

Annex L

Report of the Standing Working Group on Ecosystem Modelling

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1. INTRODUCTORY ITEMS

1.1 Introductory remarks

Kitakado welcomed the members of the Standing Working Group on Ecosystem Modelling (hereafter Working Group).

1.2 Election of Chair

Kitakado was elected Chair.

1.3 Appointment of rapporteurs

Herr and Archer were appointed rapporteurs.

1.4 Adoption of agenda

The adopted agenda is included as Appendix 1.

1.5 Documents available

The documents available to the Working Group were identified as SC/68A/EM/01-04, SC/68A/SP/05, Watari *et al.* (2018) and Cunen *et al.* (2019).

2. REVIEW ISSUES RELEVANT TO ECOSYSTEM MODELLING WITHIN THE SCIENTIFIC COMMITTEE

2.1 Modelling of relationship between whales and prey

Appendices 1 and 2 of SC/68A/SP/05 reported the final conclusions of the estimates of prey consumption of sei, Bryde's, and common minke whales in the offshore area, and common minke whale in the coastal areas, respectively, based on JARPNII samples. The analyses took into consideration some analytical recommendations from the IWC SC. The effect of sampling design on prey consumption estimates in the coastal and offshore areas was assessed by 'CATDAP', one of the categorical data analysis tools based on AIC. Results showed that sampling design had a negligible effect on the estimates of prey consumption. Uncertainties associated to relevant parameters such as consumption estimate equations, body weight of whales, and caloric value of prey species, were treated with Monte Carlo simulations. The prey consumption during May-September in the offshore area by common minke, Bryde's, and sei whales were 1.2 and 1.3 million tons *per year*, for the periods 2000-07 and 2008-16, respectively. The range of CVs was 0.12-0.22. In the coastal area off Sanriku, prey consumption during March-June by common minke whales was 4,498 tons, 2,154 tons and 1,097 tons per year in 2005, 2006 and 2012, respectively. The range of CVs were between 0.08 and 0.09. In the coastal area off Kushiro, prey consumption during September-October by common minke

whales varied between 783 and 4,030 tons per year during 2002 to 2012. The range of CVs was 0.20-0.27. Results of the updated analyses confirmed those presented to the 2016 JARPNII final review.

In discussion, the consideration of interactions of explanatory variables in the analyses was discussed. The authors explained that they had not investigated inclusion of interactions of explanatory variables. It was assumed that they were not supportive, due to the sparseness of the data. Furthermore, clarification regarding uncertainty in the analyses was needed as the updated estimates of prey consumption is based on Monte Carlo methods involving uniform distributions for various parameters. The rationale for choice of parameters of the uniform distributions needs to be more fully justified. In addition, some of the parameters relate to parameters that pertain to the entire population and others to individuals within the population. Therefore, clarification of what the reported CVs relate to is required. The Working Group appreciated the updated analyses and recognised that the recommendations of the 2009 and 2016 JARPNII workshops had been followed.

Attention: SC

The Working Group recommended a further investigation of the possibility of using interaction terms as well as providing further clarification on the distribution of the uncertainties.

Watari *et al.* (2018) reported the results of an ecosystem modelling exercise in the western North Pacific in 2013 using Ecopath which focused on small pelagic fishes. At the time of the JARPNII review workshop held in 2016, the results of an ecosystem modelling approach using Ecopath with Ecosim in the western North Pacific from 1994 to 2013 were presented. The model presented to the review meeting has now been improved and this paper presents a part of the improvements. The Ecopath model had the sub-model structure with three blocks to take account of physical and biological differences by regions. In accordance with the guideline to develop the Ecopath model, the quality of the input data was assessed by pedigree, and a series of pre-balance diagnostics was conducted to evaluate the initial static energy budget. An ecological index, L-index, suggested that the state of the ecosystem in the western North Pacific in 2013 was intermediate between overexploited and sustainably fished. The outcome of the Ecopath model also indicated that the contribution of small pelagic fishes to both predator production and commercial catch of other species in the western North Pacific is high compared with many other ecosystems. This static, mass-balanced Ecopath model is considered a first step towards understanding the ecosystem of the western North Pacific. Development of the Ecosim component is still ongoing but it is expected that the result will contribute strategic consideration to fisheries management of the western North Pacific at the ecosystem level.

