SC/68C/REP/03

Sub-committees/working group name: REP

Report of the IWC-CMS Workshop on Cetacean Ecosystem Functioning, virtual 19-21 April 2021

REPORT OF THE IWC-CMS WORKSHOP ON CETACEAN ECOSYSTEM FUNCTIONING

Annexes

The Workshop was held from 19-21 April 2021 virtually via Zoom. A list of participants is provided as ANNEX E.

1. INTRODUCTORY ITEMS

1.1 Welcoming remarks

Ritter, the convenor of the workshop, welcomed all attendants and thanked the International Whaling Commission (IWC) and Convention on Migratory Species (CMS) for co-hosting the workshop and invited them to provide opening remarks.

Melanie Virtue, Head of Aquatic Species at CMS, welcomed the participants and thanked the workshop organizers for their efforts in planning and preparing the workshop. She noted how proud CMS is to be co-hosting the workshop and how this workshop is only the latest collaboration between IWC and CMS. She highlighted the workshop's importance given the ecological importance of whales in the marine environment, the necessity to understand their role in ecosystems, and the need to address challenges facing the species and their ecosystems.

Rebecca Lent, IWC Executive Secretary, also welcomed participants to the workshop. She noted that planning for the workshop had been underway for some time but that it had been delayed due to the pandemic. She noted that the Commission recognizes the importance of this workshop and had reiterated its support during the last Commission meeting in 2018. The outcomes of the workshop will provide an important foundation for a second workshop, as well as for a separate Conservation Committee (CC) workshop later this year. She expressed thanks to the co-chairs, rapporteurs, and researchers for their presentations and participation. She also thanked those providing funding for the workshop, including the Animal Welfare Institute (AWI), Whale and Dolphin Conservation (WDC), Pro Wildlife, OceanCare, and the Scientific Committee (SC). The Executive Secretary said that the IWC was pleased to partner with CMS and expressed hope that a partnership on this issue can also be developed with the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR).

Ritter explained that the original intent was to host this workshop in person. He expressed thanks to members of the workshop Steering Group and to the non-governmental organizations for providing funding. He reminded participants that IWC Resolution 2016-03 provided the basis for this workshop, which asked the SC to screen the existing research studies on the contribution of cetaceans to ecosystem functioning, to develop a gap analysis regarding research, and to develop a plan for remaining research needs. The primary objective for this workshop is to conduct the requested gap analysis.

1.2 Election of Chairs

Ritter and Kitakado were appointed as co-chairs of the workshop.

1.3 Appointment of rapporteurs

Schubert and James were appointed as rapporteurs to assist in the preparation of the workshop report.

1.4 Adoption of Agenda

The draft agenda was discussed, amended, and adopted (ANNEX A).

1.5 Review of documents

The participants were reminded that workshop documents were available on the workshop's Sharepoint site. These documents include: the two primary review reports, the workshop agenda, copies of the presentations, and other relevant documents.

2. REVIEW OF THE TERMS OF REFERENCE

According to the Terms of Reference (ToR) (see ANNEX B), the workshop aimed to review existing knowledge on the contribution of cetaceans to ecosystem functioning based on two primary review reports and additional presentations. The objectives of the workshop were: (1) to summarize existing knowledge, (2) to identify data gaps, (3) to determine what can realistically and reliably be quantified at this time, (4) to identify geographical areas and species/taxa which are of special interest or which may not have been well studied, and (5) to prioritize a list of future scientific research to better understand how cetaceans affect ecosystem functioning.

3. BACKGROUND ON CETACEAN ECOSYSTEM FUNCTIONING

Two primary review reports (SC/68C/EM05 and SC/68C/EM02) were prepared for the workshop to provide perspectives on the role of cetaceans in ecosystem functioning.

It was noted that some terms relating to ecosystem functioning have multiple or different meanings depending on context, including in legal contexts. Therefore, a glossary of terms was created defining how such terms had been used during this workshop (see ANNEX D).

