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CMS Scientific Council (ScC-SC7)**

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**REPORT OF THE 2<sup>ND</sup> IWC-CMS WORKSHOP ON CETACEAN ECOSYSTEM FUNCTIONING**

*(Prepared by the International Whaling Commission)*

Summary:

The enclosed report pertains to UNEP/CMS/ScC-SC7/Doc.6.2.1.

# SC/69B/REP/04

**Sub-committees/working group name: REP**

## **REPORT OF THE 2nd IWC-CMS WORKSHOP ON CETACEAN ECOSYSTEM FUNCTIONING**

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# **REPORT OF THE 2<sup>nd</sup> IWC-CMS WORKSHOP ON CETACEAN ECOSYSTEM FUNCTIONING**

The 2<sup>nd</sup> IWC-CMS Workshop on Cetacean Ecosystem Functioning was held at the headquarters of the Convention on Migratory Species of Wild Animals in Bonn, Germany from 14-16 November 2023. A list of participants is provided in Annex A.

## **1. INTRODUCTORY ITEMS**

### **1.1 Welcoming remarks**

Schubert, the organizing convenor, welcomed all workshop participants and thanked the International Whaling Commission (IWC) and Convention on the Conservation of Migratory Species of Wild Animals (CMS) for co-hosting the workshop. He invited them to provide opening remarks.

Staniland, on behalf of the IWC, welcomed the workshop participants and thanked the workshop steering group, Schubert, Kitakado, and CMS for their efforts to organize the workshop, as well as CMS for its ongoing collaboration with the IWC on this topic and for providing the workshop venue. He wished everyone a productive meeting.

Virtue, on behalf of CMS, welcomed all participants and thanked the workshop organizers for their efforts in planning the event. She noted the previous successful collaborations between CMS and IWC. She explained that CMS covers all migratory species (aquatic, avian, and terrestrial). Her team works at the global level, but also with regional agreements focused on specific species. CMS recognizes the important role that cetaceans play in a healthy environment. Virtue wished everyone a successful workshop.

### **1.2 Election of Chair**

Kitakado was appointed as the Chair of the workshop.

### **1.3 Appointment of rapporteurs**

Schubert was appointed the primary rapporteur of the workshop to be assisted by Katara and other workshop participants.

### **1.4 Adoption of Agenda**

The draft agenda was discussed, amended, and adopted (Annex B).

### **1.5 Review of documents**

Workshop documents were available on the dedicated SharePoint site and included: the agenda, copies of presentations, relevant papers and publications, IWC documents including the 2016 and 2018 IWC resolutions, and information from the 1<sup>st</sup> IWC-CMS Workshop on Cetacean Ecosystem Functioning.

## **2. REVIEW OF THE TERMS OF REFERENCE**

Kitakado provided a brief history of this issue within the IWC, noting the 2016 and 2018 resolutions approved by the Commission and the results of the 1<sup>st</sup> IWC CMS workshop on cetaceans and ecosystem functioning. That workshop developed a list of six questions to be addressed at the 2<sup>nd</sup> workshop, with two objectives: the quantification of spatial difference in the ecosystem functioning of cetaceans, focusing on environments with regional ecosystem characteristics; and the quantification of temporal changes in ecosystem functioning of cetaceans, with a focus on differences between pre-whaling and current populations, and identification of information and knowledge gaps. The workshop report will be reviewed at SC69B, and then at the 69<sup>th</sup> meeting of the

Commission, both occurring in 2024.

### **3. BACKGROUND INFORMATION/MATERIALS**

#### **3.1 Summary of the IWC Resolutions (2016-3 and 2018-2)**

Galletti provided details on the Commission's approval of resolution 2016-3 at its 66<sup>th</sup> meeting in 2016 (Portoroz, Slovenia) and resolution 2018-2 at its 67<sup>th</sup> meeting in 2018 (Florianopolis, Brazil). The 2016 resolution created workstreams for both the Scientific Committee (SC) and Conservation Committee (CC) on this subject. The CC was asked to review the ecological, management, environmental, social, and economic aspects of the issue, and the SC to screen existing research and develop a gap analysis together with a plan to address remaining research needs. The CC decided to focus initially on the social and economic components. In 2016, the IWC was the first Multilateral Environmental Agreement (MEA) to recognize the contribution of cetaceans to ecosystem functioning. Since then, several other MEAs and international organizations, including CMS (see UNEP/CMS/COP12/Doc. 24.2.6), International Monetary Fund, Intergovernmental Panel on Climate Change, United Nations Framework Convention on Climate Change and United National Environment Programme Finance Initiative have addressed (and continue to address) the issue. In resolution 2018-2, the Commission thanked the SC and CC for the work completed to date, recommended further collaboration with CMS, and encouraged Contracting Governments to integrate the value of cetaceans' ecological roles into local, regional, and global organizations on biodiversity and environment, including climate change and conservation policies.

#### **3.2 Summary of 1st IWC-CMS Workshop on Cetaceans and Ecosystem Functioning (April 2021)**

Kitakado summarized the results of the 1<sup>st</sup> workshop. That workshop was tasked with reviewing the existing scientific information, assessing what ecosystem functions of cetaceans can realistically and reliably be currently quantified, identifying geographic areas and species/taxa on which to focus, identifying knowledge and data gaps, and producing prioritized recommendations for research to fill those gaps. To assist with accomplishing these objectives, two keynote papers were presented by Roman *et al.* (2021) and Wassmann *et al.* (2021), along with presentations by experts on whale falls, nutrient cycling and transport (e.g., the whale pump and the whale conveyor belt), carbon sequestration and predator-prey interactions. The results of the workshop were reflected in four tables contained in the workshop report, including a summary of selected traits of cetaceans and their related ecosystem functions and services (Table 1), ecological functions of cetaceans; research and development needs (Table 2); a list of general questions, hypotheses and tasks to be accomplished or considered during the 2<sup>nd</sup> workshop (Table 3); and a draft template providing an overview of cetacean ecosystem functions over time and space as whale abundance estimates have changed between the pre-and post-commercial whaling periods. See SC/68C/REP/03, Report of the IWC-CMS Workshop on Cetacean Ecosystem Functioning, virtual 19-21 April 2021.

#### **3.3 Summary of the work of the IWC Conservation Committee on the socio-economics of cetaceans and ecosystem functions**

Galletti summarized the work of the CC, including its hosting of a virtual workshop examining the socio-economic value of the ecosystem functions of cetaceans, held virtually in April 2022. An advisory group had been established to develop the Terms of Reference and the proposed scope of work for a pilot project to examine the socio-economic value of the ecosystem functions of cetaceans, as agreed at IWC68 in 2022. The scope of work includes assessing the economic value of species/populations to climate regulation through carbon sequestration based on biomass (and changes over time), estimating the broader values of other ecosystem functions, and designing financial and governance mechanisms to provide funds for conservation. The proposed candidate species for the pilot project were North Pacific humpback whales, the assemblage of great whales (i.e., blue, minke, humpback and fin whales) in the Southern Ocean, the South Atlantic southern right whale and the North Atlantic minke whale. Outcomes from the present workshop will inform ongoing

discussions by the advisory group regarding the draft tender for the pilot project. See CCPG/OCT23/15.

In discussion, workshop participants sought more information about the species or group of species selected for the review. It was explained that those species or groups of species were selected for consideration based on the availability and reliability of abundance estimates. Dolphins and sperm whales had been specifically discussed, and it was noted that they were not selected for inclusion in the list of target species due generally to a lack of reasonably accurate and precise abundance estimates. A new report providing updated abundance estimates for small cetaceans in European and North Atlantic waters was noted (Gilles *et al.* 2023).<sup>1</sup> The Southern Ocean and North Atlantic were selected due to the difference in the complexity of these ecosystems, thereby providing geographical differences in the roles of cetaceans in ecosystem functioning.

#### **4. KEY STEPS FOR QUANTIFYING ROLES OF CETACEANS IN ECOSYSTEM FUNCTIONING**

##### **4.1 Identify ecosystem functioning processes and associated metrics (updating the science)**

###### **4.1.1 H. Pearson - Whales in the Carbon Cycle: The Current State of Knowledge**

The great whales (baleen and sperm whales), through their massive size and wide distribution, influence ecosystem and carbon dynamics. Whales directly store carbon in their biomass and contribute to carbon export through sinking carcasses. Whale excreta may stimulate phytoplankton growth and capture atmospheric CO<sub>2</sub>; such indirect pathways represent the greatest potential for whale carbon sequestration but are poorly understood. Based on the current state of knowledge, the great whales store 2 million tons of carbon in their bodies (biomass carbon, all baleen whales globally), sequester 62,000 tons C/year in their carcasses (whale fall carbon, all baleen whales globally), fix 22 million tons C/year via nutrient recycling (whale pump and great whale conveyor belt, for four Southern Ocean baleen whale species), and export 400,000 tons C/year via nutrient export (whale pump, Southern Ocean sperm whales). Industrial whaling is estimated to have caused a 90 % decline in these carbon values. Recovery of the great whales can aid CO<sub>2</sub> removal to some degree, though it is likely to be small relative to the scale of the global carbon cycle. Integrating whale recovery into climate policy needs to be grounded in the best available information, and economic valuations of whales should incorporate this information. There is noteworthy scientific concern about the biological assumptions used by Chami *et al.* (2020) to generate monetary valuations based on whale carbon values. Given the severity of the climate and extinction crises, the precautionary principle should be applied immediately to whale conservation as a low-risk low-regret strategy with multiple benefits. The carbon values of the great whales should be viewed alongside numerous ecosystem, cultural, and moral motivations to protect them.

Pearson was thanked for her presentation. In discussion, it was noted that the estimates of carbon sequestration used in the analysis were based on cetacean abundance estimates from Smith *et al.* (2019). See Pearson (2023); Annex D. However, revised abundance estimates exist for some cetacean stocks and those carbon values could be updated. Workshop participants discussed the difference between carbon fixation and sequestration, the direct and indirect pathways for carbon sequestration, the cycling of new versus recycled nutrients depending on the diving

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<sup>1</sup> Gilles, A, Authier, M, Ramirez-Martinez, NC, Araújo, H, Blanchard, A, Carlström, J, Eira, C, Dorémus, G, FernándezMaldonado, C, Geelhoed, SCV, Kyhn, L, Laran, S, Nachtsheim, D, Panigada, S, Pigeault, R, Sequeira, M, Sveegaard, S, Taylor, NL, Owen, K, Saavedra, C, Vázquez-Bonales, JA, Unger, B, Hammond, PS (2023). Estimates of cetacean abundance in European Atlantic waters in summer 2022 from the SCANS-IV aerial and shipboard surveys. Final report published 29 September 2023. 64 pp. Available at: <https://tinyurl.com/3ynt6swa>

depth/feeding zone of whales, and the ability of the great whales to sequester carbon relative to other species/species groups.

#### **4.1.2 L. Gilbert - *Cetaceans and the whale pump: expanding the picture to more species, more ecosystems and more nutrients***

This study estimates nutrient release by cetacean communities in 14 areas located in temperate and subpolar regions of the Northern Hemisphere and tropical or subtropical regions, including a total of 38 cetacean species and eight essential nutrients. It is based on a bioenergetic model built using Monte Carlo simulations and bootstrapping, applied per species and area, and relies on data on cetacean physiology, metabolism, diet, prey composition, and abundance. At the community level, cetaceans release more nutrients in productive meso- to eutrophic regions than in the less productive oligotrophic tropical and subtropical regions, demonstrating the bottom-up effect of productivity on cetacean abundance. However, the absolute levels of nutrient release by cetaceans are not necessarily proportional to the potential top-down effect of the released nutrients on ecosystems, as this is determined by a wide range of factors, such as the nutrient background and limiting conditions in the recipient ecosystems. It is therefore possible that the relative contribution of cetaceans to ecosystem functioning through the whale pump is greater in tropical than in temperate regions. In addition, the nutrient cocktail released by cetaceans at the community level varies geographically. It is primarily determined by the specific composition of the communities, as small cetaceans, deep-diving species and baleen whales do not release the same cocktail of nutrients due to their different diets, and their relative contributions vary geographically. This also means that the communities do not contribute equally to the release of each nutrient in a given ecosystem. This suggests that their role in ecosystem functioning may vary accordingly within a given ecosystem and between ecosystems, both quantitatively in terms of the amount of nutrients released and qualitatively in terms of the potential ecosystem response to these nutrient releases. The contributions of small cetaceans and deep divers exceed those of large whales in some areas. Overall, the results demonstrate the diversity and complexity of the whale pump processes in the world's oceans.

Gilbert was thanked for her presentation. The discussion focused on the nutrient cocktail provided by cetaceans and how it can change depending on prey composition and abundance, how whale nutrient inputs compare to anthropogenic sources (e.g., Mississippi River run-off into the Gulf of Mexico), how the nutrients released by cetaceans may or may not provide a substantive benefit to the ecosystem depending on existing geochemistry of the water and other nutrient sources, and the uncertainties in the model. It was noted that there are important gaps in our knowledge of the nutrient compositions of prey. Gilbert noted that analysing the diet of the different cetacean groups as well as nutrient assimilation and release rates were the most challenging aspects to model. Regarding uncertainties in the model, there is confidence in the difference documented between the contribution of cetaceans to nutrient cycling in tropical and temperate areas, but other uncertainties warrant further investigation based on the overlap of confidence intervals between areas. However, when evaluating the spatial variability in the contribution of cetaceans to ecosystem functions, it is important to consider environmental conditions at the local level concomitantly.

#### **4.1.3 D. Costa - *Updates on cetacean bioenergetics and material flux***

There has been a lot of progress in the last few years in understanding the factors that control the cost of the existence of cetaceans. First, it is crucial to recognize that in terms of the cost of existence, cetaceans are a heterogeneous group, with a range of metabolic costs associated with their different life history patterns. For example, Mysticete cetaceans are generally capital

breeders, where they separate breeding from feeding. In contrast, most odontocete cetaceans are income breeders and feed throughout their reproductive cycle.

Additionally, deep-diving cetaceans are likely to have more conserved metabolic rate to enable their prolonged dives (Quick *et al.* 2020), while more surface-feeding cetaceans are less constrained and likely have higher metabolic rates associated with their more intense lifestyle (Aguilar Soto *et al.* 2008). The Office of Naval Research supported a Bioenergetics workshop virtually in 2021. This workshop had 62 participants and generated a series of publications, including a "horizon scan" that generated a community view of the "Key questions in marine mammal bioenergetics" (McHuron *et al.*, 2022). Some papers reviewed the cost of reproduction (McHuron *et al.* 2023), the cost of growth (Adamczak *et al.* 2023), methods for estimating energy intake (Booth *et al.* 2023), a review of the metabolic rates (Noren and Rosen 2023) and finally as assessment of the existing approaches for modeling the energy requirement of marine mammals (Pirota 2022). These papers were published in a special issue of Conservation Physiology.

Costa was thanked for his presentation. During discussion, it was noted that this work highlights the range of uncertainty associated with assessing cetacean bioenergetics. Nevertheless, the suite of papers published on this subject, including those highlighted in the presentation, can provide a baseline for this workshop and can be used to conduct a meta-analysis of bioenergetics models. Costa noted new models under development by his students that will soon be available for humpback whales and for fish versus whale models.

## **4.2 Develop conceptual models, including target species, regions, and critical parameters needed to estimate the ecosystem functioning metrics in the past and during the present time**

### **4.2.1 North Atlantic Ocean**

#### 4.2.1.1 M. BIUW - HISTORICAL ABUNDANCE RECONSTRUCTION OF KEY LARGE CETACEANS IN NORTHEAST ATLANTIC

Under this agenda item, historical reconstructions of the abundance of key large cetaceans in the Northeast Atlantic Ocean were presented. See Biuw *et al.* (2023); Annex E. Species considered included blue, fin, sei, humpback and minke whales. These analyses were carried out in response to a request by the Standing Working Group on Ecosystem Modelling (SWG EM) of IWC SC to conduct a comparative examination of the potential role of cetaceans in the marine nutrient and carbon cycle in the North Atlantic (IWC EM ToR 2.1). The analyses presented here were limited to the Northeast Atlantic basin north of ~60°N, but also include some additional regions generally covered by regional whale abundance surveys (i.e., the North Sea and areas between Greenland, Iceland, and the Faeroe Islands). The reconstructions presented were obtained using a single-species density-dependent generalized logistic growth model, implemented in a Bayesian framework using historical catch data and available abundance estimates. The model is the same as has previously been used to estimate the stock status of humpback whales in the Southwest Atlantic. While the modelling framework allows for a range of scenarios to be explored in terms of, for example, biases in catch statistics or different values for maximum population growth rate ( $R_{max}$ ), these preliminary analyses used default settings and/or uninformative priors. Preliminary results suggest that for most species of baleen whales in the Northeast Atlantic, the levels of reduction are small or moderate relative to estimated pre-exploitation levels. However, the value specified for growth rate ( $R_{max}$ ) was generally higher than those commonly assumed for these species. Alternative runs using different values for  $R_{max}$  should be explored to examine the effects of historical abundance estimates.

Biuw was thanked for his presentation. During discussion, it was noted that single-species models,

like those used in this paper, may be problematic to use in ecosystem modelling. Unlike other oceanographic regions, the great whales were not as severely depleted as in other ocean regions during the commercial whaling era in the northern regions of the Northeast Atlantic, as whalers discovered and focused on other regions, such as the Southern Ocean. There is a relatively high degree of confidence in the estimates of current abundance, while the confidence in the fitted K parameter values is less. Thus, the estimate of historical abundance is also associated with a fair amount of uncertainty. It was noted that there is not enough data to validate the models and that there is low confidence in the historical abundance estimates. For this study, the fitted values for Rmax were generally between 5 and 6 % per year, but this most likely reflects the fact that the model has not been able to estimate this parameter well; a full range of Rmax values from 0 to 12 % was recommended to be tested using the model. Initial runs using informative priors of Rmax between 1 and 8 % suggest that a common overall pattern applies. While lower Rmax values result in slightly increased estimates of K and thus historical abundance, the overall conclusion remains unchanged, namely that most stocks of great whales in the Northeast Atlantic north of 60°N were not severely depleted and/or are currently at levels around 70 to 90 % of their pre-exploitation levels.

4.2.1.2 C. FREITAS - NUTRIENT CONCENTRATIONS OF MINKE WHALE EXCRETION IN THE NORTHEAST ATLANTIC  
There is increasing interest in assessing the impact of whales on nutrient and carbon cycling in the ocean. By fertilising surface waters with nutrient-rich faeces and urine, whales may stimulate primary production and thus carbon uptake, but robust assessments of such effects are lacking. Based on the analysis of faeces and urine directly collected from minke whales off Norway, this study quantified the concentration of macro-and micronutrients in minke whale faeces and urine before their release and dissolution in seawater. Measured nutrient concentrations, combined with prey consumption and prey-assimilation estimates, were then used to estimate daily nutrient excretion in Northeast Atlantic feeding grounds. Further research is needed to quantify the implication of released nutrients to primary production at regional and global scales.

Freitas was thanked for her presentation. It was noted that this research used minke whales because they are hunted, thereby providing a source for obtaining samples including urine. Samples have also been obtained from fin whales, and these are currently being analysed. Ongoing research is being conducted to examine the sinking rate of cetacean faecal plumes, together with in situ experiments to examine the response of marine species to excretions (both urine and faeces). The need to understand the urination characteristics of the target species better (i.e., how much they urinate, where, when) was noted. In response to a question seeking clarification, Freitas advised that the contribution to primary production from minke whales off Svalbard, based on phosphorus (P) excretion via faeces, was 0.2-4 %. This assumes that there are no nitrogen limitations in seawater and that all P is used for primary production.