The implications of Ecopath as a static model being used for a dynamic system were discussed. Given the limitations of the dataset, Ecopath was undertaken under the assumption of a closed system, which in reality the study area is not,

especially east of 150°E. Particularly highly mobile whales are known to move in and out of the area. Furthermore, the possibility of an analysis of the sensitivity of temporal changes in dynamic small pelagic fish to the static assumption of Ecopath to further investigate the justification of the chosen approach was raised. The authors confirmed that future exercises will include analyses of how biomass uncertainty influences Ecopath. Furthermore, it was pointed out that small pelagic fish are very variable in biomass and thus are very difficult to handle in Ecopath as static models. Therefore, the necessity for biomass accumulation in an unbalanced system was emphasised. The general need to take models from static to dynamic was underlined, noting that in the context of the Scientific Committee work one main aim of this kind of modelling exercises is an assessment of the impact of whales on prey populations.

The Working Group congratulated the authors on the accomplished analyses and **encouraged** them to continue their work in ecosystem modelling and conservation.

Paper SC/68A/EM/04 presented a progress report on the analysis of the sandlance population off Sanriku. A state-space two-stage population dynamics model with a stock-recruitment relationship was used for expressing sandlance population dynamics. Catch and several abundance indices of sandlances and estimates of consumption of sandlances by some predators were used when estimating parameters in the population model. To consider several stochastic flexibilities such as process errors, a Bayesian method was used to estimate the parameters and latent variables in the model. The results showed that predation by the common minke whale accounts for only a little proportion of the current biomass of the sandlance population, while predation impacts by other species recently might be dominant. The results of this study are preliminary because of needs for further validation of consumption of sandlances by predator species and further modelling process for linking sandlance and several predators through simultaneous estimation of populations dynamics.

In discussion, several suggestions for consideration in the modelling approach were made. Firstly, the inclusion of CVs of the sandlance survey estimates in variance estimation was suggested, as well as presentation of posteriors and confidence intervals. Furthermore, an apparent time-related bias in the residuals was pointed out. The question of reasonable units for biomass was discussed, whether use of numbers or weight is more reasonable. It was suggested that calculation with numbers and multiplying by weight may be the easiest way forward to calculate biomass in this approach. It was suggested to use raw data on consumption as data in the model, rather than consumption trend data without uncertainty.

The Working Group thanked the authors for their updates and **encouraged** them to include the suggestions made and to continue their efforts in this research.

2.2 Modelling of competition among whales including progress with IBEMs

This topic is one of the Committee's standing items, but this year, the Working Group did not receive any updates. Nevertheless, the Working Group expressed interest in this work, and welcomed future submissions to the Scientific Committee.

2.3 Progress on considering effects of long-term environmental variability on whale populations

The Working Group noted that this was an active area of research and was of particular interest to the Committee

with regards to how long-term environmental variability might affect stock assessments. The Working Group **agreed** to continue the discussion and looked forward to future submissions to the Scientific Committee.

Attention: SC

*The Working Group **agreed** to continue the discussion about effects of long-term environmental variability on whale populations.*

2.4 Progress on body condition analysis

Paper SC/68A/EM/02 presented results of body condition analyses of common minke whales in the northeast Atlantic. The common minke whale is a boreo-arctic species, and the summer period is generally characterised by intensive feeding and consequently seasonal fattening at high latitudes. The fat deposited is stored as energy reserves for overwintering at lower latitudes where feeding is greatly reduced. It is therefore expected that their body condition on the summer grounds will reflect food availability during their most intensive feeding period and thus indicate how well the high latitude ecosystems can support the populations. During the commercial catch operations on feeding grounds in Norwegian waters, body condition data (blubber thickness and girth) have been collected from 13,216 common minke whales caught in 1993-2018. Using this time series to investigate associations between body condition and time/area in minke whales, several statistical approaches were applied. The analyses revealed a significant negative trend from the start until 2015. After 2015, the trend was reversed and body condition values increased significantly. It has previously been suggested that there may be a link between the decreased minke whale body condition and the abundance of the Barents Sea cod stock, which increased to a record high level between 2006 and 2015. Recruitment of the cod stock during more recent years has been low with a subsequent and continuous decrease in the total stock after 2015 to a current level which is presumably approximately 60% of the 2015 level. Interestingly, the observed common minke whale body condition was at its lowest in 2015, increasing afterwards. This may support a connection between cod abundance and feeding conditions for other top predators such as common minke whales.

