal	*	**	***	*	*	*	**	*	
Harbour seal	*	**	***	*	*	*	**	*	

[1]Applicability limited in time and space for logistic and political reasons.
[2]Applicability depends on information on prey distribution.

FRAMEWORK MODEL FOR QUANTITATIVE DETERMINATION OF CONSUMPTION

The annual consumption (C) by a predator of a particular species is basically calculated as:

$$C = N \times R \times p$$

where N = number of predators
R = annual food intake requirement for predator
p = proportion of diet made up by a species of interest.

The computation becomes complicated because neither N nor p are "homogeneous". Both may depend on space, time of year, predator age and predator sex. As predator requirements are in terms of energy, strictly R relates to energy rather than mass intake. This introduces further non-homogeneity considerations. First the energy content per unit mass of prey differs between prey species, and also within a species at different times of the year. Secondly, the predators own energy requirements vary with season. For ease of presentation, these considerations are not pursued further below, but the approach can readily be extended to take them into account.

Thus one needs to calculate:

$$C = \sum space \sum time \sum age \sum sex (N \times R \times p)$$

Difficulties then arise because of absence of information on either of N or p when data are disaggregated into these "strata" for the computation.

Consider a simple example for N which ignores age and sex, and has 2 strata for each of space and time. Ideally what is wanted is to estimate proportions (shown as percentages) along the lines indicated in the following matrix:

Time	**Area 1**	**Area 2**
Summer	25 ± 5	75 ± 5
Winter	60 ± 10	40 ± 10

The first figure in each block indicates the true (but unknown) average proportion of the predator population in the stratum, while the second represents the extent to which this proportion varies between years.

Typically different sources of data will provide information on some but not all of the entries in such a matrix. to be able to combine such data sources in an optimal way to best estimate the values for the matrix as a whole, it is important to clarify first as to exactly which entries each source of data provides information upon.

For example, an annual summer survey over two years would provide information on all entries in the top row of the example matrix above. In contrast, satellite tagging over one year could provide information on all average value entries in the matrix, but not on the interannual variability. Dis-aggregated information on species proportion in the diet (*p*) can be dealt with similarly to numbers (*N*) above. There are statistical methods available (e.g. maximum likelihood estimates) which can combine two such sources of information to provide best estimates of all the entries shown in the matrix, together with estimates of the precision of each.

Some methods yield information too crude to evaluate on such a basis. While best "guestimates" can be used in such circumstances, these in isolation have the problem of failing to take account of the associated uncertainty in the overall estimates of imprecision of consumption estimates. What is needed here is to select not only the single best "guestimate", but to provide a range of possible values with an informed judgement on the relative probability accorded to each. By repeated sampling from this distribution in performing computations, such uncertainty can be reflected in overall results.

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Appendix 2

AGENDA

1. Opening remarks
2. Adoption of Agenda
3. Appointment of Rapporteur
4. Review of available documents
5. Quantitative description of marine mammal diets
    - i. Stomach evacuation methods
    - ii. Diet composition from analyses of stomachs, intestines or faeces
    - iii. Diet composition from feeding behaviour
6. Estimating energy consumption
    - i. Baleen whales
    - ii. Seals
7. Methods for integrating consumption, abundance and distribution information
8. Research needs
9. Adoption of report

LIST OF DOCUMENTS

Document No.	Document Name
SC/9/EC/1	Draft list of participants
SC/9/EC/2	Draft agenda
SC/9/EC/3	Draft list of documents
SC/9/EC/4	Boyd, I.L. A generalised algorithm for estimating the energy, carbon and prey consumption of pinnipeds and penguins.
SC/9/EC/5	Stenson, G.B. and Perry, E. Incorporating uncertainty into estimates of Atlantic cod (*Gadus morhua*), capelin (*Mallotus villosus*) and Arctic cod (*Boreogadus saida*) consumption by harp seals in NAFO Divisions 2J3KL.
SC/9/EC/6	Winship, A.J, Trites, A.W. and Rosen, D.A.S. A bioenergetic model for estimating the food requirements of Steller sea lions (*Eumetopias jubatus*) in Alaska.
SC/9/EC/7	Tjelmeland, S. Consumption of capelin by harp seal in the Barents Sea - data gaps.
SC/9/EC/8	Tamura, T. Geographical and seasonal changes of prey species and prey consumption in the western North Pacific minke whales.
SC/9/EC/9	Lindstrøm, U. Foraging ecology of minke whales (*Balaenoptera acutorostrata*): Composition and selection of prey in the northeast Atlantic. Dr. Sci. Dissertation, University of Tromsø, 2001.
SC/9/EC/10	Fisheries Agency, Japan. Photographs taken during Japan's whale research in the Western North Pacific (JARPN II) in August and September 2000.

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