4.2.1.3 M. BIUW - ESTIMATING THE HISTORICAL AND CURRENT ROLE OF CETACEANS IN THE NUTRIENT BUDGET OF THE NORTHEAST ATLANTIC OCEAN

This document contains estimates of biomass, prey consumption, and nutrient excretion by rorqual whales in the Northeast Atlantic Ocean. These estimates have been compiled in response to the request by the SWG EM (IWC EM ToR 2.1). The estimates are based on modelled historical and current abundance estimates of key rorquals in the northern part of the Northeast Atlantic Ocean, recently published estimates of nutrient contents of faeces, and unpublished estimates of nutrient contents in urine from common minke whales. For simplicity, the authors assumed similar nutrient contents in excreta of all species considered in this study: blue, fin, sei, humpback, and common minke whales.

Biuw was thanked for his presentation. During the discussion, a question was asked as to what

proportion of the total primary production in the area can be attributed to nutrients released in whale urine and faeces. As a very rough comparison, it was suggested that this fraction might be less than 0.5% of total primary production (i.e., less than that reported by Freitas, but that these were “back of the envelope” calculations and the associated values may be crude).

#### 4.2.1.4 R. BOUMANS - OCEAN ECOLOGY AND WHALES

The presentation focused on the Multi Integrated Model of Ecosystem Services (MIMES) which provides a framework for spatially dynamic simulations of ecosystems and their interactions in estimating the provisioning of ecosystem services. The MIMES was applied in a project to simulate the movement and interactions of seven whale species across 167 spatial locations which together represent the North Atlantic Ocean. Each location was attributed a depth profile based on light penetration and seven interacting ecosystem components (phytoplankton, zooplankton feed fish, whale faeces, urine, carcasses and marine snow). Whale populations are represented by both biomass and counts of individuals in an age-structured Leslie matrix. Whale presence was determined based on the percentage of a whale population interacting with local ecosystems, using daily time step locations estimated from a database of whale sightings. Conclusions from the simulation results show nutrient provisioning provided by whales to the ecosystems to be important at times and at specific locations when humpback whales return from breeding to feeding grounds as they follow the Mid-Atlantic Ridge.

Boumans was thanked for his presentation. It was noted that this type of mechanistic model was good for hypothesis generation, but it was not clear if the output was sufficient to develop management advice for local decision-making. The discussion focused on the validation of the model, whether the model assumptions could be met, the source and reliability of the data used to construct the model, and when, given real-world conditions, a model is good enough to inform management advice. Boumans responded that multiple theories and assumptions are incorporated into the model, that this is a dynamic model that is subject to ongoing improvement as new data become available, and that, while it is a mechanistic model, the parameter settings/configurations are different and can be set by the analyst using unique numbers, thus providing the ability to get probability distributions for the parameters estimated. More mechanistic representation of movement was suggested, perhaps either using individual-based models or simpler step-selection models (e.g., Michelot *et al.* 2019).

#### 4.2.1.5 M. BIUW - ECOSYSTEM MODELS DEVELOPED (OR UNDER DEVELOPMENT) FOR NORWEGIAN WATERS

This paper identified various models, including some under development, of increasing levels of complexity that have/will be used in Norwegian waters. The models include Seastar, Gadget, R Chance and Necessity (RCaN), Nordic and Barents Sea Atlantis (NoBA Atlantis), Norwegian Sea Ecosystem End to End (NORWECOM E2E), Ecopath with Ecosim (EwE) and Ecospace models, constituting a range from extended single-species models to full end-to-end ecosystem models. The characteristics of each model were described.

Biuw was thanked for his presentation. During discussion, it was noted that operationally, fish stock management in Norway continues to be informed using single-species models, while ecosystem models of varying complexity (e.g., minimum realistic models also known as MICE-Models of Intermediate Complexity for Ecosystem assessments) are being developed to pursue more integrated ecosystem-based management. While there is still no formal framework in place to bring operational stock assessment and ecosystem modelling together, there is increasing interest in pursuing this. In addition, the justification for ecosystem models comes from the increasing requests from stakeholders to address questions regarding the response of ecosystems to anthropogenic activities. However, with increasing model complexity, more data are needed, but the data required are rarely readily available. If climate change effects are to be incorporated into models, the non-stationarity of

some models is problematic. When climate change is incorporated into more complex models, it will propagate through all processes.

#### **4.2.2 Southern Ocean**

##### **4.2.2.1 N. MOOSA AND D. BUTTERWORTH - MODEL ESTIMATES OF PRE- AND POST-ABUNDANCE OF THE CETACEANS IN THE ANTARCTIC ECOSYSTEMS**

This document provides a response sought by the IWC Scientific Committee to summarise estimates of abundance and related quantities of the large baleen whales south of 60°S, both now and prior to historical exploitation. See Moosa and Butterworth (2023); Annex F. Results from a number of both single- and multi-species models are provided. However, two of the multi-species models, by Moosa (2017) and by Tulloch *et al.* (unpubl.), provide the best estimates of changes since exploitation commenced, at a circumpolar level. Their calculations are based primarily on the blue, fin, humpback and minke whales. The two models, though differing in many respects, provide rather similar results, specifically that current total baleen whale biomass is about 20 % of its pre-exploitation level (although if split by Atlantic-Indian and Pacific sectors, this ratio becomes about 15 % and 50 %, respectively, for the Moosa model). For krill consumption, prey carbon and the biomass of annual whale mortalities, this current to pre-exploitation ratio, at an Antarctic-wide level, is roughly 30 % for the Moosa model. While blue and fin whales dominate the contributions to these figures historically, at present, humpback and minke whales provide the greater contributions.

Moosa and Butterworth were thanked for their presentation. The population demographics of krill in the Southern Ocean were discussed in the context of changes in krill abundance in response to large-scale hunting of blue and fin whales. For the model, krill abundance was not used for the circumpolar model given that krill surveys are restricted to certain areas, but such data are being used in the development of regional models. It was pointed out that the model did not include certain effects, such as the positive effects of whale fertilisation and some species' ability to feed in the pack ice. However, it was noted that the model's intent was to be kept as simple as possible while hopefully still being able to reflect the main features of the historical catches, the 'krill-surplus' hypothesis and the abundance data. Without additional data on the magnitude of the impact of the whale pump on krill, particularly given nutrient cycling by other species, it is not clear how the modelling results would change. The model was also not age-structured because of its intended simplicity. Biomass calculations were based on average biomass for each species independent of age; this was considered not to have an important impact on these biomass estimates. It was noted that the only forage species included was krill and that a similar ecosystem model for the North Atlantic would need to include fish prey species.

##### **4.2.2.2 V. TULLOCH ECOSYSTEM MODEL UPDATES AND ENSEMBLE PROJECTIONS FOR SOUTHERN OCEAN AND NORTH PACIFIC**

Updates to Southern Ocean ecosystem models and North-east Pacific ecosystem models that include cetaceans were presented. Tulloch is currently updating the Southern Ocean Model of Intermediate Complexity for Ecosystem Assessments (MICE) (SC/67A/EM/12) that predicts abundances of five baleen whale species and krill under the highest CO<sub>2</sub> emissions trajectory (Representative Concentration Pathways (RCP) 8.5, from the IPCC future climate scenarios). The model was originally coupled to historical and future climate outputs (phytoplankton, temperature, chlorophyll and ice extent) from the Australian Community Climate and Earth System Simulator (ACCESS-ESM1). The model is being recoupled to the alternative Earth System Model (GFDL-MOM6-COBALT2) and recalibrated to enable inter-comparison of model outputs with an ensemble of other models as part of the Southern Ocean Model Ensemble (SOMEME) being developed by researchers at the University of Tasmania that links to the Fisheries and Marine Ecosystem Model Intercomparison Project (FishMIP). An overview of the FishMIP project was provided, which aims to generate ensemble projections for marine ecosystems and species therein (including baleen whales) with nine global and 10+ regional marine ecosystem models forced by climate projections from 2/3 Earth System Models

(the Coupled Model Intercomparison Project CMIP), and four climate scenarios.<sup>2</sup> FishMIP is part of the larger Inter-Sectoral Model Intercomparison Project (ISIMIP). Tulloch noted that by recalibrating the model to include the same input variables as used in the FishMIP Model Evaluation Protocol [ISIMIP 3a], model outputs can be used to reduce the uncertainty associated with regional models and to provide robust comparative outputs for other global models under development (e.g., Southern Ocean Mizer for baleen whales and prey).

An update on modelling efforts underway for the Salish Sea region of the Northeast Pacific was also provided. Tulloch has developed a mechanistic multi-species size-spectrum model (MIZER) that includes 23 species groups including phytoplankton and zooplankton, up to cetaceans (killer whales, porpoises, with humpback whales soon to be included), that will be used to evaluate the impacts of strategic fisheries management scenarios and climate change on cetacean abundance. This model will be used in ensemble model projects with an Atlantis end-to-end (E2E) ecosystem model developed for the region (see item 4.2.4).'

Tulloch was thanked for her presentation. It was noted that there is only a slight difference between the predictions from these Southern Ocean models and those presented by Moosa and Butterworth (see section 4.2.2.1). While the models were fitted to the same abundance estimates, there were no drastic differences in changes indicated by the biomass trajectories for the biomass. In discussion, the possible need to allow for recent changes in survey estimates of krill in the Scotia Sea and for climate change effects was raised. For these Southern Ocean models, krill abundance was fitted at specific spatial scales based on regional surveys with upscaling coefficients used to provide krill abundance estimates for the entire region. The original model, which excluded climate drivers, predicted a krill surplus. When climate drivers and two-way interactions (including consumption) were included in the model, the model initially predicted a krill surplus in the Pacific region but, with the inclusion of climate drivers, the krill population biomass is predicted to decline in the latter half of the 21st century.

### **4.2.3 North Pacific**

#### **4.2.3.1 H. MORZARIA-LUNA ATLANTIS ECOSYSTEM MODEL: ASSESSING CUMULATIVE IMPACTS IN PUGET SOUND**

Morzaria-Luna's research team developed and applied ecosystem simulation models built using the Atlantis Ecosystem modelling framework to improve the management of marine systems. Atlantis models have been developed for the Gulf of Alaska, California Current, Salish Sea and Puget Sound. Atlantis is an 'end-to-end' modelling framework for marine ecosystems that integrates oceanographic, geochemical, ecological and anthropogenic processes in a three-dimensional, spatially explicit domain. The Atlantis model for Puget Sound (AMPS) was developed as part of the Salish Sea Marine Survival project, with a focus on drivers of salmon survival. The AMPS is initialized to represent recent conditions (c. 2011) and simulates food web dynamics using 73 functional groups, including 21 salmon groups, two orca populations (Bigg's whales and Southern Resident Killer Whales (SRKWs)) and gray whales. Hydrodynamics in the AMPS are driven by outputs from a Regional Ocean Modeling System model for Puget Sound. The AMPS simulates the salmon life cycle and trophic interactions in detail. The authors are using the AMPS to explore the effects of ocean warming on ecosystem indicators, including orca populations. They are also linking their model to a framework that integrates processes across the watershed, coastal and marine ecosystems in Puget Sound. They aim for the AMPS to provide strategic guidance regarding the relative cumulative impact of multiple stressors on SRKWs, and the ecosystem impacts of actions aimed at recovering this endemic orca population. To that end, they are currently improving SRKW parametrizations, including updating the diet, spatial and seasonal distributions, and they plan to assess the implications of uncertainty in fecundity rates. They expect that model results will inform indicators of the health of Puget Sound.

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<sup>2</sup> See, <https://www.isimip.org/about/marine-ecosystems-fisheries/fish-mip-documents-and-material/>

Morzaria-Luna was thanked for her presentation. It was noted that the Atlantis model is a strategic model, not a tactical model, and therefore should not be used to advise tactical decisions. Development and initial parameterization of the model required three years. The authors commented that the model is run with the highest quality data available, but updating and recalibrating the model is an ongoing process. Although the ecosystem components included in the model are not comprehensive, inferences can still be drawn from the model. The socio-economic outputs of the model take into consideration multiple stakeholders with different levels of acceptable risks and different value systems to understand how model predictions affect value systems. Any model used by decision-makers must contain information on uncertainty to avoid the over-interpretation of results and to weigh the risks of alternative decisions appropriately. For this model, uncertainty can be addressed by modelling different scenarios (e.g., varying management actions) or running the model using different parameters (such as different fertility rates for a given marine mammal group). A key structural feature of the Atlantis models is the polygon layout which is based on biogeography, current management features, and the expert elicitation process. Cross-validation is used to evaluate model performance. In the case of the Puget Sound model, reconstructed catch series were used to drive the model from 1970-2011, and the results were compared to known stock status. The California Current and Gulf of California models have been applied to test a variety of scenarios; the California Current model has undergone independent review (Kaplan and Marshall 2016). This same review framework could be applied to all Atlantis models to improve their quality and rigour. In Puget Sound, the Atlantis model will be used to examine changes in the ecosystem services of cetaceans. A series of indicators are being developed to facilitate the model's use to assess such services.

#### **4.2.4 Other modelling presentations**

##### **4.2.4.1 P. BLACKWELL COMBINING INFORMATION FROM ECOSYSTEM MODELS USING A STATISTICAL MULTI-MODEL ENSEMBLE APPROACH**

Detailed mechanistic models can be crucial to making projections about ecosystem dynamics. Often, however, there is more than one plausible and well-supported model for a given system or phenomenon. This raises important questions about how best to make predictions and account for uncertainty in such situations. For example, simply choosing the best model and treating it as if it were 'correct' typically underestimates the uncertainty in projections. The presentation gave a brief introduction to the approach developed by Spence *et al.* (2018) which involves statistically modelling the relationship between the different mechanistic models and forming a multi-model ensemble. This gives a way of allowing for both individual and shared discrepancies in the models. A toy example was outlined, together with a case study using five different models of fish dynamics in the North Sea.

Blackwell was thanked for his presentation. During the discussion, it was noted that models will agree in some aspects and disagree in others. If the model output differs from the data in a systematic way, this information will be used in the ensemble. The authors commented that such ensemble models provide the user with an understanding of the model structures and not just the model parameters. Even if the data used are not the same across all models, one fits the model with all available data and any correlations between models can be due to any common data used. If the discrepancy between the data and the model predictions changes over time (e.g. under climate change scenarios), any model will struggle to capture this (e.g. one-off events relating to climate), but one can allow for discrepancies involving future change by allowing the discrepancy to be non-stationary. For example, in the case study described in the presentation, a step change in how the discrepancy behaved was allowed in response to a change in management fisheries policy. The ensemble framework allows users to think about what is known in a more systematic way. If there is knowledge from another study/geographical area, this prior knowledge of the effects of shocks on comparable systems can help understand what discrepancies to expect. Similarly, expert knowledge needs to be incorporated into the statistical process as one needs to have an idea of what 'reasonable' discrepancies from the data might look like. When multiple plausible well-supported models on cetacean function exist, the combined output from an ensemble model can be fed into an economic model in a similar way as is

done for fisheries management.

#### **4.3 Review and discuss existing ecosystem models for the proposed regions**

In discussion, five modelling-related areas were selected as reflecting those most in need of further work:

1. Current perceptions of the status of the many whale stocks typically fail to realise that although some remain at very low levels (such as the blue whales in the Southern Ocean), others have recovered to a substantial extent (even to near pre-exploitation levels) or were never very severely depleted in the first place. The status of stocks initiative (SOSI) in the IWC SC aims to update such status estimates and to provide them for many further stocks, based on single species models, and should continue to be speedily pursued, and later extended to provide projections for the future for both large whale and small cetacean stocks. As a first step, the IWC SC and the Secretariat are encouraged to prioritize making updated tables of abundance estimates available online. This will facilitate cross-comparison between different efforts to model the pre-exploitation and current role of cetaceans in marine ecosystems.
2. Nutrient cycling field/laboratory studies and analyses should be improved and extended, and linked to phytoplankton and carbon dynamics. Inputs from Earth System Models might assist. The question of how the indirect carbon pathways across vertical and horizontal spatial scales work should be addressed, both whether the associated mechanisms are operating (nutrient cycling; carbon fixation, export and sequestration), and if so, what is the marginal contribution of whales relative to other ecosystem components.
3. The multispecies models presented at the meeting should be extended, primarily to include lower trophic levels (other than forage fish) to some extent, to be able to take account of the role played by whale excretion. Alternatively, existing models might be linked to bio-geochemical models to try to achieve this. Spatio-temporal considerations (horizontal and vertical movement) may also require some attention.
4. Modelling work should always continue to establish to what extent key results are likely to be sensitive to structural differences between alternative models. Furthermore, before large-scale experiments might be put in place, it should be clear how these results might be useful (i.e. first be clear how the results from the experiments might be used).
5. Summarize existing bio-energetic formulations and parameters to establish appropriate ranges (e.g. prey consumption rates) for use in analyses

Other modelling aspects considered to be of some importance, though of less immediate urgency, were (in no specific order):

- Allowance for climate change in models;
- Application of whole ecosystem type (i.e. Atlantis-like) models;
- Attention to further aspects of nutrient and carbon cycling – sequestration, fixing and storage in living animals;
- Data needs, particularly new estimates of population abundance and mortality rates by species and by age;
- Diagrammatic representation of models and associated aspects to aid their understanding by economists and to assist in identifying data gaps;
- Inclusion of age structure in models;

- Linking the nutrient cycling to whale population energy requirements;
- Properties of models, especially as related to their sensitivity, robustness, structure and validation.

In discussion, it was emphasized that the IWC SC Working Group on Ecosystem Modeling is currently at a strategic use point, and not at the point of providing tactical advice as to the development of models to predict the role of cetaceans in ecosystem function. It is important that the IWC Commissioners understand the time horizon needed to address the knowledge gaps associated with developing and refining such models before their tactical use can be initiated.

## **5. OTHER ITEMS**

### **5.1 Ecological economics**

#### **5.1.1 M. HERNANDEZ-BLANCO - ESTIMATING ONE OF THE MULTIPLE VALUES OF NATURE - FROM FUNCTIONS TO SERVICES**

Ecosystem services refer to the relative contribution of natural capital to the production of various human benefits, in combination with the other three forms of capital (i.e., built, human and social) In simpler terms, ecosystem services are the benefits that society obtains from ecosystems. These benefits originate when an ecosystem function has an impact on the well-being of people. Cetaceans alone do not provide ecosystem services (since quite obviously they are not an ecosystem), and therefore speaking about ecosystem services from cetaceans is conceptually wrong and misleading. Even referring to hunting (e.g., aboriginal consumption of meat) as an ecosystem service from whales is inappropriate since in this case, it would be a food provisioning service (meat from whales) provided by marine ecosystems. In terms of whale watching, this is also not an ecosystem service provided by whales; rather, it is a recreation/tourism service provided by marine systems with the opportunity to see (among other things) whales.

Cetaceans contribute to the vigour (e.g., from primary productivity) and organization (e.g., biodiversity and its interactions) of ecosystem health, which has an impact on the magnitude and quality of the benefits provided. Therefore, regarding cetaceans, the main goal should be to determine the roles of whales and dolphins, and their connections with other species and abiotic elements that contribute to ecosystem functions (e.g., nutrient circulation and ocean fertilization, carbon sequestration and habitat provision through whale falls) and ultimately to ecosystem health. The last determines the provision of ecosystem services from the marine system.

Hernandez-Blanco was thanked for his presentation. During discussion, it was noted that these economic valuation methods are well established (with most developed many decades ago). However, before these economic methods can be applied, for example as part of cost-benefit analyses, there is a need to identify the ecosystem services for which values will be estimated and the causal pathways through which these services are linked to the ecosystem functions supported by cetaceans. While whales provide multiple direct values to society, including existence values, the role they play in supporting the provision of ecosystem services is still largely unknown. The necessary type and complexity of the models used to assess these benefits depend on factors that include the type of value to be estimated, the potential magnitude of the value, the beneficiaries affected by the ecosystem service, and how the resulting information will be used to inform decisions. The selected socio-ecological models should provide the information needed to inform decisions, considering both the level of uncertainty in the model and the degree of certainty that is needed to inform particular types of decisions.