The Working Group welcomed the results of this study and appreciated the length of the time series and amount of data collected. In discussion, it was noted that data collected during JARPA between 1989 and 2004 had revealed a similar decrease in the body condition of Antarctic minke whales, but without indication of changes in prey abundance (krill). It was clarified that cod are a competitor for the same prey source, and that minke whale body condition is thought to be linked to cod population dynamics through competition for common prey resources, namely capelin, herring and krill, as indicated by stomach contents analyses. Harp seals are another abundant predator in the area, also competing for the same resource. The authors of SC/68A/EM/02 explained that the time series would be continued and that with further decreases in cod abundance they expect a continued increase in minke whale body condition.

It was suggested to take the results of SC/68A/EM/02 further and to analyse the potential implications of a decreased body condition in the population of minke whales. For example, decreased body condition may affect recruitment. Investigating the age structure of the caught animals would be one way of analysing population effects of the body condition. The authors indicated that material

for age determination was available (eye lenses, ovaries and information on pregnancies) but that age determination is still difficult and yet to be undertaken. Furthermore, analyses of stomach content were suggested to investigate functional responses of changes in body condition, e.g. selectivity of prey. The Working Group **encouraged** the authors to conduct suggested analyses and to continue ecosystem-based modelling of the data, integrating whales, seals, cod and their prey. The Working Group looked forward to receiving the results of these exercises in the future.

During SC/67b last year, it was decided that the discussion on the body condition of Antarctic minke whales be discontinued. Cunen *et al.* were encouraged to publish the results of their study in a peer-reviewed journal. Walløe reported that the paper by Cunen *et al.* (2019) has recently been accepted for publication in the *Annals of Applied Statistics*. The Working Group congratulated the authors and acknowledged that the recommendation of the Scientific Committee had been followed and completed.

The usefulness of more and more complex model development was discussed. It was raised, that after long series of model improvement, often the results and conclusions remain the same. Likewise, concern was raised, that sometimes too much importance and effort is allocated to obtaining statistical significance, while statistical significance is not required for every data application. Often a defensible estimate of error suffices. However, it was underlined that model development usually increases precision, accounting for more uncertainty, and that this is generally desirable and important for a variety of applications.

3. REVIEW INFORMATION ON KRILL DISTRIBUTION AND ABUNDANCE FROM NEWREP-A

SC/68A/EM/01 reported a krill and oceanographic survey in Antarctic Areas III-E and IV during the 2018/19 austral summer season as a part of the New Scientific Whale Research Program in the Antarctic Ocean (NEWREP-A). The survey, conducted by two research vessels *Yushin Maru* No. 2 (YS2) and *Kaiyo Maru* No. 7 (KY7), was associated with the main Objective II of NEWREP-A, ‘investigation of the structure and dynamics of the Antarctic marine ecosystem through building ecosystem models’. The krill survey was conducted along the zig-zag tracklines designed for whale sighting survey. Acoustic data using quantitative echosounders were recorded continuously for a total of 72 days and covered 7,195 n.miles. Net sampling using a small ring net and an Isaak-Kid Midwater Trawl (IKMT) was carried out to identify species and size composition of plankton echo signs at 54 and 22 stations, respectively. Oceanographic observations using CTDs and sea water sampling were also conducted. Krill and oceanographic data are currently being examined, and results will be reported to related CCAMLR working group meetings.

The sampling station design was discussed, raising the issue of if stations were representative of the acoustic densities. For better assessment, a presentation of acoustic densities along the tracklines would be desirable.