#### **5.1.2 R. Johnston - Use of benefit transfer approaches to heterogenous large-scale applications of ecosystem service valuation**

Applied ecosystem service valuation to inform large-scale decisions generally requires benefit

transfer. Benefit transfer is the use of information on economic (often non-market) values from pre-existing primary studies at one or more sites, or policy contexts (called study sites) to predict economic value estimates for other, typically unstudied sites or policy contexts (called policy sites). Benefit transfer allows ecosystem service values to be quantified for sites at which no primary valuation studies have been conducted. The accuracy of estimates of benefit transfers, however, depends on the methods that are applied, and some ecosystem service benefit transfers in the academic literature have applied methods that are either inaccurate or conceptually flawed. This presentation provides an overview of benefit transfer methods applicable to large-scale ecosystem services valuation. Among the different approaches, there is emerging consensus over the potential advantages of valuation meta-regression models (MRMs). These models synthesize data from many prior studies that have estimated similar types of economic value for similar ecosystem services. The resulting parameterized benefit functions can be used to predict ecosystem service values at policy sites where no original valuation studies have been conducted. The use of MRMs for applied benefit transfer is illustrated using a case study of water quality improvements in the New York, New Jersey Harbor Estuary (USA). The case study demonstrates how this approach allows value predictions to be adjusted for characteristics of ecosystem service changes, affected human populations and other characteristics of the affected policy site(s), thereby promoting more valid and reliable value predictions.

Johnston was thanked for his presentation. A key point noted in the discussion was that to enable the valuation of ecosystem service values supported by cetaceans, it is necessary to understand the causal linkages that connect the effects of these species on ecosystems to ecosystem services that are valued by beneficiaries. These effects will likely vary depending on multiple factors, such as location and the type of cetacean species, among others. The accuracy of these models also depends on the range of available data. In a novel situation, if one is far outside of one's data envelope, the reliability of the model outputs may decrease. The contribution of cetaceans to the provision of marine ecosystem services could potentially be factored into benefit transfer functions and/or meta-analysis. Carbon sequestration is a very important value/service. Once the quantity of carbon sequestered by whales is understood, the social value of that sequestration can be calculated readily using a consensus estimate of the social cost of carbon (agreed by scientists). However, the accuracy of these predictions depends on the underlying accuracy of biophysical models used to predict the amount of carbon sequestration that is caused by cetaceans in different ecosystems. To assess the economic value of whales fully, there is a need to highlight the knowledge gaps and the research needed to fill these gaps. Notably, there are uncertainties in all ecological processes and any uncertainty in the biology or the ecological models will propagate through to economic predictions of ecosystem service values.

### ***5.1.3 C. Fullenkamp - A valuation method for great whales and forest elephants; connecting financial markets to conservation and restoration***

This presentation discusses the valuation approach used by the Blue Green Future team to place monetary values on living natural resources such as megafauna. The approach is motivated by the goal of encouraging action to preserve and restore living nature, combined with the realization that financial markets as well as policymakers and individuals must be convinced to take action. This leads to an approach to valuation that explicitly acknowledges that it is not estimating the total economic or intrinsic value of any natural resource, but provides a lower bound on value that is nonetheless capable of prompting action. The presentation then gives an overview of the valuation process used by Blue Green Future, emphasizing its focus on integrating scientific research, modelling and measurement of the environmental services produced by natural resources into a standard market-based discounted expected value framework for estimating the value of each resource. The presentation emphasizes the application of Blue Green Future's valuation methodology to African forest elephants and great whales, showing that estimated lower bounds for the values of these species are appreciable. Such values can then form the basis of positive actions to preserve and restore

megafauna, or to calculate damages or set fines to discourage the harming or killing of these species.

Fullenkamp was thanked for his presentation. It was noted that this methodology is based on a 'willingness to pay' approach tied to the price of carbon in the market, but that, if considering the overall value of a whale to society, different methodologies would be applicable. It is important to consider the types of values that are predicted by different types of economic models. In this case, the value is based on the current population and future offspring. As whales are considered an "international public good", their management and conservation require international cooperation. While the current voluntary market for carbon offsets and reductions needs restructuring, by using live whales as a carbon credit, there is the potential to sell those credits to raise funds to conserve whales; however, questions were asked about the lack of any guarantee that the whale will survive (including outside a country's Exclusive Economic Zone). There may be value in transitioning this work from a partial equilibrium to a full equilibrium model while also keeping in mind other interactions and feedback loops (e.g., how changes in fish stocks occur as a consequence of the ecosystem functions supported by cetaceans) even if not modeled. There was also discussion about some of the biological assumptions used in the monetary valuation, a major one being the one percent global increase in primary productivity linked to the nutrient cycling of whales including the origins of that estimate, given that most carbon fixed by phytoplankton is respired back into the atmosphere with only a small fraction sequestered. In response, it was argued that the model is based on an assumption of a steady state increase in the phytoplankton that would permanently fix carbon, and has an overarching goal of valuing the functions of cetaceans to, for example, promote the creation of more or expanded Marine Protected Areas to benefit wildlife conservation more generally. Nevertheless, some present expressed the view that the argument for how carbon fixation/primary production equates to carbon sequestration and value on the carbon market was unclear, and goes beyond the scope of current biological understanding. It was noted that biological models should inform the economic models but it was not clear to what extent biological models have to be developed or advanced to make progress on economic models.

#### 5.1.4 R. MOLINA AND J.C. VILLASEÑOR-DERBEZ - A MODEL FOR MONETIZING WHALE CONSERVATION

Whales store enormous amounts of carbon in their bodies, stimulate primary production through nutrient recycling, and sequester carbon when they die. These carbon benefits are diminished when whales are removed from the environment but are increased when the population grows compared to the current baseline. Here, a bio-economic model is built that couples an age-structured whale population, its contributions to the carbon cycle, and economic principles to calculate the implied cost of whale mortality and, by implication, the carbon benefits associated with their conservation. In the analysis, it was found that the main carbon cost of removing a whale accrues due to the ensuing population dynamics following its removal (forgone reproductive potential), and not due to the carbon that was once stored in that whale. Taking these dynamics into account, the per-whale costs of human-induced whale mortality range from \$5,410 ± 2,093 (mean ± standard deviation) for small-bodied and fast-growing species such as minke whales (*Balaenoptera acutorostrata*) to \$74,153 ± 2,349 for large-bodied and slow-growing species like fin whales (*B. physalus*). Further, after examining catch data reported by the IWC, it was found that the implied foregone benefits induced by global whaling of fin, humpback, minke and gray whales only are at least USD 8.35 million per year. These findings establish a lower bound for the potential benefits of whale conservation, underscored by additional gains from ecosystem services and ecotourism.

Renato was thanked for his presentation. During the discussion, it was noted that one of the benefits that humans derive from whales that could be elicited in the simplest (and therefore easiest) terms is their existence value. Existence values are not linear and can change based on species abundance, biological and social carrying capacities, perceived or actual risks to the species, and due to cultural factors. The contribution of cetaceans to the ecosystem services of carbon storage and sequestration

via direct carbon pathways is currently reasonably estimable. Some inquired about the need to use an age-class model given the uncertainty associated with the additional parameters. Renato explained that they had run robustness tests, but still needed to check if using more parsimonious models would render similar results. Furthermore, it was noted that additional research would be valuable to determine the correlation between such lower-bound estimates and the expected total value of the whale, which can be influenced by a number of variables.

In a broader discussion, workshop participants noted that while the value of the climate regulation services supported by whales can already be determined (conditional on the accuracy of the biogeochemical modelling used to predict the quantity of carbon sequestered via direct carbon pathways), more data are needed to estimate the value provided through other ecosystem functions (e.g., nutrient cycling and impact on primary productivity) accurately. The intent behind the pilot project to assess the socio-economic value of the ecosystem functions of cetaceans is not to provide a value for every function or service, but to assess the sources of potential value where possible (i.e., where there are sufficient data to do so) and then to provide a framework to assess additional values when the data are available. Participants sought to identify the “low-hanging fruit” in the context of the functions or services that can be valued and recognized the value of the ecological models in informing the economic models. They noted that a guidance document containing information about species, populations, abundance estimates and variability and other resources may be useful for the economists. Developing a causal chain between a whale function and how it creates a service that is valued by humans is a critically important exercise to inform any economic valuation further. Broadly speaking, a key consideration in this assessment is to determine how the economic valuation data will be used, by whom, and to articulate the objectives in conducting the analyses. It was also suggested that there is a need to identify the questions to be answered first before proceeding. Based on this discussion, the Chair created two in-session working groups asking them to develop a series of questions related to the socio-economics of the ecosystem functions of cetaceans and ecosystem modeling of cetaceans, respectively. The results of these in-session working group discussions are contained in Annexes G and H.

## **5.2 Research approach**

### **5.2.1 H. Pearson - A research pathway for advancing understanding of the indirect carbon and nutrient cycling roles of the great whales**

The great whales are integral components of healthy ecosystems that exert strong effects on the carbon (C) cycle. Understanding the great whales’ indirect C effects through fertilization of surface waters via their excreta is a major knowledge gap that must be addressed before considering great whale recovery as a nature-based solution. The authors propose a study to critically examine and estimate the C effects of one indirect C pathway- the whale pump - using empirical field tests, laboratory experiments and numerical modelling. The first objective is to assess if whale hot spots and hot moments enhance the biological carbon pump. Satellite measurements of chlorophyll-a will be used to detect changes in phytoplankton biomass, growth rate, and community composition, together with size in areas and times with versus without great whales. Bulk sinking rate experiments will also be conducted to assess the species, size, and amount of phytoplankton stimulated in regions with versus without feeding whales. The second objective is to estimate how much new vs recycled primary production whales stimulate. The Savoca *et al.* (2021) model that relates whale foraging data, prey type, and nutrient recycling rates will be expanded by incorporating precise measurements of prey nutrient content and the proportion of dives above vs below the maximum annual mixed layer depth. Incubation experiments will also be conducted to determine the potential for great whale faeces to stimulate phytoplankton growth. The third objective is to determine the impact of whale-derived nutrients on C export and sequestration. A Community Earth System Model will be used to quantify the impact of whale-mediated nutrient inputs and C export on the patterns and rates of marine net primary productivity, new vs recycled nutrient budgets, and the strength of the biological carbon

pump and associated ocean C sequestration. Taken together, this project will advance understanding of the potential for recovery of the great whales to aid in CO<sub>2</sub> removal.

Pearson was thanked for her presentation. Workshop participants welcomed the research proposal and some expressed interest in collaborating. It was noted that such models are dependent on having current data on the status of whale stocks. In addition, it is important to use such models to determine not only if the whale pump works, but also to consider the role of other species that engage in nutrient cycling to better understand the proportional role of the different species groups in this process. It was noted that various biogeochemical models exist and, instead of creating new models, existing models could potentially be used to provide a rapid way forward. What is most critical is ensuring that the results of the exercise will provide meaningful answers to the questions.

### **5.3 Discussion of the valuation of the economic functions of cetaceans**

In discussion, it was considered of greatest importance that the pilot project should focus on creating a research framework to assess the economic role of cetaceans in supporting marine ecosystem services. This framework would explore all potential ecosystem services supported by cetaceans and identify what data gaps can be addressed in the future to allow economic valuation of these ecosystem services.

It was noted that there were already some carbon sequestration economic valuation models available that consider biomass and primary productivity. However, these valuations were limited to one ecosystem service only (i.e., climate regulation through carbon sequestration via direct pathways). It was also noted that the value of carbon sequestration has been considered extensively in economic valuation models. Hence the primary question concerning cetaceans is not the underlying value of carbon sequestration (which is well-studied in the economics literature), but rather the net amount of carbon sequestered due to cetaceans (the biophysical question).

There could be many other ecosystem services of interest. Examples could include those derived from the impact on primary production determined from the whale pump on fish stocks or the impact of whale falls on the provision of habitat to biodiversity and bioprospecting opportunities. In addition, the pilot project could then apply some of these models (conditional on the availability of ecological and economic data) to a specific population/area as a general case study.

Furthermore, the group agreed that the framework should provide general guidelines on how these economic valuations can be used to influence whale conservation and management, either through market or policy developments.

Critical questions that the pilot project should consider to the extent possible:

What are the ecosystem services to which cetaceans contribute?

What are the linkages between the ecosystem services to which cetaceans contribute (e.g., climate regulation, nutrient cycling contributing to primary productivity and habitat provisioning)?

Which ecosystem services can be valued with existing data and current economic valuation tools?

How do these values change as cetacean populations increase or decline due to natural and anthropogenic drivers of change?

Which ecosystem services to which cetaceans contribute should be prioritized for analysis (considering the availability of data and models, together with the likely [relative] magnitude of the associated values)?

How can economic valuations of the ecosystem services to which cetaceans contribute be used to inform whale conservation and management?

## **6. SUMMARY AND RESEARCH NEEDS**

Several research teams have made appreciable progress in studying the ecosystem functions of cetaceans around the world including in the Southern Ocean, North Atlantic and North Pacific oceans.

Further research by interdisciplinary teams of scientists is necessary to further elucidate the ecosystem functions and services provided by cetaceans and other taxa, including small cetaceans and marine invertebrates, in all oceanographic regions. This is recommended to provide additional data related to their role in carbon sequestration, nutrient cycling and its impact on primary production, biodiversity (including the benefits of dead animals (e.g., whale/cetacean falls) on seafloor biodiversity) to facilitate a comparison with the proportional impact of all taxa in providing such services.

It is imperative that such interdisciplinary research teams include marine biologists, ecosystem modellers, oceanographers, statisticians, ecological economists and others with relevant expertise and skills to facilitate collaboration amongst such experts. Such diversity will benefit independent and collective research efforts to maximize opportunities to design study methodologies and collect data that can be used in ecosystem modelling that will inform the development of economic valuation assessments.

Ecological economists play a critical role in providing valuation assessments of cetaceans and other species that can aid decision-makers, industry, civil society and philanthropic organizations in making conservation and management decisions or in allocating funding to support conservation initiatives.

Future research needs for modelling analysis of the ecosystem functions provided by cetaceans are identified and addressed in 4.3.

Future activities to develop an economic valuation of the functions and/or services provided by cetaceans are identified and addressed in 5.1.5.

## **7. RECOMMENDATIONS FROM THE WORKSHOP**

The question of how the indirect whale carbon pathways operate across vertical and horizontal spatial scales needs to be addressed, both whether the associated mechanisms are operating (nutrient cycling; carbon fixation, export and sequestration), and if so what is the contribution of whales relative to other ecosystem components.

Develop a framework illustrating the causal linkages between the ecosystem services to which cetaceans contribute (e.g., climate regulation, nutrient cycling contributing to primary productivity, habitat provisioning), cetacean functions in the ecosystem and the potential values to beneficiaries.

Place the ecosystem services to which cetaceans contribute in priority order for analysis.

## **8. ADOPTION OF THE WORKSHOP REPORT**

The report was adopted on 16 November 2023, 17:50.

## Annex A

### Invited participants list (in person)

Name	Affiliation
Biuw, Martin	Institute of Marine Research (Norway)
Blackwell, Paul	University of Sheffield (United Kingdom)
Boumans, Roelof	Boston University Pardee School of Global Studies (United States); Accounting for Desirable Futures (aka Affordable Futures) (United States)
Butterworth, Doug	University of Cape Town (South Africa)
Freitas, Carla	Institute of Marine Research (Norway)
Fullenkamp, Connel	Duke University (United States)
Galletti, Barbara	Centro de Conservación Cetacea (Chile)
Gilbert, Lola	La Rochelle Universite (France)
Hernández-Blanco, Marcello	Conservation Strategy Fund (Costa Rica)
Johnston, Robert	Clark University (United States)
Kitakado, Toshihide	Tokyo University of Marine Science (Japan)
Molina, Renato	University of Miami, Rosenstiel School Environmental and Resource Economics (United States)
Moosa, Naseera	University of Cape Town (South Africa)
Pearson, Heidi	University of Alaska Southeast (United States)

### Invited participants list (virtual)

Name	Affiliation
Costa, Daniel	University of California, Santa Cruz (United States)
Friedlaender, Ari	University of California at Santa Cruz (United States)
Kelly, Nat	Australian Antarctic Division (Australia)
Kizska, Jeremy	Florida International University (United States)
Letscher, Robert	University of New Hampshire (United States)
Morzaria-Luna, Hem Nalini	NWFSC-NOAA
Savoca, Matt	Stanford University (United States)
Tulloch, Viv	University of British Columbia (Canada)
Villaseñor-Derbez, Juan Carlos	University of California, Santa Barbara (United States)

### Other attendees (in-person or virtual)

Nominee	Affiliation
Cabrera, Elsa	Centre de Conservacion Cetacea – Chile
Ferguson, Megan	Biodiversity Research Institute (United States)
Frisch-Nwakanma, Heidrun	Convention on Conservation of Migratory Species of Wild Animals
Fuchs, Astrid	Whale and Dolphin Conservation
Iniguez, Miguel	Argentina
Katara, Isidora	International Whaling Commission
Porter, Lindsay	IWC SC Vice Chair
Rennell, Jenny	Convention on Conservation of Migratory Species of Wild Animals

Schubert, DJ	Animal Welfare Institute
Staniland, Iain	IWC Head of Science
Tossenberger, Vanessa	Fundacion Cethus
Virtue, Melanie	Convention on Conservation of Migratory Species of Wild Animals
Vrooman, Jip	Wageningen University & Research (Netherlands)
Zerbini, Alex	IWC SC Chair

## Annex B

### Agenda

1. Opening of the Workshop
  - 1.1 Welcome and introduction of workshop participants
    - 1.1.1 Welcoming Remarks from the IWC
    - 1.1.2 Welcoming Remarks from CMS
    - 1.1.3 Technical Arrangements
  - 1.2 Appointment of Chair
  - 1.3 Appointment of Rapporteurs
  - 1.4 Adoption of Agenda
  - 1.5 Review of available documents
2. Review of Terms of Reference
3. Background information/materials
  - 3.1 Summary of the IWC Resolutions (2016-3 and 2018-2)
  - 3.2 Summary of 1<sup>st</sup> IWC-CMS workshop on cetaceans and ecosystem functioning (in April 2021)
  - 3.3 Summary of the work of the IWC Conservation Committee's Advisory group on the socio-economics of cetaceans and ecosystem functions
4. Key steps for quantifying of roles of ecosystem functioning
  - 4.1 Identify ecosystem functioning processes and associated metrics (updating the science)
    - 4.1.1. Whales in the carbon cycle; the current state of knowledge (H. Pearson)
    - 4.1.2. Cetaceans and the whale pump: expanding the picture to more species, more ecosystems and more nutrients (L. Gilbert)
    - 4.1.3 Updates on cetacean bioenergetics and material flux (D. Costa)
  - 4.2 Develop conceptual models, including target species, regions, and critical parameters needed to estimate the ecosystem functioning metrics in the past and during the present time
    - 4.2.1 North Atlantic Ocean
      - 4.2.1.1 Historical abundance reconstruction of key large cetaceans in Northeast Atlantic (M. Biuw)
      - 4.2.1.2 Nutrient concentrations of minke whale excretion in the Northeast Atlantic (C. Freitas)
      - 4.2.1.3 Estimating the historical and current role of cetaceans in the nutrient Budget of the Northeast Atlantic (M. Biuw)
      - 4.2.1.4 Ocean ecology and whales (R. Boumans)
    - 4.2.2 Southern Ocean
      - 4.2.2.1 Model estimates of pre and post-abundances of the cetaceans in the Antarctic ecosystems (N. Moosa)
      - 4.2.1.2 Ecosystem model updates and ensemble projections for Southern Ocean and North Pacific (V. Tulloch)
    - 4.2.3 North Pacific
      - 4.2.4.1 Atlantis ecosystem model: assessing cumulative impacts in Puget Sound (H. Morzaria-Luna)
    - 4.2.4 Other modeling presentations
      - 4.2.3.1 Combining information from ecosystem models using a statistical multi-model ensemble approach
  - 4.3 Review and discussion of existing ecosystem models for the proposed regions

5. Other items
  - 5.1 Ecological economics
    - 5.1.1 Estimating one of the multiple values of nature – from functions to services (M. Hernandez)
    - 5.1.2 Use of benefit transfer approaches to heterogenous large scale applications of ecosystem service valuation (R. Johnston)
    - 5.1.3 A valuation method for great whales and forest elephants (C. Fullenkamp)
    - 5.1.4 A model for monetizing whale conservation (R. Molina & J.C. Villaseñor-Derbez)
  - 5.2 Research approach
    - 5.2.1 A research pathway for advancing understanding of the indirect carbon and nutrient cycling roles of the great whales (H. Pearson)
  - 5.3 Discussion of the valuation of the economic functions of cetaceans
6. Summary and research needs
7. Recommendations from the workshop
8. Adoption of workshop report

## Annex C

### References

Adamczak, S. K., McHuron, E. A., Christianen, F., Dunkin, R., McMahon, C.R., Noren, S., Pirota, E., Rosen, D., Sumich, J., and Costa, D. 2023. Growth in marine mammals: a review of growth patterns, composition and energy investment. *Conservation Physiology*, 11:coad035.

Aguilar Soto, N., M. P. Johnson, P. T. Madsen, F. Diaz, I. Dominguez, A. Brito, and P. Tyack. 2008. Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). *Journal of Animal Ecology* 77: 936-947.

McHuron, E. A., Adamczak, S., Arnould, J.P.Y., Ashe, E., Booth, C., Bowen, W.D., Christiansen, F., Biuw, M., Solvang, H., Lindstrøm, U. 2023. Update to: Reconstruction of historical abundance of rorquals in the Northeast Atlantic. Institute of Marine Research. IWC-CMS 2nd Workshop on Cetaceans and Ecosystem Functions, November 2023, Bonn, Germany. See Annex F.

Booth, C. G., Guilpin, M., Drias-O'Hara, A.K., Ransjin, J.M., Ryder, M., Rosen, D., Pirota, E., Smout, S., McHuron, E.A., Nabe-Nielsen, J., and Costa, D.P. 2023. Estimating energetic intake for marine mammal bioenergetic models. *Conservation Physiology*, 11: coac083.

Chami, R., Cosimano, T., Fullenkamp, C., Berzaghi, B., Español-Jiménez, S., Marcondes, M., and Palazzo, J. 2020. On valuing nature-based solutions to climate change: a framework with application to elephants and whales. In ERID Working Paper Number 279, Duke University. Available at: [https://papers.ssrn.com/sol3/papers.cfm?abstract\\_id=3686168](https://papers.ssrn.com/sol3/papers.cfm?abstract_id=3686168)

Gilles, A., Authier, M., Ramirez-Martinez, N.C., Araújo, H., Blanchard, A., Carlström, J., Eira, C., Dorémus, G., FernándezMaldonado, C., Geelhoed, S.C.V., Kyhn, L., Laran, S., Nachtsheim, D., Panigada, S., Pigeault, R., Sequeira, M., Sveegaard, S., Taylor, N.L., Owen, K., Saavedra, C., Vázquez-Bonales, J.A., Unger, B., and Hammond, P.S. 2023. Estimates of cetacean abundance in European Atlantic waters in summer 2022 from the SCANS-IV aerial and shipboard surveys. Final report published 29 September 2023. 64 pp. Available at: <https://tinyurl.com/3ynt6swa>

[International Whaling Commission/Conservation Committee Planning Group. 2023.](#) Invitation to Tender. Contracted Expert/Team/Organization to conduct the pilot project to assess the socioeconomic value of the ecosystem services provided by cetaceans. DRAFT. CCPG/OCT23/15

International Whaling Commission and Convention on Migratory Species. 2021. SC/68C/REP/03, Report of the IWC-CMS Workshop on Cetacean Ecosystem Functioning, 19-21 April 2021 (Virtual). Available at: <https://archive.iwc.int/pages/view.php?ref=19252&k=>

Kaplan, I.C., and Marshal, K.N. 2016. A guinea pig's tale: learning to review end-to-end marine ecosystem models for management applications. *ICES Journal of Marine Science*, 73(7), 1715–1724. doi:10.1093/icesjms/fsw047.

McHuron, E. A., Adamczak, S., Arnould, J.P.Y., Ashe, E., Booth, C., Bowen, W.D., Christiansen, F., Chudzinska, M., Costa, D.P., Fahlman, A., Farmer, N.A., Fortune, S.M.E., Gallagher, C.A., Keen, K.A., Madsen, P.T., McMahon, C.R., Nabe-Nielsen, J., Noren, D.P., Noren, S.R., Pirota, E., Rosen, D.A.S., Speakman, C.N., Villegas-Amtmann, S., and Williams, R. 2022. Key questions in marine mammal bioenergetics. *Conservation Physiology*. 10:coac055.

- McHuron, E. A., Adamczak, S., Costa, D.P., and Booth, C. 2023. Estimating reproductive costs in marine mammal bioenergetic models: a review of current knowledge and data availability. *Conservation Physiology*. 11:coac080.
- Michelot, T., Blackwell, P.G., and Matthiopoulos, J. 2019. Linking resource selection and step selection models for habitat preferences in animals. *Ecology*. 100(1), p.e02452. Available at: <https://esajournals.onlinelibrary.wiley.com/doi/pdf/10.1002/ecy.2452>
- Noren, S. R., and Rosen, D.A.S. 2023. What are the Metabolic Rates of Marine Mammals and What Factors Impact this Value: A review. *Conservation Physiology*. 11:coad077.
- Moosa, N. 2017. An updated model of the krill-predator dynamics of the Antarctic ecosystem. MSc thesis, UCT. 251 pp.
- Moosa, N., and Butterworth, D.S. 2023. Model estimates of pre- and post- abundances of the cetaceans in the Antarctic Ecosystem. University of Cape Town. Report IWC SC/CMS/N23/01 IWC-CMS 2nd Workshop on Cetaceans and Ecosystem Functions, November 2023, Bonn, Germany. See Annex G.
- Pirotta, E. 2022. A review of bioenergetic modelling for marine mammal populations. *Conservation Physiology* 10: 10.1093/conphys/coac036.
- Pearson, H. 2023. Basis of Biomass and Whalefall C Values (Presented in Pearson *et al.* (2022)). Report of the IWC-CMS 2nd Workshop on Cetaceans and Ecosystem Functions, November 2023, Bonn, Germany. See Annex E.
- Quick, N. J., Cioffi, W.R., Shearer, J.M., Fahlman, A., and Read, A.J. 2020. Extreme diving in mammals: first estimates of behavioural aerobic dive limits in Cuvier's beaked whales. *Journal of Experimental Biology*, 223: jeb222109.
- Roman, J., Kiszka, J., Pearson, H., Savoca, M., and Smith, C. 2021. Ecological Roles and Impacts of Large Cetaceans in Marine Ecosystems. IWC SC/68C/EM/05
- Smith, C.R., Roman, J., and Nation, J.B. 2019. A metapopulation model for whale-fall specialists: The largest whales are essential to prevent species extinctions. *Journal of Marine Research*, 77, Supplement, 283–302. Available at [https://elischolar.library.yale.edu/journal\\_of\\_marine\\_research/481/](https://elischolar.library.yale.edu/journal_of_marine_research/481/)
- Wassmann, P., Biuw, M., and Haug, T. 2021. A critical evaluation of whales as ecosystem engineers. IWC SC/68C/EM/02
- Savoca, M.A., Czapanskiy, M.F., Kahane-Rapport, S.R., Gough, W.T., Fahlbusch, J.A., Bierlich, K.C., Segre, P.S., De Clemente, J., Penry, G.S., Wiley, D.N., Calambokidis, J., Nowacek, D.P., Johnston, D.W., Pyenson, N.D., Friedlaender, A.S., Hazen, E.L., and Goldbogen, J.A. 2021. Baleen whale prey consumption based on high-resolution foraging measurements. *Nature*, 599; 85-90. Available at: <https://par.nsf.gov/servlets/purl/10315593>
- Spence, M.A., Blanchard, J.L., Rossberg, A.G., Heath, M.R., Heymans, J.J., Mackinson, S., Serpetti, N., Speirs, D.C., Thorpe, R.B., and Blackwell, P.G. 2018. A general framework for combining ecosystem models. *Fish and Fisheries*, 19(6); 1031-1042. Available at: <https://onlinelibrary.wiley.com/doi/pdfdirect/10.1111/faf.1231>

## Annex D

Basis of Biomass and Whalefall C Values (Presented in Pearson *et al.* (2022))  
Heidi Pearson

THE SEA: THE CURRENT AND FUTURE OCEAN  
*Journal of Marine Research*, 77, Supplement, 283-302, 2019

A metapopulation model for whale-fall specialists: The largest whales are essential to prevent species extinctions

By Craig R. Smith, Joe Roman, and J.B Nation

From Smith *et al.* (2019)

Basis of Biomass and Whalefall C Values Presented in Pearson *et al.* (2022)

Table 2. Prewhaling occupancy rate of whale falls ( $P_0$ ) needed to ensure long-term survival of a whale-fall specialist after whaling for different ocean regions. Lengths before ( $L_0$ ) and after ( $L_1$ ) whaling are given in meters, and population sizes before ( $N_0$ ) and after ( $N_1$ ) whaling are in thousands.

Basin	$L_0$	$L_1$	$N_0$	$N_1$	$P_0$
North Atlantic	15.9	12.3	875	369	0.91
North Pacific	17.5	14.9	712	296	0.87
Southern Hemisphere	17.0	10.1	2,461	819	0.98
Global	16.8	11.6	4,049	1,484	0.96

Global

$L_0$	$L_1$	$N_0$	$N_1$
16.8	11.6	4,048.5	1,487
$L_1/L_0 = 0.689$		$N_1/N_0 = 0.367$	

Table 3. Estimates for historical and current whale populations and lengths. Lengths are given in meters, and populations in thousands.

Basin	Species	$L_0$	$L_1$	$N_0$	$N_1$
North Atlantic					
	Blue ( <i>Balaenoptera musculus</i> )	27	22	7.5	0.4
	Bowhead ( <i>Balaena mysticetus</i> )	20	20	80	8
	Common minke ( <i>Balaenoptera acutorostrata</i> )	7	7	211	157
	Fin ( <i>Balaenoptera physalus</i> )	23	20	73	56
	Humpback ( <i>Megaptera novaeangliae</i> )	16	16	112	20
	Right ( <i>Eubalaena glacialis</i> )	16	16	14	0.5
	Sei ( <i>Balaenoptera borealis</i> )	16	14	10.6	7
	Sperm ( <i>Physeter microcephalus</i> )	18.5	14.5	367	120
	Means/totals	15.9	12.3	875.1	368.9
		$L_1/L_0 = 0.775$		$N_1/N_0 = 0.422$	

Smith et al. (2019)

Basin	Species	$L_0$	$L_1$	$N_0$	$N_1$
North Pacific					
	Blue ( <i>Balaenoptera musculus</i> )	27	22	6	3
	Bowhead ( <i>Balaena mysticetus</i> )	20	20	30	18
	Bryde's ( <i>Balaenoptera brydei</i> )	15	15	52	41
	Common minke ( <i>Balaenoptera acutorostrata</i> )	7	7	47	32
	Fin ( <i>Balaenoptera physalus</i> )	23	20	65	31
	Gray ( <i>Eschrichtius robustus</i> )	15	15	25	16
	Humpback ( <i>Megaptera novaeangliae</i> )	16	16	20	20
	Right ( <i>Eubalaena japonica</i> )	16	16	32	0.4
	Sei ( <i>Balaenoptera borealis</i> )	16	14	68.4	14.7
	Sperm ( <i>Physeter microcephalus</i> )	18.5	14.5	367	120
	Means/totals	17.5	14.9	712.4	296.1
		$L_1/L_0 = 0.851$		$N_1/N_0 = 0.416$	

Smith et al. (2019)

Basin	Species	$L_0$	$L_1$	$N_0$	$N_1$
Southern Hemisphere					
	Antarctic minke ( <i>Balaenoptera bonaerensis</i> )	7	7	670	515
	Blue ( <i>Balaenoptera musculus</i> )	27	22	290	2
	Bryde's ( <i>Balaenoptera brydei</i> )	15	15	94	91
	Fin ( <i>Balaenoptera physalus</i> )	23	20	625	23
	Humpback ( <i>Megaptera novaeangliae</i> )	16	16	170	30
	Right ( <i>Eubalaena australis</i> )	16	16	78	13.6
	Sei ( <i>Balaenoptera borealis</i> )	16	14	167	27.4
	Sperm ( <i>Physeter microcephalus</i> )	18.5	14.5	367	120
		17.0	10.1	2,461	822
		$L_1/L_0 = 0.595$		$N_1/N_0 = 0.334$	

Smith *et al.* (2019)

Sources for Population Estimates (pp. 297-300 in Smith *et al.* 2019)

- Christensen (2006): Marine Mammal Populations: Reconstructing historical abundances at the global scale. Fisheries Centre Research Reports 14(9)
- Antarctic minke whales: Ruegg *et al.* (2010) and IWC (2013a)
- Southern right whales: IWC (2013b)
- Bowhead whales in the North Atlantic: Allen and Keay (2006), Cooke and Reeves (2018), Vacquié-Garcia *et al.* (2017)
- Bowhead whales in the North Pacific: Cooke and Reeves (2018), Givens *et al.* (2016), Shpak *et al.* (2017)
- Blue whales in the Southern Hemisphere: Branch *et al.* (2004) and Branch *et al.* (2007)
- Sperm whales: Whitehead (2002) "He estimated that 33% of the global population would be found in the North Atlantic, and we assumed a 50% split of the remainder between the North Pacific and Southern Hemisphere."

#### References:

Allen, R. C., and I. Keay. 2006. Bowhead whales in the eastern Arctic, 1611–1911: Population reconstruction with historical whaling records. *Environment and History*, 12, 89–113. doi: 10.3197/096734006776026791

Branch, T. A., K. Matsuoka, and T. Miyashita. 2004. Evidence for increases in Antarctic blue whales based on Bayesian modelling. *Marine Mammal Science*. 20, 726–754. doi: 10.1111/j.1748-

7692.2004.tb01190.x

Branch, T. A., K. M. Stafford, D. M. Palacios, C. Allison, J. L. Bannister, C. L. K. Burton, E. Cabrera, *et al.* 2007. Past and present distribution, densities and movements of blue whales *Balaenoptera musculus* in the Southern Hemisphere and northern Indian Ocean. *Mammal Review*, 37, 116–175. doi: 10.1111/j.1365-2907.2007.00106.x

Christensen, L. B. (2006). Marine mammal populations: Reconstructing historical abundances at the global scale [R]. doi:<http://dx.doi.org/10.14288/1.0074757>

Cooke, J. G., and R. Reeves. 2018. *Balaena mysticetus*, in The IUCN Red List of Threatened Species, e.T2467A50347659. doi: 10.2305/IUCN.UK.2018-1.RLTS.T2467A50347659.en

Givens, G. H., S. L. Edmondson, J. C. George, R. Suydam, R. A. Charif, A. Rahaman, D. Hawthorne, *et al.* 2016. Horvitz-Thompson whale abundance estimation adjusting for uncertain recapture, temporal availability variation, and intermittent effort. *Environmetrics*, 27, 134–146. doi: 10.1002/env.2379

International Whaling Commission. 2013a. Reports of the Subcommittee on In-Depth Assessments. *Journal Cetacean Research and Management (Suppl.)*, 14, 195–213.

International Whaling Commission. 2013b. Report of the workshop on the assessment of southern right whales. *Journal of Cetacean Research and Management. Journal Cetacean Research and Management. (Suppl.)*, 14, 437–462.

Ruegg, K. C., E. C. Anderson, C. S. Baker, M. Vant, J. A. Jackson, and S. R. Palumbi. 2010. Are Antarctic minke whales unusually abundant because of 20th century whaling? *Molecular Ecology*, 19, 281–291. doi: 10.1111/j.1365-294X.2009.04447.x

Smith, C.R., Roman, J., and Nation, J.B. 2019. A metapopulation model for whale-fall specialists: The largest whales are essential to prevent species extinctions. *Journal of Marine Research*, 77, Supplement, 283–302. Available at: [https://elischolar.library.yale.edu/journal\\_of\\_marine\\_research/481/](https://elischolar.library.yale.edu/journal_of_marine_research/481/)

Vacquié-García, J., C. Lydersen, T. A. Marques, J. Aars, H. Ahonen, M. Skern-Mauritzen, N. Øien, *et al.* 2017. Late summer distribution and abundance of ice-associated whales in the Norwegian High Arctic. *Endangered Species Research*, 32, 295–304. doi: 10.3354/esr00791

Whitehead, H. 2002. Estimates of current global population size and historical trajectory for sperm whales. *Marine Ecology Progress Series*, 242, 295–304. doi: 10.3354/meps242295

## Annex E

### Update to: Reconstruction of historical abundance of rorquals in the Northeast Atlantic

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#### Introduction

During the 2nd CMS-IWC workshop on Cetacean Ecosystem Functioning in Bonn, Nov 14-16 2023, we presented preliminary analyses based on single-species population modeling of key rorqual species in the Northeast Atlantic basin north of 60°N. At the workshop, several suggestions were made in terms of testing different prior settings for the  $r_{max}$  parameter. This was due to the fact that the wide uniform prior generally resulted in posterior distributions not substantially different from the priors, suggesting that the model was not able to estimate this parameter satisfactorily. To reflect the entire range of possible population trajectories from these relatively simple models, the workshop participants recommended testing a set of plausible narrower priors for  $r_{max}$ , ranging from 0 to 12 (i.e. roughly the maximum possible growth rate estimated for humpback whales [e.g. Zerbini *et al.* (2011)]).

In response to these requests, we ran a series of models with narrow priors of  $r_{max}$ , as specified in Table 1.

Table 1: Prior  $r_{max}$  settings for the set of models fitted to all rorqual stocks in the Northeast Atlantic north of 60°N

Model	Prior
R0.5	$r_{max} \sim \text{rnorm}(0.005, 0.0005)$
R1	$r_{max} \sim \text{rnorm}(0.01, 0.0010)$
R2	$r_{max} \sim \text{rnorm}(0.02, 0.0020)$
R4	$r_{max} \sim \text{rnorm}(0.04, 0.0040)$
R6	$r_{max} \sim \text{rnorm}(0.06, 0.0060)$
R8	$r_{max} \sim \text{rnorm}(0.08, 0.0080)$
R10	$r_{max} \sim \text{rnorm}(0.1, 0.0100)$
R12	$r_{max} \sim \text{rnorm}(0.12, 0.0120)$

The following sections, tables and figures present the output from these additional runs. For each model, the standard deviation was set to 10% of the respective mean. All other inputs were kept constant, and models were compared with regard to their negative log-likelihoods.

#### Blue whales

Table 2 presents the candidate models fitted to the blue whale data.

Table 2: Model comparison for blue whales. Models are ordered by their negative log-likelihood.