Concern about generally low estimates of krill biomass were raised, recalling the assumed biomass that once must have sustained great numbers of whales prior to exploitation by commercial whaling. The representativeness of krill surveys in general was discussed and the wish for guidance from CCAMLR and krill experts on this matter was expressed. From a Scientific Committee perspective, the

relationship of current krill biomass estimates in Area V and consumption rates of whales are of high interest. According to results from JARPAII, 30% of the estimated krill biomass is consumed annually by fin, humpback, and Antarctic minke whales (Murase *et al.*, 2006). Although these results for krill biomass have not yet been standardised.

The Working Group looked forward to receiving the abundance estimates from the krill survey in the future and underlined the importance of krill biomass data to inform ecosystem function models.

4. PROGRESS ON SPECIES DISTRIBUTION MODELS AND ENSEMBLE AVERAGING, INCLUDING PREPARATION OF GUIDELINES

An update on the intersessional correspondence group on the applications of species distribution models (SDMs) was presented to the Working Group. While there was not significant progress between meetings, the Working Group **agreed** that developing guidelines for best practice for species distribution models (SDM) was important, and that the correspondence group should be retained.

As a key species linking primary producers to the higher trophic levels in the Antarctic ecosystem, the Antarctic krill (*Euphasia superba*) plays an important role in the Antarctic ecosystem. Therefore, knowing the plausible spatial distribution of krill will be useful for resource management and conservation in this area. Species distribution models (SDMs) can help predict the spatial species density by quantifying the relationship between the observed species distribution and its influencing factors. In general, although both statistical models and machine learning methods can be applied as SDMs, there is still an open question regarding the estimation performance of those SDMs for Antarctic krill. When it comes to krill surveys, tooth-shaped track lines have been preferred over zig-zag track lines, which are conventionally used in cetacean surveys. However, some surveys aim at combined cetacean and krill surveys, e.g. NEWREP-A.

Paper SC/68A/EM/03 introduced the results of simulation performance tests to address two questions: (1) how do the performance of machine learning methods compare to conventional statistical methods? and (2) what is the difference in performance between the two survey designs? Therefore, two different density distributions of krill were conditioned using actual krill density observation taken from the US AMLR Program in 2011. Using the assumed true spatial density surfaces, simulation data were repeatedly generated under the two designs, and then SDMs were applied to the data, two statistical models, and four machine learning methods. Machine learning methods were proven to have higher and more reliable prediction abilities than traditional statistical models. Random forests (RF) and boosted regression trees (BRT) were revealed to be the most reliable machine learning methods in this study. In addition, the zigzag-shaped and tooth-shaped designs were found to have comparable performances, and both of them can be applied in krill field surveys.

The working group took note the outcome of the study, that a zig zag survey design could be used just as well as a tooth-shaped design for krill surveys. It was noted, that NEWREP-A surveys followed a zig zag design, and that krill was sampled along these tracks. The results of SC/68A/EM/03 promise a reasonable evaluation of the NEWREP-A krill data and will facilitate concurrent assessments of whales and krill in the future. The authors intend to present these results to CCAMLR as well.

The testing of more complex statistical models for evaluation of the simulated data was discussed, for example, if soap smoothers could improve statistical model performance. However, it was recognised that possible model development, available time for implementation and usefulness of potential results had to be balanced.

Attention: SC

*The Working Group **agreed** that developing guidelines for best practice for species distribution models (SDMs) is important, and that the intersessional correspondence group should be re-established to work on this before SC/68B.*

5. PROGRESS WITH PREPARATION OF WORKSHOP ON ECOSYSTEM FUNCTIONING

In the intersessional period the Convenor of the Workshop Steering Group liaised with NGOs who agreed to provide additional funding dedicated to the envisioned review, and also with external experts who identified Joe Roman as a potential contractor for the review. An official letter to CMS to co-host the workshop was sent by the Secretariat. An informal agreement has been received, but a formal statement is pending. Also, Belgium confirmed provision of a venue in Brussels as long as the workshop takes place in 2019. The subsequent discussions in the Steering Group were dedicated to the exact focus of the workshop and also on the budget, how to process the additional NGO funding (dedicated to the review), the possible co-operation with CMS, potential dates, venues and potential workshop participants.