	$r_{max}$	$NLL$
<b>blueR2</b>	0.02 (0.017-0.023)	37.03
<b>blueR4</b>	0.04 (0.033-0.047)	37.24
<b>blueR1</b>	0.01 (0.0084-0.012)	37.26
<b>blueBaseRel</b>	0.051 (0.0093-0.11)	37.41
<b>blueR0.5</b>	0.005 (0.0041-0.0058)	37.53
<b>blueR6</b>	0.06 (0.05-0.069)	37.67
<b>blueR8</b>	0.081 (0.069-0.093)	37.81
<b>blueR10</b>	0.099 (0.084-0.11)	37.81
<b>blueR12</b>	0.12 (0.12-0.12)	37.83

As shown in Table 2, the best supported model for blue whales was one with an  $r_{max}$  of 0.02 (0.017-0.023). This model estimated historical and current abundances of 1,927 (1,726-2,238) and 1,607 (1,121-2,198) respectively, giving a ratio of current to historical abundance of 0.83 (0.62-0.97) (Table 3).

Table 3: Comparison of estimates of historical and current abundance of blue whales from all candidate models. The modeled trajectory from the best supported model is shown in 1.

	$K$	$N_{2023}$	$Ratio$
<b>blueR2</b>	1,927 (1,726-2,238)	1,607 (1,121-2,198)	0.83 (0.62-0.97)
<b>blueR4</b>	1,512 (1,332-1,955)	1,458 (1,159-2,107)	0.96 (0.83-1)
<b>blueR1</b>	2,470 (2,177-2,854)	1,623 (1,049-2,301)	0.65 (0.48-0.8)
<b>blueBaseRel</b>	1,722 (1,197-2,530)	1,527 (1,081-2,248)	0.91 (0.53-1)
<b>blueR0.5</b>	2,898 (2,538-3,331)	1,543 (984-2,277)	0.53 (0.39-0.67)
<b>blueR6</b>	1,489 (1,179-2,079)	1,483 (1,135-2,236)	0.99 (0.95-1)
<b>blueR8</b>	1,494 (1,092-2,040)	1,493 (1,064-2,247)	1 (0.99-1)
<b>blueR10</b>	1,490 (1,076-2,110)	1,490 (1,020-2,226)	1 (1-1)
<b>blueR12</b>	1,475 (1,024-2,082)	1,475 (985-2,211)	1 (1-1)

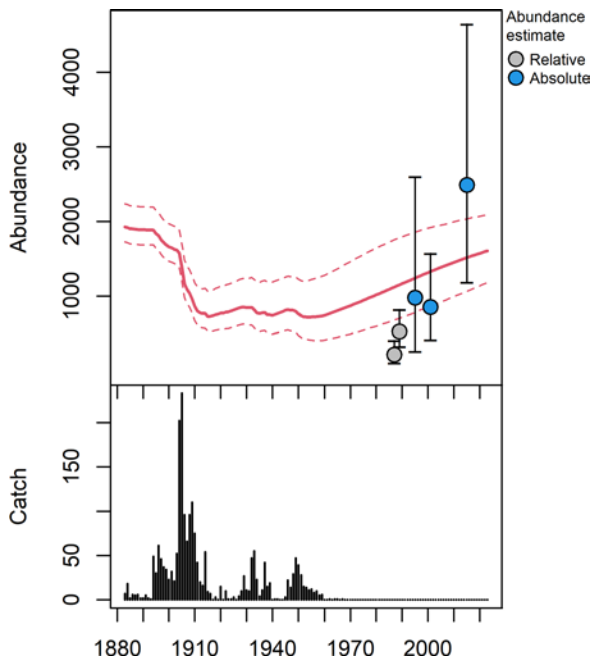


Figure 1: Blue whale population trajectory and catch statistics, based on the best supported model (see text for further details).

We should note that in these new runs we have included all historical catches occurring throughout the entire Northeast Atlantic. During the initial preliminary runs, we limited the catches to the region west of 5°W, as these were considered to correspond more closely to the area covered by the abundance surveys. However, given the very small number of blue whale observations in Norwegian surveys, we have now assumed that the abundance estimates based on Icelandic and Faeroese vessels in the area between Greenland, Iceland and the Faeroe islands is representative of the entire basin.

### Fin whales

Table 4 presents the candidate models fitted to the fin whale data.

Table 4: Model comparison for fin whales. Models are ordered by their negative log-likelihood.

	$r_{max}$	$NLL$
<b>finR1</b>	0.01 (0.0085-0.012)	47.23
<b>finR2</b>	0.02 (0.017-0.023)	47.27
<b>finR0.5</b>	0.005 (0.0042-0.0058)	47.33
<b>finR4</b>	0.04 (0.033-0.047)	47.46
<b>finBase.comb</b>	0.056 (0.0063-0.11)	47.48
<b>finR8</b>	0.08 (0.067-0.093)	47.48
<b>finR10</b>	0.099 (0.084-0.11)	47.49
<b>finR12</b>	0.11 (0.096-0.12)	47.5
<b>finR6</b>	0.06 (0.051-0.07)	47.5

As shown in Table 4, the best supported model for fin whales was one with an  $r_{max}$  of 0.01 (0.0085-0.012). This model estimated historical and current abundances of 58,117 (52,579-64,247) and 46,407 (39,820-54,187) respectively, giving a ratio of current to historical abundance of 0.8 (0.74-0.85) (Table 5).

Table 5: Comparison of estimates of historical and current abundance of fin whales from all candidate models The modeled trajectory from the best supported model is shown in 2.

	$K$	$N_{2023}$	Ratio
<b>finR1</b>	58,117 (52,579-64,247)	46,407 (39,820-54,187)	0.8 (0.74-0.85)
<b>finR2</b>	48,903 (43,477-55,175)	45,841 (39,568-53,240)	0.94 (0.9-0.96)
<b>finR0.5</b>	66,833 (61,094-72,760)	45,685 (38,586-53,207)	0.68 (0.63-0.73)
<b>finR4</b>	45,146 (39,265-51,206)	44,633 (37,879-52,102)	0.99 (0.98-0.99)
<b>finBase.comb</b>	48,007 (39,667-64,942)	45,136 (38,044-53,148)	0.95 (0.63-1)
<b>finR8</b>	44,918 (39,083-51,415)	44,749 (38,051-52,603)	1 (0.99-1)
<b>finR10</b>	44,660 (38,636-50,821)	44,546 (37,609-52,246)	1 (1-1)
<b>finR12</b>	44,756 (38,920-51,084)	44,662 (37,739-52,257)	1 (1-1)
<b>finR6</b>	44,590 (38,600-51,084)	44,330 (37,318-52,182)	0.99 (0.99-1)

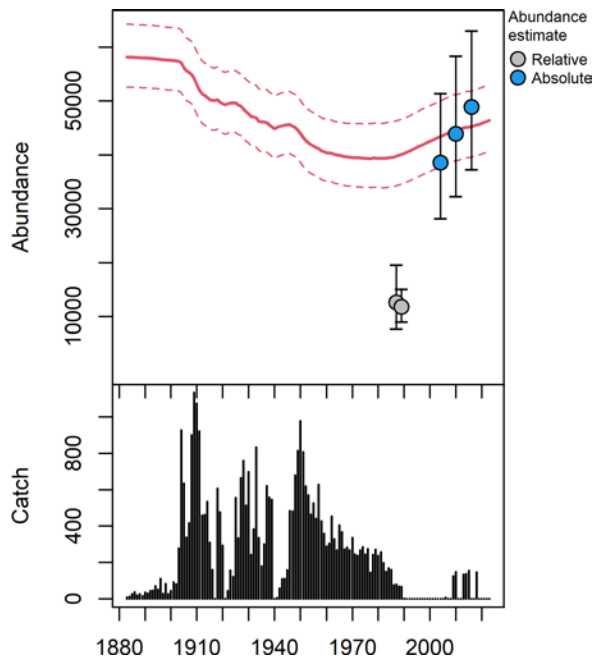


Figure 2: Fin whale population trajectory and catch statistics, based on the best supported model (see text for further details).

### Sei whales

Table 6 presents the candidate models fitted to the sei whale data.

Table 6: Model comparison for sei whales. Models are ordered by their negative log-likelihood.

	$r_{max}$	$NLL$
<b>seiR2</b>	0.02 (0.017-0.023)	17.26
<b>seiR1</b>	0.01 (0.0083-0.012)	17.29
<b>seiR4</b>	0.039 (0.033-0.046)	17.3
<b>seiR0.5</b>	0.005 (0.0042-0.0058)	17.38
<b>seiR6</b>	0.059 (0.05-0.069)	17.41
<b>seiR8</b>	0.08 (0.067-0.094)	17.53
<b>seiR12</b>	0.11 (0.096-0.12)	17.53
<b>seiR10</b>	0.099 (0.083-0.11)	17.58
<b>seiBase</b>	0.061 (0.0049-0.11)	45.42

As shown in Table 6, the best supported model for sei whales was one with an  $r_{max}$  of 0.02 (0.017-0.023). This model estimated historical and current abundances of 7,731 (6,854-9,018) and 4,762 (2,324-8,370) respectively, giving a ratio of current to historical abundance of 0.61 (0.33-0.89) (Table 7).

Table 7: Comparison of estimates of historical and current abundance of sei whales from all candidate models The modeled trajectory from the best supported model is shown in 3.

	$K$	$N_{2023}$	$Ratio$
<b>seiR2</b>	7,731 (6,854-9,018)	4,762 (2,324-8,370)	0.61 (0.33-0.89)
<b>seiR1</b>	9,902 ( 8,739-11,567)	4,499 (2,153-8,627)	0.44 (0.25-0.69)
<b>seiR4</b>	5,666 (5,003-7,087)	4,761 (2,779-7,861)	0.83 (0.52-1)
<b>seiR0.5</b>	11,525 ( 9,945-13,981)	4,268 (1,887-8,424)	0.36 (0.19-0.58)
<b>seiR6</b>	4,931 (4,128-7,065)	4,696 (3,226-8,251)	0.95 (0.73-1)
<b>seiR8</b>	4,704 (3,584-7,288)	4,643 (3,340-8,143)	0.98 (0.87-1)
<b>seiR12</b>	4,668 (3,238-7,373)	4,663 (3,169-8,146)	1 (0.98-1)
<b>seiR10</b>	4,763 (3,354-7,531)	4,752 (3,256-8,420)	1 (0.97-1)
<b>seiBase</b>	4,939 (2,590-8,468)	4,364 (2,200-8,214)	0.91 (0.43-1)

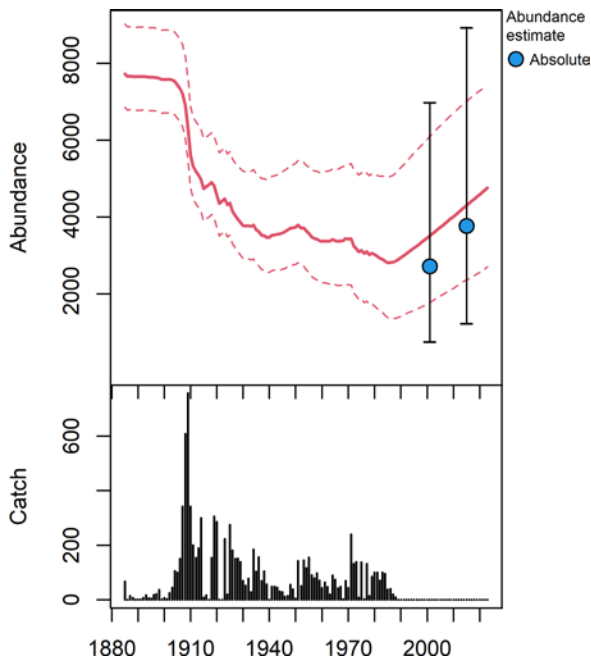


Figure 3: Sei whale population trajectory and catch statistics, based on the best supported model (see text for further details).

Two things should be noted with these new model runs. Firstly, given the very small number of sei whale observations in Norwegian surveys, we have assumed that the survey-based estimates from the Icelandic and Faeroese vessels in the region between Greenland, Iceland and the Faeroe Islands are representative the entire component of the stock that regularly occurs in the entire region of consideration here. As in the case of blue whales, we have therefore included all historical catches from the entire region in these updated model runs. In the previous runs, we excluded catches from east of 5°W. The current analyses should therefore be considered more conservative. Secondly, we chose to use only the absolute abundance estimates in these runs, as including the highly variable relative estimates caused problems with model convergence. Again, we argue that limiting the analyses to only the absolute abundance estimates provides the most conservative view of the current status of this stock relative to pre-exploitation abundance.

### Humpback whales

Table 8 presents the candidate models fitted to the humpback whale data.

Table 8: Model comparison for humpback whales. Models are ordered by their negative log-likelihood.

	$r_{max}$	$NLL$
<b>humpR10</b>	0.097 (0.082-0.11)	50.57
<b>humpR1</b>	0.0099 (0.0085-0.012)	50.6
<b>humpR6</b>	0.061 (0.051-0.07)	50.63
<b>humpR12</b>	0.11 (0.097-0.12)	50.67
<b>humpR2</b>	0.02 (0.017-0.024)	50.68
<b>humpR0.5</b>	0.0049 (0.0042-0.0056)	50.69

	$r_{max}$	$NLL$
<b>humpR4</b>	0.04 (0.035-0.046)	50.74
<b>humpR8</b>	0.08 (0.067-0.092)	50.76

As shown in Table 8, the best supported model for humpback whales was one with an  $r_{max}$  of 0.097 (0.082-0.11). This model estimated historical and current abundances of 26,024 (20,715-32,030) and 26,024 (18,440-33,391) respectively, giving a ratio of current to historical abundance of 1 (1-1) (Table 9).

Table 9: Comparison of estimates of historical and current abundance of humpback whales from all candidate models. The modeled trajectory from the best supported model is shown in 4.

	$K$	$N_{2023}$	$Ratio$
<b>humpR10</b>	26,024 (20,715-32,030)	26,024 (18,440-33,391)	1 (1-1)
<b>humpR1</b>	26,291 (20,457-34,231)	26,192 (19,439-34,506)	1 (0.99-1)
<b>humpR6</b>	25,998 (20,645-33,673)	25,998 (19,946-37,420)	1 (1-1)
<b>humpR12</b>	26,287 (19,946-34,138)	26,287 (19,258-35,114)	1 (1-1)
<b>humpR2</b>	26,285 (20,748-34,866)	26,277 (19,631-35,889)	1 (1-1)
<b>humpR0.5</b>	26,099 (20,160-32,064)	25,721 (18,698-34,224)	0.99 (0.98-0.99)
<b>humpR4</b>	25,714 (19,135-35,912)	25,714 (18,388-37,125)	1 (1-1)
<b>humpR8</b>	26,749 (20,362-35,595)	26,749 (19,938-36,495)	1 (1-1)

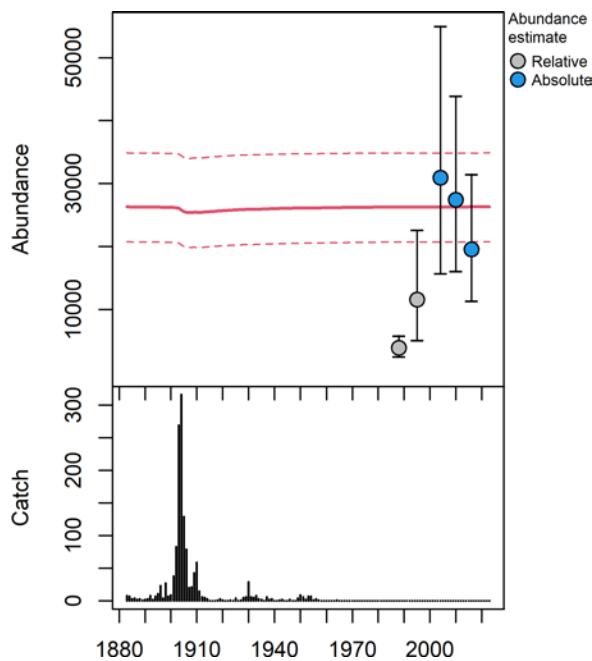


Figure 4: Humpback whale population trajectory and catch statistics, based on the best supported model (see text for further details).

It should be noted, that all humpback whale models gave very similar results, and all suggested that the

population has remained relatively stable throughout the time period since catches began. While there is consistency in the model with respect to the small catches relative to the estimated abundance, the results should nevertheless be treated with caution.

### Minke whales

Table 10 presents the candidate models fitted to the minke whale data.

Table 10: Model comparison for minke whales. Models are ordered by their negative log-likelihood.

	$r_{max}$	$NLL$
<b>minkeR2</b>	0.02 (0.017-0.023)	56.13
<b>minkeR8</b>	0.079 (0.068-0.089)	56.2
<b>minkeR0.5</b>	0.0051 (0.0044-0.0059)	56.21
<b>minkeR6</b>	0.059 (0.049-0.07)	56.28
<b>minkeR12</b>	0.11 (0.095-0.12)	56.29
<b>minkeR1</b>	0.0099 (0.0083-0.011)	56.29
<b>minkeR10</b>	0.098 (0.084-0.11)	56.34
<b>minkeR4</b>	0.04 (0.034-0.046)	56.39

As shown in Table 10, the best supported model for sei whales was one with an  $r_{max}$  of 0.02 (0.017-0.023). This was the same model resulting from the preliminary runs presented at the workshop in Bonn. To reiterate, this model estimated historical and current abundances of 185,591 (170,329-206,281) and 152,071 (132,257-180,094) respectively, giving a ratio of current to historical abundance of 0.82 (0.75-0.88) (Table 9).

Table 11: Comparison of estimates of historical and current abundance of minke whales from all candidate models

	$K$	$N_{2023}$	$Ratio$
<b>minkeR2</b>	185,591 (170,329-206,281)	152,071 (132,257-180,094)	0.82 (0.75-0.88)
<b>minkeR8</b>	146,250 (125,977-163,570)	143,111 (120,792-162,745)	0.98 (0.97-0.98)
<b>minkeR0.5</b>	242,769 (224,958-262,934)	141,776 (120,825-166,013)	0.58 (0.53-0.63)
<b>minkeR6</b>	146,715 (127,161-168,651)	142,314 (118,456-166,204)	0.97 (0.96-0.98)
<b>minkeR12</b>	145,828 (124,619-163,433)	143,582 (118,998-162,384)	0.98 (0.98-0.99)
<b>minkeR1</b>	218,488 (199,865-236,859)	146,132 (117,760-176,464)	0.67 (0.6-0.72)
<b>minkeR10</b>	146,306 (125,720-169,773)	143,807 (120,338-168,403)	0.98 (0.98-0.99)
<b>minkeR4</b>	154,730 (133,698-179,761)	146,609 (119,497-178,562)	0.95 (0.92-0.96)

The modeled trajectory from the best supported model is shown in 5.

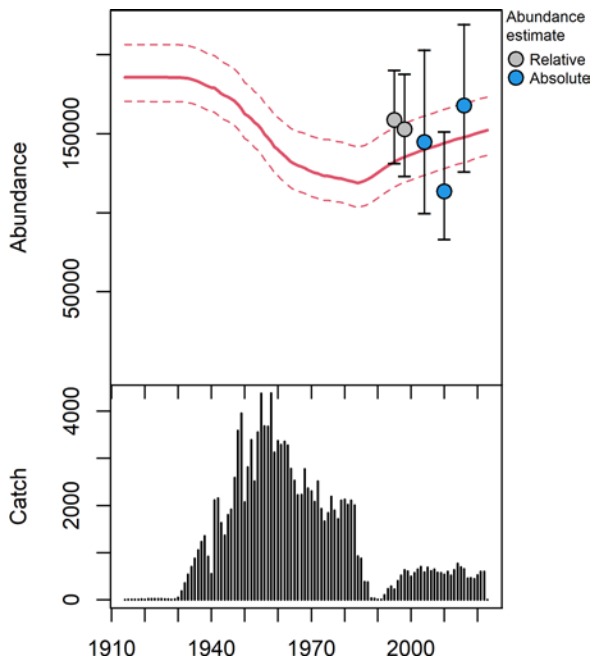


Figure 5: Minke whale population trajectory and catch statistics, based on the best supported model (see text for further details).

## Discussion

This update provides a more comprehensive overview of estimated current and historical abundance for rorquals in the Northeast Atlantic north of 60N, albeit based on a relatively simple single-species model. Overall, the results suggest that the preliminary runs resulted in estimated  $r_{max}$  that were likely too high. Table 11 shows the best supported models for each species.

Table 12: Best supported models for all species

	$r_{max}$	K	N_2023	R_2023
<b>blueR2</b>	0.02 (0.017-0.023)	1,927 (1,726-2,238)	1,607 (1,121-2,198)	0.83 (0.62-0.97)
<b>finR1</b>	0.01 (0.0085-0.012)	58,117 (52,579-64,247)	46,407 (39,820-54,187)	0.8 (0.74-0.85)
<b>seiR2</b>	0.02 (0.017-0.023)	7,731 (6,854-9,018)	4,762 (2,324-8,370)	0.61 (0.33-0.89)
<b>humpR10</b>	0.097 (0.082-0.11)	26,024 (20,715-32,030)	26,024 (18,440-33,391)	1 (1-1)
<b>minkeR2</b>	0.02 (0.017-0.023)	185,591 (170,329-206,281)	152,071 (132,257-180,094)	0.82 (0.75-0.88)

The best models provided support for an  $r_{max}$  of 0.01 or 0.02 for all species except for humpback whales, where all models produced similar results irrespective of the prior on  $r_{max}$ . While these smaller  $r_{max}$  values for the selected models did result in slightly higher estimates for the historical abundance  $K$ , the ratios of current to historical abundances were generally relatively high, ranging from 0.61 (0.33-0.89) for sei whales to 1 for humpback whales.

## References

Zerbini, A. N., Ward, E. J., Kinas, P. G., Engel, M. H., and Andriolo, A. 2011. A Bayesian assessment of the conservation status of humpback whales (*Megaptera novaeangliae*) in the western South Atlantic Ocean. *J. Cetacean Res. Manag.*: 131–144.

## Annex F

### Model estimates of pre- and post- abundances of the cetaceans in the Antarctic Ecosystem

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#### Abstract

IWC document SC/68D/EM/WP04 provided a list of pre-exploitation estimates of abundance for the Antarctic blue, fin, humpback, minke, southern right, sei and Bryde's whales in the region(s) south of 60°S, based on modelling studies. The authors were tasked with compiling this list as part of the intersessional steering group on the ecosystem functioning of cetaceans in the Southern Ocean. This document summarises what has been accomplished for this task (last presented to the IWC Scientific Committee in April 2023), as well as providing updates to this work through considering prey carbon content and 'whale falls'. Both the Moosa and Tulloch ecosystem models estimate the present large baleen whale biomass south of 60°S to be about 20% of its value before exploitation commenced.

#### Keywords

cetaceans, ecosystem functioning, single-species model, multi-species model, International Whaling Commission (IWC), pre-exploitation abundance, current abundance, whale biomass, prey consumption, prey carbon content, whale falls

#### Acknowledgements

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#### Pre- and post- abundances of the Antarctic cetaceans:

The second ToR (ToR 2.2), as agreed by the EM (Ecosystem Modelling) Sub-Committee at the 2022 IWC SC meeting for work needed to advance the understanding of the ecosystem functioning of cetaceans, reads as follows:

[To] compile a list of pre-exploitation estimates of abundance for these same species [as mentioned in ToR 2.1] for part or all of the region south of 60 degrees based on modelling studies

Towards this end, tables of the existing ecosystem and single-species model-based estimates of these quantities have been prepared (see Table 2, Table 7 and Table A1). These tables are considered to provide a comprehensive list of the available abundance estimates for the region south of 60 degrees south from models (ecosystem and single-species models respectively) at a management area level or larger. Estimates of whale abundance from CCAMLR studies pertain to a smaller spatial scale. As that information is not pertinent to the objective of this compilation, it has been noted for future reference only.

The quantities presented in Tables 2 and 7 are themselves based on abundance estimates from surveys. The abundance estimates (absolute and relative) used in the analysis of Moosa (2017), Mori and Butterworth (2006), Christensen (2006) and Tulloch *et al.* (2018, 2019) are listed in Tables 8 - 13.

In Moosa (2017), IDCR/SOWER survey data are used to calculate absolute whale abundance estimates due to their circumpolar nature and better standardised conduct of the surveys, while JARPA survey data, due to their time series nature, are used to calculate relative whale abundance estimates and trends.

The results outlined in Tables 2 and 6 are put forward as sufficient to address the requirement of ToR 2.2. of the 2022 EM Sub-Committee report.

Appendix A1 lists the pre-exploitation and current abundance estimates from existing ecosystem models.

**Whale biomass:**

The EM Sub-Committee also requested that results be given in terms of whale biomasses as well as numbers. Details of those calculations are given below, with the results shown in Table 3. The ratio of the overall current whale biomass to the overall historical whale biomass between the two ‘main’ Antarctic studies are of similar order (about 20%). This suggests little difference in terms of cetacean biomass with respect to two different ecosystem modelling frameworks (see Appendix A2 for more details of these modelling frameworks).

The average of the male and female whale mean masses from Trites and Pauly (1998) are used to determine an average mass (mt) for the large baleen whales considered (Table 1).

**Table 1:** Table that lists the average body weights for the large baleen whale species considered.

Whale Species	Average Body Weight (mt)
<b>Antarctic blue</b> ( <i>B. musculus</i> )	102.74
<b>Fin</b> ( <i>B. physalus</i> )	55.59
<b>Humpback</b> ( <i>M. novaeangliae</i> )	30.41
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	6.57

More information regarding these quantities can be found in Moosa (2017) and Moosa and Butterworth (2017).

The whale biomass ( $B$ ) in metric tonnes is calculated as follows:

$$B = w \times N_y \quad (1)$$

where  $w$  is the average weight (mt) of the large baleen whale species considered (see Table 1), and  $N_y$  is the abundance in year  $y$  of the large baleen whale species considered.

**Whale estimated prey consumption and prey carbon content:**

The EM Sub-Committee further requested that the estimated prey consumption and prey carbon content of the Antarctic cetaceans be calculated. The estimated prey consumption is summarised in Table 4 and is detailed in Moosa (2017): the average body weight information comes from Trites and Pauly (1998) (see Table 1) and the residence time information comes from Kasamatsu (2000). The same method as outlined in Wassmann *et al.* (2021) is followed to give an estimate of the amount of carbon released annually by the large baleen whales in the Southern Ocean (Table 5), i.e. 20% of the total consumption is assumed to reflect prey dry weight, 10% to be prey carbon content, 2% to be faecal dry weight and 1% to be faecal carbon content.

There is a greater amount of carbon released from the humpback and minke whales recently (minke contributing more than humpbacks) compared to the blue and fin whales – this is due to the former’s current biomasses being greater than their historical biomasses.

### **Whale falls**

The EM Sub-Committee also requested that the historical and current carbon contributions of the Antarctic cetacean ‘whale falls’ (i.e. when a whale carcass falls to the ocean floor) be calculated. To estimate these ‘whale fall’ values, the ‘best’ model estimate of the annual natural mortality proportion ( $M$ ) from the Base Case of Moosa (2017) is multiplied by the historical and current abundances and biomasses (Table 3). These results are presented in Table 6.

Whale falls during historical times are greater than those at present. As was seen with the prey carbon, whale falls from the humpback and minke whales (minke contributing more than humpbacks) are more than those from the blue and fin whales recently – this is due to the former’s current biomasses being greater than their historical biomasses.

Appendix 3 lists estimates for these and earlier-summarised quantities from the Moosa (2017) model split by the Atlantic-Indian (AI) and Pacific-Only (PO) Regions. In terms of total whale biomass, the former is currently more depleted (to about 13%) than the latter (to about 49%) when compared to pre-exploitation levels.

### **References**

- 1) Baker, C.S. and Clapham, P.J. 2004. Modelling the past and future of whales and whaling. *Trends in Ecology and Evolution*, 18 (7): 365 – 371 pp.
- 2) Bannister, J.L. 1994. Continued increase in humpback whales off Western Australia. Report of the International Whaling Commission, 44: 309 – 310 pp.
- 3) Branch, T.A. 2008. Current status of Antarctic blue whales based on Bayesian modelling. IWC document, SC/60/SH7: 10 pp.
- 4) Branch, T.A. 2007. Abundance of Antarctic blue whales south of 60°S from three complete circumpolar sets of surveys. *JCRM*, 9 (3): 253 – 262 pp.
- 5) Branch, T.A. 2003. Updated circumpolar abundance estimates for Southern Hemisphere minke whales including results from the 1998/99 to 2000/01 IDCR-SOWER surveys. Report of the Scientific Committee, Annex G, Appendix 3. *JCRM (suppl.)*, 5: 271-275 pp.
- 6) Branch, T.A. and Butterworth, D.S. 2001. Estimates of abundance south of 60°S for cetacean species sighted frequently on the 1978/79 – 1997/98 IWC/IDCR-SOWER sighting surveys. *JCRM*, 3 (3): 251 – 270 pp.
- 7) Branch, T.A. and Rademeyer, R.A. 2003. Blue whale estimates from the IDCR-SOWER surveys: updated comparisons including results from the 1998/99 to 2000/01 surveys. *JCRM (suppl.)*, 5: 291 – 292 pp.
- 8) Branch, T.A., Matsuoka, K. and Miyashita, T. 2004. Evidence for increases in Antarctic blue whales based on Bayesian modelling. *Marine Mammal Science*, 20 (4): 726 – 754 pp.
- 9) Borchers, D.L., Butterworth, D.S. and Kasamatsu, F. 1990. Southern hemisphere whale abundance estimates south of 30°S derived from IWC/IDCR survey and Japanese scouting vessel data. SC/42/SHMi18. IWC document: unpublished.
- 10) Brown, M.R., Field, M.S., Clarke, E.D., Butterworth, D.S. and Bryden, M.M. 1997. Estimates of abundance and rate of increase for East Australian humpback whales from the 1996 land-based survey at Point Lookout, North Stradbroke Island, Queensland. SC/49/SH35. IWC document: 15 pp.

- 11) Butterworth, D.S., Borchers, D.L., Chalis, S. and DeDecker, J.B. 1995. Estimation of abundance for Southern Hemisphere blue, fin, sei, humpback, sperm, killer and pilot whales from the 1978/79 to 1990/91 IWC/IDCR sighting survey cruises, with extrapolation to the area south of 30° for the first five species based on Japanese scouting vessel data. *SC/46/SH24*. IWC document: 54 pp (unpublished)
- 12) Christensen, L.B. 2006. Marine mammal populations: reconstructing historical abundances at the global scale. *Fisheries Centre Research Reports, University of British Columbia, Canada*, 14 (9): 165 pp.
- 13) Cummings, W.C. 1985. Right whales: *Eubalaena glacialis* (Muller, 1776) and *Eubalaena australis* (Desmoulins, 1822). In Ridgway, S.H. and Harrison, R.J. (Eds). *Handbook of Marine Mammals, Vol 3*. Academic Press, London: 275 – 304 pp.
- 14) Hakamada, T., Matsuoka, K., Nishiwaki, S. and Kitakado, T. 2013. Abundance estimates and trends for Antarctic minke whales (*Balaenoptera bonaerensis*) in Antarctic Areas IV and V for the period 1989/90 – 2004/05. *JCRM*, 13 (2): 123 – 151 pp.
- 15) IWC. 2013. Report to the Scientific Committee, Annex G – Report of the Sub-Committee on In-depth Assessments. *JCRM (suppl.)*, 14: 195 – 213 pp.
- 16) IWC. 2004. Whale population estimates. International Whaling Commission <http://www.iwcoffice.org/conservation/estimate.htm>
- 17) IWC. 2003. Report of the Scientific Committee. *JCRM (suppl.)*, 5: 1 – 499 pp.
- 18) IWC. 2001. Report of the workshop on the comprehensive assessment of right whales: a worldwide comparison. *JCRM (Special Issue)*, 2: 1–60 pp.
- 19) IWC. 1998. Workshop on the comprehensive assessment of right whales. *SC/50/REP4*. IWC document: unpublished.
- 20) IWC. 1996a. Report of the sub-committee on Southern Hemisphere baleen whales – Annex E. Report of the International Whaling Commission 46: 117 – 131 pp.
- 21) IWC. 1996b. Report of the subcommittee on Southern Hemisphere baleen whales. *JCRM (Special Issue)*, 46: 117-138 pp.
- 22) IWC. 1995. Report of the subcommittee on Southern Hemisphere baleen whales. *JCRM (Special Issue)*, 45: 123 pp.
- 23) IWC. 1991. Report of the sub-committee on Southern Hemisphere minke whales. Report of the International Whaling Commission 4: 113 – 131 pp.
- 24) Jackson, J.A., Ross-Gillespie, A., Butterworth, D.S., Findlay, K., Holloway, S., Robbins, J., Rosenbaum, H., Weinrich, M., Baker, C.S. and Zerbini, A. 2015. Southern Hemisphere humpback whale comprehensive assessment – a synthesis and summary: 2010 – 2015. IWC document, *SC/66a/SH03*: 38 pp.
- 25) Kasamatsu, F. 2000. Kujira no seitai. Kouseishakouseikaku, Tokyo, Japan. 230 pp (in Japanese)
- 26) Klinowska, M. 1991. Dolphins, porpoises, and whales of the world: the IUCN red data book. *IUCN – the World Conservation Union*: 429 pp.
- 27) Law, R.M., Ziehn, T., Matear, R.J., Lenton, A., Chamberlain, M.A., Stevens, L.E., Wang, Y.P., Srbinovsky, J., Bi, D., Yan, H. and Vohralik, P.F. 2015. The carbon cycle in the Australian Community Climate and Earth System Simulator (ACCESS-ESM1) – Part 1: Model description and pre-industrial simulation. *Geoscience Model Development*, 8 (9): 8063 – 8116.
- 28) Laws, R.M. and Hofman, R.J. 1977. Seals and whales of the southern ocean. *Philosophical Transactions of the Royal Society of London (Series B)*, 279: 81 – 96 pp.
- 29) Masaki, Y. 1972. Estimation of abundance of whales by means of whale sighting in the Antarctic. Tokyo. IWC document: unpublished.
- 30) Matear, R.J. and Hirst, A.C. 1999. Climate change feedback on the future oceanic CO<sub>2</sub> uptake. *Tellus B: Chemical and Physical Meteorology*, 51 (3): 722 – 733.

- 31) Matsuoka, K. and Hakamada, T. 2014. Estimates of abundance and abundance trends of the blue, fin and southern right whales in the Antarctic Areas III-E-VI-W, south of 60°S, based on JARPA and JARPAII sighting data (1989/90 – 2008/09). IWC document, *SC/F14/J05*: 27 pp.
- 32) Matsuoka, K., Hakamada, T., Kiwada, H., Murase, H. and Nishiwaki, S. 2011. Abundance estimates and trends for humpback whales (*Megaptera novaeangliae*) in Antarctic Areas IV and V based on JARPA sightings data. *JCRM (special issue) 3*: 75 – 94 pp.
- 33) Moosa, N. 2017. An updated model of the krill-predator dynamics of the Antarctic ecosystem. MSc thesis, UCT. 251 pp.
- 34) Moosa, N. and Butterworth, D.S. 2023. An addition to the EM WP 01 addendum. *SC/69A/EM/WP06*. IWC document: 2 pp.
- 35) Moosa, N. and Butterworth, D.S. 2023. The existing estimates of pre-exploitation and current abundances of whale populations in the Southern Ocean – Addendum. *SC/69A/EM/WP01/Addendum*. IWC document: 1 pp.
- 36) Moosa, N. and Butterworth, D.S. 2017. Summary of an update of the Mori-Butterworth (2006) model of the krill-predator dynamics of the Antarctic ecosystem. Submitted to the IWC Scientific Committee, Slovenia. *SC/67A/EM/14*. 31 pp.
- 37) Moosa, N., Tulloch, V., Kelly, N. and Butterworth, D.S. 2023. The existing estimates of pre-exploitation and current abundances of whale populations in the Southern Ocean. *SC/69A/EM/WP01*. IWC document: 12 pp.
- 38) Mori, M. 2005. Modelling the krill-predator dynamics of the Antarctic ecosystem. PhD thesis, UCT. 302 pp.
- 39) Mori, M. and Butterworth, D.S. 2006. A first step towards modelling krill-predator dynamics of the Antarctic ecosystem. *CCAMLR Science*, 13: 217 – 277 pp.
- 40) Mori, M. and Butterworth, D.S. 2005. Some advances in the application of ADAPT-VPA to minke whales in Areas IV and V. *SC/57/IA17*. IWC document: 27 pp.
- 41) Ohsumi, S. 1981. Further estimation of population sizes of Bryde's whales in the South Pacific and Indian Ocean using sighting data. Reports of the International Whaling Commission, 31: 407 – 415 pp.
- 42) Perry, S.L, DeMaster, D.P. and Silber, G.K. 1999. The great whales: history and status of six species listed as endangered under the US Endangered Species Act of 1973. *Marine Fisheries Review (special issue)*: 74 pp.
- 43) Plagányi, É.E., Punt, A.E., Hillary, R., Morello, E.B., Thébaud, O., Hutton, T., Pillans, R.D., Thorson, J.T., Fulton, E.A., Smith, A.D.M., Smith, F., Bayliss, P., Haywood, M., Lyne, V. and Rothlisberg, P.C. 2014. Multi-species fisheries management and conservation: tactical applications using models of intermediate complexity. *Fish and Fisheries*, 15: 1 – 22.
- 44) Punt, A.E. 2014. Additional applications of the Statistical Catch-at-age Analysis for Southern Hemisphere minke whales. IWC document, *SC/65b/IA03*: 15 pp.
- 45) Punt, A.E., Bando, T., Hakamada, T. and Kishiro, T. 2013. Assessment of Antarctic Minke whales using Statistical Catch-at-age Analysis. *SC/65a/IA01*. IWC document: 48 pp.
- 46) Rademeyer, R., Brandão, A., Mori, M. and Butterworth, D. 2003. Trends in Antarctic blue whale populations taking account of area effects or A response to Joe Horwood, 1990, RIWS 40: 47, footnote 2. *SC/55/SH20*. IWC document: 17 pp.
- 47) Tamura, T. and Ohsumi, S. 2000. Regional assessments of prey consumption by marine cetaceans in the world. *SC/52/E6*. IWC document: 41 pp (unpublished).
- 48) Tamura, T. and Ohsumi, S. 1999. Estimations of total food consumption by cetaceans in the world's oceans. ICR document: 15 pp.
- 49) Trites, A. W. and Pauly, D. 1998. Estimating the mean body masses of marine mammals from maximum body lengths. *Canadian Journal of Zoology*, 76 (5): 886 – 896.
- 50) Tulloch, V.J.D., Plagányi, É.E., Matear, R., Brown, C.J. and Richardson, A.J. 2019. Future recovery of baleen whales is imperiled by climate change. *Global Change Biol.*, 25: 1263 – 81 pp.

- 51) Tulloch, V.J.D., Plagányi, É.E., Matear, R., Brown, C.J. and Richardson, A.J. 2018. Ecosystem modelling to quantify the impact of historical whaling on Southern Hemisphere baleen whales. *Fish and Fisheries*, 19: 117 – 37 pp.
- 52) Tulloch, V.J.D., Plagányi, É.E., Matear, R., Brown, C.J. and Richardson, A.J. 2017. Ecosystem modelling to quantify the impact of historical whaling on Southern Hemisphere baleen whales. *Fish and Fisheries*, 19 (Special Issue 2): 1 – 21.
- 53) Wassmann, P., Haug, T. and Biuw, M. 2021. A critical evaluation of whales as ecosystem engineers – Methods description. *SC/69A/EM/WP07*. IWC document: 4 pp.