The Working Group discussed that the workshop will need to focus on specific questions and hypotheses that need be identified beforehand. It was emphasised that these questions should address matters that can be quantified, and that the questions should be chosen with respect to the potential for being answered. While there are many interesting questions that could be raised, ultimately quantitative answers will be needed to demonstrate ecosystem functions of whales. The Working Group collected a number of initial candidate questions which will need further categorization according to specific ecosystem functions of whales and a prioritisation (see Appendix 3). This will be further elaborated in the intersessional period under the steering group.

It was emphasised that the workshop should include people from outside the whale research community, e.g. experts on primary production, fish specialists and biological oceanographers. The function of whales in the ecosystem needs to be investigated holistically and not separate from other functions within the same system. A number of potential candidates for participation in the workshop were identified. A shortlist of participants will be finalised by the Workshop Steering Group in the intersessional period.

Furthermore, the importance of identifying geographical areas, where such research could take place was highlighted. It was noted that the Antarctic Ocean is a prime candidate for studies on the role of cetaceans in ecosystem function, because it is a whale dominated system and very different from other ecosystems, particularly due to the absence of zooplankton-eating fish. The Working Group **agreed** that the workshop should explore conducting analyses for regions outside of the Antarctic Ocean to compare the function of whales between different ecosystems. It was noted, that the choice of ecosystems should be guided by availability of data. It will be easier to quantify the function of whales within well studied ecosystems for which information on many other functions and processes already exists.

The question of how functions could be quantified was discussed. The comparison of areas with and without whales was detailed as one option. Spatial as well as temporal scenarios could serve for comparison, e.g. areas with whales migrating in and out could be investigated. Or, areas that saw a steep decline in whale numbers over time could be analysed, if historical data useful to ecosystem functioning analyses were available. Likewise, the impact of a certain species could be compared between different ecosystems, e.g. blue whales in the Antarctic Ocean, Chile and Australia.

Attention: SC

*The Working Group **agreed** that the Workshop on Ecosystem Functioning should explore conducting analyses for regions outside of the Antarctic Ocean to compare the function of whales between different ecosystems.*

5.1 Review of Terms of Reference

The Working Group reviewed the Terms of Reference of the workshop. A revised list of the Terms of Reference and the revised draft agenda for the workshop are provided in Appendix 2. Furthermore, the Steering Group of the workshop developed the terms of reference for the review of the roles of cetaceans in ecosystem functioning. These will be finalised by the Steering Group soon after this meeting.

5.2 Contribution of whales to ecosystem functioning

Joe Roman presented an overview of how our understanding of the ecological functions of whales has changed in the past decade. Most studies before 2010 focused on the role of whales as predators, but since that time, there has been increased attention on the ecological role of whale carcasses, especially in the deep sea, on nutrient transfer (via the whale pump and long distance movements during migration), and on the role of whales as prey and in trophic cascades. The increased attention on these functions has also brought to light the potential role of whales in biogeochemical cycles, including carbon, nitrogen, phosphorus, and iron. To date, the role of whale carcasses (in biodiversity and the carbon cycle) has perhaps been the best studied, but increased efforts also examine the role of whales in nutrient cycling, and we have a new understanding of interactions between killer whales and baleen whales and how these interactions could shape behavior and choice of breeding grounds.

Discussion indicated that there was a range of views about the importance of the roles of whales in the ecosystem and that these different views would need to be represented in discussions at the workshop.

5.3 Work plan for final Workshop preparations

The Working Group re-established the Steering Group on 'Cetacean and Ecosystem Functioning: a gap analysis workshop' to finalise preparations for the upcoming workshop with a membership of Ritter (Convenor), Butterworth, Donovan, Ferris, Galletti, Haug, Kitakado, McKinley, Punt, Roman, Smith, Suydam, Virtue (a CMS representative).

6. ECOSYSTEM MODELLING IN THE ANTARCTIC OCEAN

This is an active area of research of particular interest to the working group with regards to investigating ecological functions of whales in the ecosystem. The Antarctic Ocean is considered as a prime area for this research. However, this year no new information has been received. It was noted

Table 1
Summary of work plan for the EM Working Group.