**Table 2:** Pre-exploitation and current estimates of abundance for the Antarctic blue, fin, humpback, minke, southern right and sei whales in the region(s) south of 60°S, based on ecosystem modelling studies.

New to this table (highlighted in grey) is an unpublished analysis conducted by V. Tulloch that uses the abundance estimates that were input to the analysis of Moosa (2017). The original table is presented in Table A1. The aim of this exercise was to see how the pre-exploitation and current estimates of abundance differed in terms of model structure (in the case of Tulloch *et al.*, 2019 and Moosa, 2017) when the same estimates of abundance were used.

Whale Species	Moosa (2017)			Mori-Butterworth (2006)			Tulloch <i>et al.</i> (2018)		
	Historical (1780/81)	Current (2014/15)	Ratio	Historical (1780)	Current (2000)	Ratio	Historical (1890)	Current (2015)	Ratio
<b>Antarctic blue</b> ( <i>B. musculus</i> )	198 805	5 140	0.026	189 193	1 867	0.010	115 817	1 468	0.013
<b>Fin</b> ( <i>B. physalus</i> )	321 032	52 278	0.163	238 692	38 010	0.159	250 771	16 849	0.067
<b>Humpback</b> ( <i>M. novaeangliae</i> )	117 722	98 999	0.841	118 684	9 905	0.084	78 600	18 192	0.232
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	368 442	573 252	1.556	318 875	746 561	2.341	275 129	376 841	1.370
<b>Southern right</b> ( <i>E. australis</i> )	-	-	-	-	-	-	498	5 875	11.798
<b>Southern right</b> ( <i>E. australis</i> ), pre 1800	-	-	-	-	-	-	-	-	-
Whale Species	Tulloch <i>et al.</i> (2019) - incl climate drivers			Tulloch <i>et al.</i> (2019) - excl climate drivers			Tulloch <i>et al.</i> (unpub) - incl climate drivers		
	Historical (1890)	Current (2014/15)	Ratio	Historical (1890)	Current (2014/15)	Ratio	Historical (1890)	Current (2014/15)	Ratio
<b>Antarctic blue</b> ( <i>B. musculus</i> )	236 240	3 841	0.016	236 224	3 724	0.016	236 203	4 940	0.021
<b>Fin</b> ( <i>B. physalus</i> )	462 591	39 529	0.086	462 488	41 509	0.090	464 797	53 973	0.116
<b>Humpback</b> ( <i>M. novaeangliae</i> )	141 712	68 213	0.481	141 724	71 449	0.504	144 920	108 941	0.752
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	257 668	777 298	3.017	271 061	732 073	2.701	215 193	601 501	2.795
<b>Southern right</b> ( <i>E. australis</i> )	1 045	10 969	10.497	1 045	11 279	10.793	1 045	10 969	10.497
<b>Southern right</b> ( <i>E. australis</i> ), pre 1800	143 760		0.076	143 743		0.079	143 748		0.076

**Table 3:** Table of whale numbers and whale biomass as requested from the EM session on the 25<sup>th</sup> April 2023; whale biomass estimates have been included for the large baleen whales considered, only where pertinent. Note, the overall ratio (highlighted in grey) for the two studies are very similar.

Whale Species	Moosa (2017)				
	Historical (1780/81)	Current (2014/15)	Ratio	Historical Biomass (1780/81) × 10 <sup>6</sup> (mt)	Current Biomass (2014/15) × 10 <sup>6</sup> (mt)
<b>Antarctic blue</b> ( <i>B. musculus</i> )	198 805	5 140	0.026	20.425	0.528
<b>Fin</b> ( <i>B. physalus</i> )	321 032	52 278	0.163	17.846	2.906
<b>Humpback</b> ( <i>M. novaeangliae</i> )	117 722	98 999	0.841	3.580	3.011
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	368 442	573 252	1.556	2.421	3.776
<b>Total</b>	1 006 001	729 669	0.725	44	10 (Ratio: 0.231)
Whale Species	Tulloch <i>et al.</i> (unpub) - incl climate drivers				
	Historical (1890)	Current (2014/15)	Ratio	Historical Biomass (1890) × 10 <sup>6</sup> (mt)	Current Biomass (2014/15) × 10 <sup>6</sup> (mt)
<b>Antarctic blue</b> ( <i>B. musculus</i> )	236 203	4 940	0.021	24.268	0.508
<b>Fin</b> ( <i>B. physalus</i> )	464 797	53 973	0.116	25.838	3.000
<b>Humpback</b> ( <i>M. novaeangliae</i> )	144 920	108 941	0.752	4.407	3.313
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	215 193	601 501	2.795	1.414	3.952
<b>Southern right</b> ( <i>E. australis</i> )	1 045	10 969	10.497	-	-
<b>Southern right</b> ( <i>E. australis</i> ), pre 1800	143 748		0.076	-	-
<b>Total</b> <b>(w/out right whales)</b>	1 061 113	769 335	0.725	56	11 (Ratio: 0.193)
<b>Total</b> <b>(with right whales)</b>	1 205 906	780 324	0.647	-	-

**Table 4:** Table of estimated prey consumption including: pre-exploitation and post-exploitation abundances, average body weight (kg), residence time (days), per capita consumption of krill (mt) and the pre-exploitation and post-exploitation total krill consumption (mt).

Whale Species (Antarctic)	Historical Abundance (1780/81)	Current Abundance (2014/15)	Average Body Weight (kg)	Residence Time (days)	Per Capita Consump. (mt)	Historical Total Krill Consumption (1780/81), $\times 10^3$ (mt)	Current Total Krill Consumption (2014/15), $\times 10^3$ (mt)
<b>Antarctic blue</b> ( <i>B. musculus</i> )	198 805	5 140	102.74	125	490.8	97.57	2.52
<b>Fin</b> ( <i>B. physalus</i> )	321 032	52 278	55.59	120	310.4	99.65	16.23
<b>Humpback</b> ( <i>M. novaeangliae</i> )	117 722	98 999	30.41	100	200.7	23.63	19.87
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	368 442	573 252	6.57	90	63.2	23.29	36.23

**Table 5:** Table of whale total prey consumption, prey dry weight, prey carbon content, faecal dry weight and faecal carbon content (in 10<sup>3</sup> mt) as per the method outlined in SC/69A/EM/WP07.

Whale Species (Antarctic)	Per Capita Consump. (mt)	Historical Total Krill Cons (mt) (1780/81) × 10 <sup>3</sup>	Current Total Krill Cons (mt) (2014/15) × 10 <sup>3</sup>	Historical Prey Dry Weight (1780/81) × 10 <sup>3</sup> (mt)	Current Prey Dry Weight (2014/15) × 10 <sup>3</sup> (mt)	Historical Prey Carbon (1780/81) × 10 <sup>3</sup> (mt)	Current Prey Carbon (2014/15) × 10 <sup>3</sup> (mt)	Historical Faecal Dry Weight (1780/81) × 10 <sup>3</sup> (mt)	Current Faecal Dry Weight (2014/15) × 10 <sup>3</sup> (mt)	Historical Faecal Carbon (1780/81) × 10 <sup>3</sup> (mt)	Current Faecal Carbon (2014/15) × 10 <sup>3</sup> (mt)
<b>Antarctic blue</b> ( <i>B. musculus</i> )	490.8	97.573	2.523	19.515	0.505	9.757	0.252	1.951	0.050	0.976	0.025
<b>Fin</b> ( <i>B. physalus</i> )	310.4	99.648	16.227	19.930	3.245	9.965	1.623	1.993	0.325	0.997	0.162
<b>Humpback</b> ( <i>M. novaeangliae</i> )	200.7	23.627	19.869	4.725	3.974	2.363	1.987	0.473	0.397	0.236	0.199
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	63.2	23.286	36.230	4.657	7.246	2.329	3.623	0.466	0.725	0.233	0.362

**Table 6:** Table of the pre-exploitation and post-exploitation abundances and biomasses as well as the pre-exploitation and post-exploitation of numbers and biomasses of the whales dying annually (relating to ‘whale falls’).

Whale Species	Historical Abundance (1780/81)	Current Abundance (2014/15)	Historical Biomass (1780/81) $\times 10^3$ (mt)	Current Biomass (2014/15) $\times 10^3$ (mt)	Annual Natural Mortality Prop. assumed*, $yr^{-1}$	Historical Number of Whales Dying Annually (1780/81)	Current Number of Whales Dying Annually (2014/15)	Historical Biomass of Whales Dying Annually (1780/81) $\times 10^3$ (mt)	Current Biomass of Whales Dying Annually (2014/15) $\times 10^3$ (mt)	Ratio
<b>Antarctic blue</b> ( <i>B. musculus</i> )	198 805	5 140	20 425.23	528.08	0.04	7 952	206	817.01	21.12	0.026
<b>Fin</b> ( <i>B. physalus</i> )	321 032	52 278	17 846.17	2 906.13	0.03	9 631	1 568	535.39	87.18	0.163
<b>Humpback</b> ( <i>M. novaeangliae</i> )	117 722	98 999	3 579.93	3 010.56	0.03	3 532	2 970	107.40	90.32	0.841
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	368 442	573 252	2 420.66	3 766.27	0.09	33 160	51 593	217.86	338.96	1.556

\*These values are the model estimates for estimable parameter  $M_j$ , the annual natural mortality proportion for the krill-predator species  $j$ , from the Moosa (2017) Base Case.

**Table 7:** Table of pre-exploitation (historical) and current abundance estimates from existing **single-species** models. These analyses have generally not provided a CV for the historical and current abundances (more for the historical than current); hence why this measure has been excluded from the table.

Whale Species	Punt (2014)			Branch (2008)			Jackson <i>et al.</i> (2015)		
	Historical (1930)	Current (2013)	Ratio	Historical (1904)	Current (2005*)	Ratio	Historical (1900)	Current (2015)	Ratio
<b>Antarctic blue</b> ( <i>B. musculus</i> )	-	-	-	256 000	2 600	0.010	-	-	-
<b>Fin</b> ( <i>B. physalus</i> )	-	-	-	-	-	-	-	-	-
<b>Humpback</b> ( <i>M. novaeangliae</i> )	-	-	-	-	-	-	137 972	96 675	0.701
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	365 850	301 400	0.824	-	-	-	-	-	-
<b>Southern right</b> ( <i>E. australis</i> )	-	-	-	-	-	-	-	-	-
<b>Sei</b> ( <i>B. borealis</i> )	-	-	-	-	-	-	-	-	-
Whale Species	Branch <i>et al.</i> (2004)			Matsuoka and Hakamada (2014) – Area IV			Rademeyer <i>et al</i> (2003)		
	Historical (1905)	Current (1996)	Ratio	Historical (1989/90)	Current (2007/08)	Ratio	Historical (1905)	Current (2002)	Ratio
<b>Antarctic blue</b> ( <i>B. musculus</i> )	239 000	1 700	0.007	300	1 222	4.073	214 293	4 274	0.020
<b>Fin</b> ( <i>B. physalus</i> )	-	-	-	4 966	17 591	3.542	-	-	-
<b>Humpback</b> ( <i>M. novaeangliae</i> )	-	-	-	-	-	-	-	-	-
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	-	-	-	-	-	-	-	-	-
<b>Southern right</b> ( <i>E. australis</i> )	-	-	-	42	1 557	37.071	-	-	-
<b>Sei</b> ( <i>B. borealis</i> )	-	-	-	-	-	-	-	-	-

\*The current year of 2005 is not explicitly stated in the paper but rather taken from Figure 3 in Branch (2008).

**Table 7 continued:** Table of pre-exploitation (historical) and current abundance estimates from existing **single-species** models. These analyses have generally not provided a CV for the historical and current abundances (more for the historical than current); hence why this measure has been excluded from the table.

Whale Species	Baker and Clapham (2004)			Hakamada <i>et al.</i> (2013) – Area IV			Hakamada <i>et al.</i> (2013) – Area V		
	Historical (1770)	Current (1997)	Ratio	Historical (1989/90)	Current (2003/04)	Ratio	Historical (1990/91)	Current (2004/05)	Ratio
<b>Antarctic blue</b> ( <i>B. musculus</i> )	-	-	-	-	-	-	-	-	-
<b>Fin</b> ( <i>B. physalus</i> )	-	-	-	-	-	-	-	-	-
<b>Humpback</b> ( <i>M. novaeangliae</i> )	-	-	-	-	-	-	-	-	-
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	-	-	-	29 993	32 970	1.099	100 745	74 030	0.735
<b>Southern right</b> ( <i>E. australis</i> )	150 375	7 571	0.050	-	-	-	-	-	-
<b>Sei</b> ( <i>B. borealis</i> )	-	-	-	-	-	-	-	-	-
Whale Species	Matsuoka <i>et al</i> (2011) – Area IV			Matsuoka <i>et al</i> (2011) – Area V			Punt <i>et al.</i> (2013)		
	Historical (1989/90)	Current (2003/04)	Ratio	Historical (1990/91)	Current (2004/05)	Ratio	Historical (1930)	Current (2000)	Ratio
<b>Antarctic blue</b> ( <i>B. musculus</i> )	-	-	-	-	-	-	-	-	-
<b>Fin</b> ( <i>B. physalus</i> )	-	-	-	-	-	-	-	-	-
<b>Humpback</b> ( <i>M. novaeangliae</i> )	5 325	27 783	5.218	602	9 342	15.518	-	-	-
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	-	-	-	-	-	-	154 435	307 924	1.994
<b>Southern right</b> ( <i>E. australis</i> )	-	-	-	-	-	-	-	-	-
<b>Sei</b> ( <i>B. borealis</i> )	-	-	-	-	-	-	-	-	-

**Table 8:** Summary of the observed/inferred absolute abundance estimates for the krill-eating whale species considered in Moosa (2017).

Species		Abundance Estimate	CV	Source
Name	Region and Abundance Year**			
Blue whale	$N_{1997/98}^{b, AI}$	853	0.33	Branch (2007)
	$N_{1997/98}^{b, PO}$	1 353	0.35	
Fin whale	$N_{1997/98}^{f, AI}$	10 591	0.5	see Moosa (2017)
	$N_{1997/98}^{f, PO}$	27 594	0.5	
Humpback whale	$N_{2014/15}^{h, AI}$	66 182	0.07	see Moosa (2017)
	$N_{2014/15}^{h, PO}$	31 893	0.06	
Minke whale	$N_{1997/98}^{m, AI}$	183 256	0.13	IWC (2013)
	$N_{1997/98}^{m, PO}$	286 611	0.08	

**Table 9:** Summary of the observed abundance trend (relative trend) estimates for the krill-eating whale species considered in Moosa (2017). The relative trend estimates are shown as a proportional change per year, this is except for blue whales where successive circumpolar estimates of abundance (\*) are given; they then provide a basis to infer a trend estimate within the model-fitting process.

Species		Abundance Estimate	CV	Source
Name	Region and Abundance Year**			
Blue whale	$N_{1980/81}^b$	592*	0.40	Branch (2007)
	$N_{1987/88}^b$	686*	0.47	
	$N_{1997/98}^b$	2 249*	0.36	
Fin whale	$N_{1995/96-2007/08}^{f, AI}$	0.116	0.39	see Moosa (2017)
	$N_{1996/97-2008/09}^{f, PO}$	0.116	0.39	
Humpback whale	$N_{2010/11-2014/15}^{h, AI}$	0.025	0.20	see Moosa (2017)
	$N_{2010/11-2014/15}^{h, PO}$	0.058	0.11	
Minke whale	$N_{1945/46-1967/68}^{m, AI}$	0.013	-	Punt (2014)
	$N_{1968/69-1987/88}^{m, AI}$	-0.029	-	
	$N_{1988/89-2003/04}^{m, AI}$	0.010	-	
	$N_{1945/46-1967/68}^{m, PO}$	0.020	-	
	$N_{1968/69-1987/88}^{m, PO}$	-0.030	-	
	$N_{1988/89-2003/04}^{m, PO}$	-0.003	-	

\*\*The Antarctic ecosystem model developed in Moosa (2017) divides the Antarctic into two regions: Region AI which combines the IWC Areas in the Atlantic and Indian sectors of the Southern Ocean, and Region PO which contains the IWC Areas in the Pacific sector of the Southern Ocean only.

**Table 10:** Summary of the observed/inferred absolute abundance estimates for the krill-eating whale species considered in Mori and Butterworth (2006).

Species		Abundance Estimate	CV	Source
Name	Region and Abundance Year**			
Blue whale	$N_{2000}^{b,AI}$	1 104	0.4	Rademeyer <i>et al.</i> (2003)
	$N_{2000}^{b,PO}$	762	0.4	
Fin whale	$N_{1997}^{f,AI}$	10 591	0.5	Mori (2005)
	$N_{1997}^{f,PO}$	27 594	0.5	
Humpback whale	$N_{1997}^{h,AI}$	5 044	0.07	Branch and Butterworth (2001)
	$N_{1997}^{h,PO}$	4 868	0.06	
Minke whale	$N_{1985}^{m,AI}$	327 369	0.1	IWC (1991)
	$N_{1985}^{m,PO}$	420 572	0.1	

**Table 11:** Summary of the observed abundance trend (relative trend) estimates for the krill-eating whale species considered in Mori and Butterworth (2006). The relative trend estimates are shown as a proportional change per year, this is except for blue whales where successive circumpolar estimates of abundance (\*) are given; they then provide a basis to infer a trend estimate within the model-fitting process.

Species		Abundance Estimate	CV	Source
Name	Region and Abundance Year**			
Blue whale	$N_{1981}^b$	546*	0.41	Branch and Rademeyer (2003)
	$N_{1988}^b$	680*	0.52	
	$N_{1996}^b$	1 891*	0.42	
Fin whale	NA			
Humpback whale	$N_{1977-1991}^{h,AI}$	0.11	0.14	Bannister (1994) †
	$N_{1981-1996}^{h,PO}$	0.12	0.07	Brown <i>et al.</i> (1997) ††
Minke whale	$N_{1970-2000}^{m,AI}$	-0.024	0.31	Mori (2005), Mori and Butterworth (2005) †††
	$N_{1970-2000}^{m,PO}$	-0.024	0.31	

\*\*The Antarctic ecosystem model developed in Mori and Butterworth (2006) divides the Antarctic into two regions: Region AI which combines the IWC Areas in the Atlantic and Indian sectors of the Southern Ocean, and Region PO which contains the IWC Areas in the Pacific sector of the Southern Ocean only.

† For west Australia (IWC Area IV) only.

†† For east Australia (IWC Area V) only.

††† For IWC Areas IV and V only.

**Table 12:** Summary of the abundance points used in the model-fitting process for the krill-eating whale species considered in Christensen (2006).

Species		Abundance Estimate	CV	Source
Name	Region and Abundance Year			
Blue whale	$N_{1980-2000}^b$	900	NA	IWC (1996a, 2004), Perry <i>et al.</i> (1999)
Fin whale	$N_{1978-1988}^f$	15 178		IWC (1996a), Perry <i>et al.</i> (1999)
Humpback whale	$N_{1980}^h$	19 851		Butterworth <i>et al.</i> (1995), IWC (1996a), Laws and Hofman (1977), Tamura and Ohsumi (1999), Perry <i>et al.</i> (1999)
	$N_{1985}^h$	20 000		
	$N_{1995}^h$	17 000		
Minke whale	$N_{1995}^m$	312 000		IWC (2003)
Bryde's whale	$N_{1975}^{br}$	89 000		Ohsumi (1981), Tamura and Ohsumi (2000)
Right whale	$N_{1972}^r$	4 300		Masaki (1972), Cummings (1985), IWC (1998), Perry <i>et al.</i> (1999)
Sei whale	$N_{1965}^s$	40 000		Borchers <i>et al.</i> (1990), Klinowska (1991), IWC (1996a), Perry <i>et al.</i> (1999)

**Table 13:** Summary of the observed/inferred absolute abundance estimates for the krill-eating whale species (female only) considered in Tulloch *et al.* (2018) and Tulloch *et al.* (2019) – total whale survey estimates were divided by ‘q’ (proportion of female whales, calculated from historical catches) in the model.