Item	Intersessional 2019/20	2020 Annual Meeting (SC/68b)
(1) Ecosystem modelling in the Antarctic Ocean	Continue further analyses	Review results of further analyses
(2) Application of species distribution models (SDM)	Intersessional Working Group activity	Review progress of Working Group
(3) Effect of long-term environmental variability on whale populations	Continue further analyses and literature review	Review results of further analyses and progress of Working group on literature review
(4) Further development of individual-based energetic models	Continue further analyses	Review results of further analyses
(5) Modelling of competition among whales and relationship between whales and prey	Continue further analyses	Review results of further analyses
(6) Update of any exercises on krill distribution and abundance	Conduct krill surveys and analyses of the data	Review results of survey and analyses
(7) Cetacean and ecosystem functioning: a gap analysis workshop	Continue analyses and preparation of workshop	Review result of analyses and outcomes of workshop

that data from JARPAII and NEWREP-A are still being analysed and will be submitted in the future. The Working Group looked forward to future submissions to the Scientific Committee.

Furthermore, the Working Group **encouraged** contributions from areas other than the Antarctic Ocean. Future work of the Working Group will not be limited to Ecosystem Modelling of the Antarctic Ocean but aims at comparing different ecosystems and the functions of whales therein.

It was noted, that the joint IWC-CCAMLR workshop had been postponed, now to take place in the period 2020-21. It is expected that by then progress will have been made by both the Working Group and CCAMLR in identifying information gaps and necessary research. It is envisaged to invite a member of CCAMLR (e.g. George Watters) to the Working Group for future Scientific Committee meetings to function as a bridge between CCAMLR and the Working Group.

7. WORK PLAN

See Table 1 above.

8. ADOPTION OF REPORT

The report was adopted on 18 May 2019 at 14:00. The Chair expressed his sincere appreciation to the rapporteurs, Herr and Archer, for their excellent work and thanked the participants, including remote accesses of Roman and Galletti, for their valuable contributions. The Working Group thanked Kitakado for his leadership.

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Appendix 1

AGENDA

1. Introductory items
 - 1.1 Introductory remarks
 - 1.2 Election of Chair
 - 1.3 Appointment of rapporteurs
 - 1.4 Adoption of agenda
 - 1.5 Documents available
2. Review issues relevant to ecosystem modelling within the Scientific Committee
 - 2.1 Modelling of relationship between whales and prey
 - 2.2 Modelling of competition among whales including progress with IBEMs
 - 2.3 Progress on considering effects of long-term environmental variability on whale populations
 - 2.4 Progress on body condition analysis
3. Review the information on krill distribution and abundance from NEWREP-A
4. Progress on species distribution models (SDMs) and ensemble averaging, including preparation of guidelines
5. Progress with preparation of Workshop on Ecosystem Functioning
 - 5.1 Review of Terms of Reference
 - 5.2 Contribution of whales to ecosystem functioning
 - 5.3 Work plan
6. Ecosystem modelling in the Antarctic Ocean
7. Work plan
8. Adoption of Report

Appendix 2

TERMS OF REFERENCE AND DRAFT AGENDA FOR THE 'CETACEANS AND ECOSYSTEM FUNCTIONING: A GAP ANALYSIS' WORKSHOP

Terms of Reference

- (1) Review existing scientific information through:
 - (a) a review of relevant scientific studies on the contribution of cetaceans to ecosystem functioning [this will be accomplished in advance of the Workshop through contract, results to be presented at Workshop (see ToR for the contract)]; and
 - (b) presentations from selected experts on their research into how cetaceans affect ecosystem functions.
- (2) Assess what can realistically and reliably be quantified currently.
- (3) Identify potential geographical areas and species/taxa on which to focus.
- (4) Identify knowledge gaps as well as data gaps in our understanding of cetaceans and their impact and role in ecosystem functioning.
- (5) Develop a prioritised list of recommendations for scientific research to fill identified knowledge gaps, including studies on methodological approaches to study how cetaceans affect ecosystem function and (quantitative) ecosystem modelling of such impacts.

Expected outcomes: A meeting report that will include a comprehensive summary of the Workshop which will cover the objectives identified above and deliver according recommendations.

Draft Agenda

1. Presentations of existing knowledge [*review paper to be produced ahead of the workshop and other presentations*]. Consideration of cetaceans' actual and relative contribution to:
 - 1.1 Nutrient circulation: carbon sequestration; nutrient flux, etc.
 - 1.2 Ocean fertilisation (vertical: 'whale pump' and horizontal: 'whale conveyor belt')
 - 1.3 Whale falls
 - 1.4 Cetaceans as predators (trophic cascades)
 - 1.5 Current quantification/modelling approach
2. Identification of key data needs and gaps
 - 2.1 Nutrient circulation: carbon sequestration; nutrient flux, etc.
 - 2.2 Ocean fertilisation (vertical: 'whale pump' and horizontal: 'whale conveyor belt')
 - 2.3 Whale falls
 - 2.4 Cetaceans as predators (trophic cascades)
 - 2.5 Current quantification/modelling approaches
3. Ways forward and recommendations (including the role of stakeholders: scientists and organisations)
4. Conclusions and review of report
 - 4.1 Defining research needs
 - 4.2 Identifying quantitative models
 - 4.3 Identifying future focus (plus proposed work plan)

Appendix 3

HYPOTHESES AND QUESTIONS FOR THE WORKSHOP ON ECOSYSTEM FUNCTIONING

Note: The list below represents a collation of initial ideas by members of the Working Group. There was insufficient time to discuss these in detail and so they are not in order of priority.

- (1) How important is whale movement between large depths and surface water to overall nutrient recycling?
- (2) What contribution do whale carcasses on the ocean floor make to overall nutrient recycling?
- (3) What is the proportional role of: (a) top predators; and (b) whales in both the use and fertilisation of primary production?
- (4) What effect does species specific behavior of whales have on their function in the ecosystem? (Different species of whales have a very different diving behaviour: sperm whales are deep divers and e.g. minke whales usually feed near the surface).
- (5) What are the ecosystem-specific functions of whales? e.g. it is important to discriminate between the possible function of the hypothetical whale pump mechanism in the arctic oceans (North Pacific and North Atlantic) where fish species are present which eat zooplankton (capelin and herring etc.) and the Southern Ocean where such fish species are lacking. The vertical movements of these fish species must be considered in the northern oceans.
- (6) What is the impact/function of whales in the ecosystem in relation to the impact of other top predators? (Even if the 'whale pump mechanism' can be shown to be important, other top predators than whales could be equally or more important for this mechanism. In the Southern Ocean, the Weddell seal, which is a deep diver and are present in high abundance, could be important).
- (7) What is the whales' (quantitative) contribution to a defined ecosystem function, e.g. how much carbon is sequestered in a whale carcass?
- (8) Do whales have functions in the ecosystem that are unique, i.e. no other species occupy these functions?
- (9) A key consideration is which species are non-redundant in the system.
- (10) Does the vertical and horizontal transport of nutrients by whales benefit each ecosystem equally or is the effect of the benefit depending on factors such as the biogeochemistry of the water (or other characteristics of the area/water); temperature, ocean floor substrate, or water biogeochemistry.
- (11) What is the relation between the N, Fe and C produced/sequestered and the increase of primary productivity or carbon sequestration from the atmosphere?
- (12) What are the differences between the ecosystem functions occupied by cetaceans in relation to geographical areas? Is there a difference between breeding areas vs feeding areas and if so, what would it be?
- (13) Do size, abundance or metabolic rates of cetaceans involved matter? If yes, how?
- (14) What is the role of small cetaceans and beaked whales?
- (15) What influence had the severe depletion of whales through whaling on the overall ecosystem functions?
- (16) Multiple ecosystems should be reviewed, especially data-rich ones, to see if any contrasts.

Proposed areas ecosystems for investigation

- Southern Ocean ecosystem.
- North Eastern Atlantic.
- Barents Sea.
- New England?
- North Pacific?