Species		Abundance Estimate (female proportion only)	CV	Source
Name	Region and Abundance Year**			
Blue whale	$N_{1981}^b$	263	0.41	Branch and Rademeyer (2003)
	$N_{1988}^b$	326	0.52	
	$N_{1996}^b$	907	0.42	
	$N_{1998}^b$	1 104	0.83	Branch (2007)
	$N_{2000}^{b,AI}$	532	0.4	Rademeyer <i>et al.</i> (2003)
	$N_{2000}^{b,PO}$	762	0.4	
Fin whale	$N_{1974}^f$	4 445	0.47	IWC (1995)
	$N_{1983}^f$	8 044	0.4	IWC (1996b)
	$N_{1997}^{f,AI}$	5 083	0.4	Mori and Butterworth (2006)
	$N_{1997}^{f,PO}$	27 594	0.4	Mori and Butterworth (2006)
Humpback whale	$N_{1987}^h$	4 876	0.37	Mori and Butterworth (2006), Branch and Butterworth (2001)
	$N_{1999}^h$	22 154	0.36*	see Tulloch <i>et al.</i> (2018)
	$N_{2008}^{h,AI}$	33 972**	0.36	
	$N_{2008}^{h,PO}$	6 895**	0.27	
Minke whale	$N_{1988}^m$	403 200***	0.33	see Tulloch <i>et al.</i> (2018)
	$N_{2012}^m$	288 400	0.35	
	$N_{1985}^{m,AI}$	163 685	0.1	IWC (1991), Mori and Butterworth (2006)
	$N_{1985}^{m,PO}$	210 286	0.1	
	$N_{1996}^{m,AI}$	91 664***	0.1	Branch (2003)
	$N_{1996}^{m,PO}$	117 760***	0.1	
Right whale	$N_{1920}^r$	141	0.57*	IWC (2001), see Tulloch <i>et al.</i> (2018)
	$N_{2009}^r$	5 460	0.5*	IWC
	$N_{2007}^{r,A}$	141	0.4*	see Tulloch <i>et al.</i> (2018)
	$N_{2007}^r$	5 460	0.4*	

\* Variance estimated

\*\* Combined fine-scale areal population estimates for all surveyed areas in our respective regions, collated by IWC (<https://iwc.int/estimate>). Average growth rate was used to calculate abundances for those stocks that do not have recent population estimates. CV's are calculated using available estimates.

\*\*\* Estimate derived from multi-year circumpolar surveys. Calculations used the middle of the period to which the survey estimate refers. CV's were calculated from 95% CI's.

**Appendix A1:** Pre-exploitation and current abundance estimates from existing ecosystem models.

**Table A1:** Table of pre-exploitation (historical) and current abundance estimates from existing **ecosystem** models. These analyses have generally not provided a CV for the historical and current abundances (more for the historical than current); hence why this measure has been excluded from the table.

Whale Species	Moosa (2017)			Mori-Butterworth (2006)			Christensen (2006)		
	Historical (1780/81)	Current (2014/15)	Ratio	Historical (1780)	Current (2000)	Ratio	Historical (1990)	Current (2001)	Ratio
<b>Antarctic blue</b> ( <i>B. musculus</i> )	198 805	5 140	0.026	189 193	1 867	0.010	327 000	1 180	0.004
<b>Fin</b> ( <i>B. physalus</i> )	321 032	52 278	0.163	238 692	38 010	0.159	625 000	23 300	0.037
<b>Humpback</b> ( <i>M. novaeangliae</i> )	117 722	98 999	0.841	118 684	9 905	0.084	199 000	22 500	0.113
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	368 442	573 252	1.556	318 875	746 561	2.341	379 000	318 000	0.839
<b>Southern right</b> ( <i>E. australis</i> )	-	-	-	-	-	-	86 100	6 740	0.078
<b>Sei</b> ( <i>B. borealis</i> )	-	-	-	-	-	-	167 000	27 400	0.164
<b>Bryde's</b> ( <i>B. brydei</i> )	-	-	-	-	-	-	94 100	91 300	0.970
Whale Species	Tulloch <i>et al.</i> (2019) - including climate drivers			Tulloch <i>et al.</i> (2019) - excluding climate drivers			Tulloch <i>et al.</i> (2018)		
	Historical (1890)	Current (2014/15)	Ratio	Historical (1890)	Current (2014/15)	Ratio	Historical (1890)	Current (2015)	Ratio
<b>Antarctic blue</b> ( <i>B. musculus</i> )	236 240	3 841	0.016	236 224	3 724	0.016	115 817	1 468	0.013
<b>Fin</b> ( <i>B. physalus</i> )	462 591	39 529	0.086	462 488	41 509	0.090	250 771	16 849	0.067
<b>Humpback</b> ( <i>M. novaeangliae</i> )	141 712	68 213	0.481	141 724	71 449	0.504	78 600	18 192	0.232
<b>Antarctic minke</b> ( <i>B. bonaerensis</i> )	257 668	777 298	3.017	271 061	732 073	2.701	275 129	376 841	1.370
<b>Southern right</b> ( <i>E. australis</i> )	1 045	10 969	10.497	1 045	11 279	10.793	498	5 875	11.798
<b>Southern right</b> ( <i>E. australis</i> ), pre 1800	143 760		0.076	143 743		0.079	-	-	-

## **Appendix A2: Summaries of bases for models used**

### **Mori-Butterworth (2006) and Moosa (2017)**

The Mori-Butterworth (2006) model is an age-aggregated production Model of Intermediate Complexity for Ecosystems (MICE - see Plagányi *et al.* (2014) for more information on the MICE approach) which considered the major krill-predators only, i.e., four baleen whale species and two seal species at a circumpolar level in their model framework. The aim of their model was to ascertain whether the observed population trends of these major krill-predators could be explained by predator-prey interactions alone. Their study concluded that it was possible to explain the population dynamics of the major krill-predators through predator-prey interactions only, but that there was room for improvement of their approach. One such possible improvement to their model was to develop estimates of krill consumption by other krill-predators such as birds and fish in order to determine whether these predators' merited inclusion in a refined ecosystem model. The Mori-Butterworth (2006) model was updated and refined in Moosa (2017), where krill consumption estimates of other seal, bird and fish krill-predators were developed. The analyses of Moosa (2017) provide the basis for ecosystem models developed for the Antarctic ecosystem and in this paper. The Moosa (2017) model includes a 'depensatory' effect for the Antarctic fur seals.

### **Tulloch *et al.* (2017; 2018; 2019)**

The Tulloch *et al.* (2017) study also used a MICE approach coupled with a Nutrient-Phytoplankton-Zooplankton-Detritus (NPZD) global climate model (Law *et al.*, 2015; Matear and Hirst, 1999) so as to consider the extent that plankton/zooplankton dynamics, phytoplankton (primary production) dynamics and physical climate drivers influence the prey dynamics, and in turn the dynamics of the krill-predators. Tulloch *et al.* (2017) considered five baleen whale species also at a circumpolar level and assumed that "the overall predation of krill by other predators is constant". Their study concluded that their findings improved upon the understanding of the Southern Hemisphere pelagic ecosystem, and contributed towards global efforts for defining appropriate current and future conservation and management strategies for EBFM, in particular the Southern Hemisphere ecosystem.

### **Christensen (2006)**

Christensen (2006) uses a Stochastic Stock Reduction Analysis (SSRA). This is a single-species modelling approach, which ignores species interactions effects.

### Appendix A3: Regional Split of the Antarctic

The Antarctic ecosystem model in Moosa (2017) is divided into two regions, Region Atlantic-Indian (AI) and Region Pacific-Only (PO), defined as follows (see Figure A1):

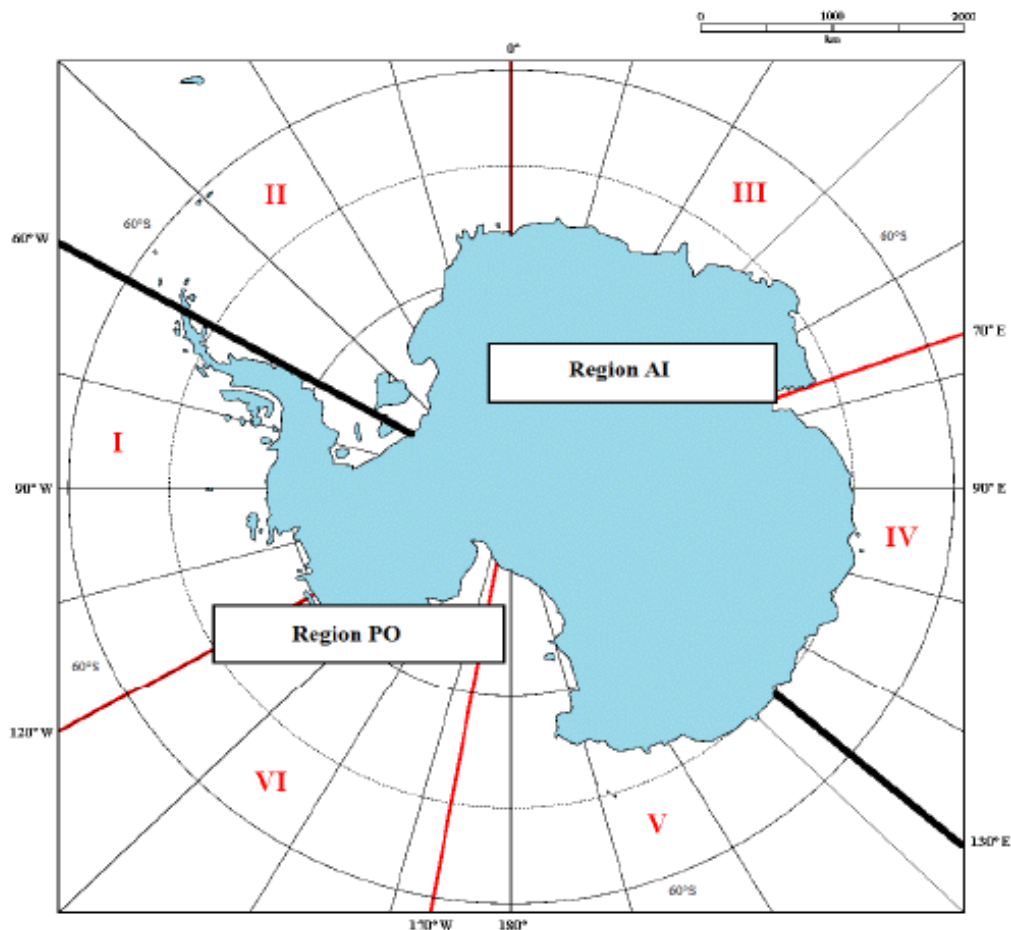
Region AI = IWC Area II + IWC Area III + IWC Area IV

Region PO = IWC Area V + IWC Area VI + IWC Area I

Mori and Butterworth (2006) also used the same regions in their ecosystem model. They argued that these divisions are reasonable as majority of the large baleen whale and commercial whale harvesting occurred in Region AI. The harvesting in this region nearly rendered some of the whale stocks extinct. By comparison, large baleen whales were harvested in fewer numbers in region PO. This suggests that the pre-exploitation distribution of the large baleen whales reflected more abundant in Region AI and less in Region PO. This regional split is evident in Tables A2 and A3 below, which lists the abundances, biomass, total krill consumption, prey carbon content and biomass of whales dying annually (related to 'whale falls') for the large baleen whales considered.

In terms of current large whale biomass, Region AI is currently at about 13% of its historical level whilst Region PO is at about 49%. For the estimated total krill consumption and prey carbon content, Region AI is currently at about 17% of its historical level whereas Region PO is about 60%. The current biomass of large baleen whales dying annually is at about 16% of its historical level in Region AI and about 67% in Region PO. This suggests a slower recovery of the large baleen whales in Region AI than in Region PO due to the heavy harvesting of these whale species in the former.

Figure A1: Map of the IWC Management areas and the two regions, Region AI and Region PO (from [http://luna.pos.to/whale/img/gen\\_map\\_ant.gif](http://luna.pos.to/whale/img/gen_map_ant.gif) [Accessed on 05/05/2016])



**Appendix Table A2:** Table of pre- and post- exploitation abundance (number), biomass (mt), estimated total prey consumption (mt), prey carbon content (mt) and biomass of whales dying annually (relating to 'whale falls') for the krill-eating whale species for **Region AI**.

Whale species	Region AI – Moosa (2017)									
	Pre-exploitation (1780/81)					Post-exploitation (2014/15)				
	Abund.	Biomass × 10 <sup>6</sup> (mt)	Total krill consump. × 10 <sup>6</sup> (mt)	Prey Carbon × 10 <sup>6</sup> (mt)	Biomass of whales dying annually × 10 <sup>6</sup> (mt)	Abund.	Biomass × 10 <sup>6</sup> (mt)	Total krill consump. × 10 <sup>6</sup> (mt)	Prey Carbon × 10 <sup>6</sup> (mt)	Biomass of whales dying annually × 10 <sup>6</sup> (mt)
<b>Blue</b>	162 532	16.699	79.77	7.977	0.668	1 226	0.126	0.60	0.060	0.005
<b>Fin</b>	221 724	12.326	68.82	6.882	0.370	15 047	0.837	4.67	0.467	0.025
<b>Humpback</b>	71 206	2.165	14.29	1.429	0.065	67 117	2.041	13.47	1.347	0.061
<b>Minke</b>	68 442	0.450	4.33	0.433	0.041	153 861	1.011	9.72	0.972	0.091
<b>Total</b>	523 903	31.639	167.21	16.721	1.143	237 251	4.014	28.47	2.847	0.182

**Appendix Table A3:** Table of pre- and post- exploitation abundance (number), biomass (mt), estimated total prey consumption (mt), prey carbon content (mt) and biomass of whales dying annually (relating to 'whale falls') for the krill-eating whale species for **Region PO**.

Whale Species	Region PO – Moosa (2017)									
	Pre-exploitation (1780/81)					Post-exploitation (2014/15)				
	Abund.	Biomass × 10 <sup>6</sup> (mt)	Total krill consump. × 10 <sup>6</sup> (mt)	Prey Carbon × 10 <sup>6</sup> (mt)	Biomass of whales dying annually × 10 <sup>6</sup> (mt)	Abund.	Biomass × 10 <sup>6</sup> (mt)	Total krill consump. × 10 <sup>6</sup> (mt)	Prey Carbon × 10 <sup>6</sup> (mt)	Biomass of whales dying annually × 10 <sup>6</sup> (mt)
<b>Blue</b>	36 273	3.727	17.80	1.780	0.149	3 914	0.402	1.92	0.192	0.016
<b>Fin</b>	99 308	5.521	30.83	3.083	0.166	37 231	2.070	11.56	1.156	0.062
<b>Humpback</b>	45 567	1.416	9.35	0.935	0.043	31 882	0.970	6.40	0.640	0.029
<b>Minke</b>	300 000	1.971	18.96	1.896	0.177	419 391	2.755	26.51	2.650	0.248
<b>Total</b>	482 147	12.634	76.93	7.693	0.535	492 418	6.197	46.38	4.638	0.355

## Annex G

Small group report on the socio-economics of the ecosystem functions of cetaceans:

It was considered of greatest importance that the pilot project should center around creating a research framework to assess the economic role of cetaceans in supporting marine ecosystem services. This framework would explore all potential ecosystem services supported by cetaceans and identify what data gaps can be addressed in the future to allow economic valuation of these ecosystem services.

It was noted that there were already some carbon sequestration economic valuation models available that consider biomass and primary productivity. However, these valuations were limited to only one ecosystem service (i.e., climate regulation through carbon sequestration via direct pathways). It was also noted that the value of carbon sequestration has been considered extensively in economic valuation models. Hence the primary question with regard to cetaceans is not the underlying value of carbon sequestration (which is well studied in the economics literature), but rather the net amount of carbon sequestered due to cetaceans (the biophysical question).

There could be many other ecosystem services of interest, including those derived from the impact on primary production derived from the whale pump on fish stocks or the impact of whale falls on the provision of habitat to biodiversity and bioprospecting opportunities. In addition, the pilot project could then apply some of these models (with available ecological and economic data) to a specific population/area as a general case study.

Furthermore, the group agreed that the framework should provide general guidelines on how these economic valuations can be used to influence whale conservation and management, either through market or policy developments.

Critical questions that the pilot project should consider to the extent possible:

What are the ecosystem services to which cetaceans contribute?

What are the linkages between the ecosystem services to which cetacean contribute (e.g., climate regulation, nutrient cycling contributing to primary productivity, habitat provisioning)?

Which ecosystem services can be valued with existing data and current economic valuation tools?

How do these values change as cetacean populations increase or decline due to natural and anthropogenic drivers of change?

Which ecosystem services to which cetaceans contribute should be prioritized for analysis (considering the availability of data and models, together

with the likely magnitude of the associated values)?

How can economic valuations of the ecosystem services to which cetaceans contribute be used to inform whale conservation and management?

## Annex H

Small group report on ecosystem modelling of cetaceans:

Five modelling-related areas were selected as reflecting those most in need of further work:

1. Current perceptions of the status of the many whale stocks typically fail to realise that although some remain at very low levels (such as the blue whales in the Southern Ocean), others have recovered to a substantial extent (even to near pre-exploitation levels or were never very severely depleted in the first place). The current status of stocks initiative (SOSI) in the IWC SC is to update such status estimates and to provide them for many further stocks, based on single species models, should continue to be speedily pursued, and later extended to provide projections for the future for both large whale and small cetacean stocks. As a first step, the IWC SC and the Secretariat are encouraged to prioritize making updated tables of abundance estimates available online. This will facilitate cross-comparison between different efforts to model the pre-exploitation and current role of cetaceans in marine ecosystems.
2. Nutrient cycling field/lab studies and analyses should be improved and extended, and linked to phytoplankton and carbon dynamics. Inputs from Earth System Models might assist. The question of “Does/How the whale pump works?” needs to be addressed, both whether the associated mechanisms are operating (nutrient cycling; carbon fixation, export, sequestration), and even if so, what is the marginal contribution of whales relative to other ecosystem components.
3. The multispecies models presented at the meeting should be extended, primarily to include lower trophic levels (other than forage fish) to some extent, so as to be able to take account of the role played by whale excretion. Alternatively, existing models might be linked to bio-geochemical models to try to achieve this. Spatio-temporal considerations (horizontal and vertical movement) may also require some attention.
4. Modelling work should always continue to establish to what extent key results are likely to be sensitive to structural differences between alternative models. Furthermore, before large scale experiments might be put in place, it should be clear how these results might be useful (i.e. first be clear how the results from the experiments might be used).
5. Summarize existing bio-energetic formulations and parameters with a view towards establishing appropriate ranges (e.g. prey

consumption rates) for use in analyses.

Other modelling aspects considered to be of some importance, though of less immediate urgency, were (in no specific order):

- Allowance for climate change in models
- Application of whole ecosystem type (i.e. Atlantis-like) models
- Attention to further aspects of nutrient and carbon cycling – sequestration, fixing and storage in living animals
- Data needs, particularly new estimates of population abundance and mortality rates by species and by age
- Diagrammatic representation of models and associated aspects to aid their understanding by economists and to assist identify data gaps.
- Inclusion of age-structure in models
- Linking the nutrient cycling to whale population energy requirements
- Properties of models, especially as related to their sensitivity, robustness, structure and validation