3.1 Review of existing knowledge

3.1.1 Keynote review I: Cetacean ecosystem functions

Roman presented his keynote presentation on the "Ecological Roles and Impacts of Large Cetaceans in Marine Ecosystems" (SC/68C/EM/05). The ecological role and importance of marine animals, from sea otters to large whales, have received increased focus in recent years. As the largest animals ever to have existed on the planet, whales are expected to have top-down impacts on their prey, but their influence on communities and ecosystems is a relatively new area of research. The state of the science for the consumptive and non-consumptive effects of whales, including their role as predators, their prey, and their influence on behavior-mediated impacts, was summarized. Further, whale carcasses provide nutrients and deep-sea habitat for hundreds of species, including more than 100 endemic species, several of which rely on chemosynthetic bacteria. SC/68C/EM05 stated that whale falls thus play a vital role for deep sea species diversity and evolution. The biological pump, or marine carbon pump, is a well-studied process in which oceanic organic matter and nutrients are removed from surface waters, as result of photosynthesis, vertical transport, gravity, and death and decomposition. Whales play a role in the movement of nutrients and organic matter in at least three ways: 1. as whale falls to the deep sea, 2. during their vertical movement between foraging dives and rest and respiration at the surface (the "whale pump"), and 3. during long-distance migrations from high-latitude foraging areas to winter grounds, where many species calve and breed (the "great whale conveyor belt"). Whales play a role as nutrient vectors in at least two ways: during their vertical movement between foraging dives and rest and respiration at the surface (the "whale pump") and during long-distance migrations from high-latitude foraging areas to winter grounds, where many species calve and breed (the "whale conveyor belt"). The review also discussed the research on three nutrients - iron, nitrogen, and phosphorus - and the role of whales in marine biogeochemical cycles, e.g. nutrient recycling and concentration of nutrients through their feces and urine. These can be particularly important in nutrient-limited oceans, as well as in whale "hot-spots" and during "hot moments." Examples were also given of whale carcasses washed up on land which constituted major local feeding opportunities for terrestrial ecosystems. Whales can also make physical changes in the oceans through benthic and bubble-net feeding and swimming through the pycnocline, thus resuspending and/or (re-)distributing nutrients. Due to their body mass, whales can also contribute to carbon storage leading to carbon sequestration when their carcasses are removed from the carbon cycle, like when a whale falls in the deep sea. Population declines from commercial whaling likely affected all of these processes. Threats from climate change and increased industrialization of the ocean are also expected to have an impact on individual whales, whale populations, and their ecological roles. North Atlantic right whales, for example, have been reduced from more than 10,000 individuals to fewer than 500, and are functionally extinct from much of their previous range. Further details are provided in SC/68C/EM/05.

The Workshop thanked Roman for his thorough review covering various key subjects related to the ecosystem functioning of cetaceans. During discussion, Ritter proposed that Tables 1 and 7 of SC/68C/EM/05 could be a valuable baseline to work from throughout the workshop and suggested expanding these tables to provide an overview of existing knowledge.

3.1.2 Keynote review II: A critical evaluation of whales as ecosystem engineers

Wassmann presented the second keynote address entitled "A critical evaluation of whales as ecosystem engineers" (see SC/68C/EM/02_rev1). The role of the great whales in world ocean ecosystem engineering was investigated through a systems ecology perspective. The function of the whale pump for the recycling of limiting nutrients for primary production and of whale falls for the sequestration of carbon on the sea-floor was explored. SC/68C/EM/02_rev1 argued that the former can be important in the Southern Ocean, but is almost certainly negligible in the Northern Pacific and Atlantic Oceans. It also argued that the whale pump has probably no impact on carbon sequestration in the form of vertical export of detrital carbon, but does impact carbon sequestration on the sea-floor through whale falls. Nutrients from sediment resuspension by feeding whales only play a role for biogeochemical cycling in the shallowest regions, which rarely face nutrient limitations, and is limited to deep-diving species that feed along the bottom. At a global scale, the contribution of whale falls to the deep oceans is in the range of a few mg C m-2 y-1, which is orders of magnitude lower than the main vertical carbon source, detritus. For organisms ranging from local, sessile or slow moving to highly mobile, areas of detection and attraction to whale falls of 10,000 m^2, 1, 10 and 100 km^2, respectively, were assumed. For these four detection and attraction ranges, a large whale carcass of 5t C represents 500, 5, 0.05 and 5 10-3 times the ambient vertical C supply, respectively. This suggests widely different feeding and evolutionary strategies for deep-sea biota. The probability of a whale fall in a 100 km^2 area during pre-industrial times was one in a few years. This assumes that whale falls take place in only 10% of the deep-sea region. The probability in present times is one per decade. The importance of stranding falls for global biogeochemical cycling is small. The overall effect of the great whales as ecosystem engineers is widely different in the various regions of the world's oceans. Whales as ecosystem engineers have an impact on the biogeochemical cycling of the oceans, which varies from negligible to essential and needs to be carefully evaluated for each region, and within a comparative context that also accounts for other organisms substantially contributing to ecosystem functioning.

The Workshop thanked Wassmann and colleagues for their review covering several key subjects. The workshop considered questions on the keynote reviews.

Pershing believed the system approach used by Wassmann and colleagues is appropriate, commended them on their modeling and calculations, but raised concerns about their overall conclusions. Specifically, he emphasized that their work reaches similar conclusions about the scale of processes like carbon sequestration, but the difference in conclusions about the importance of the processes arises from Wassmann's benchmarking against global numbers. Pershing clarified that his work (Pershing et al. 2010) clearly states that carbon flux from whales is small relative to the global carbon cycle, but that rebuilding whale populations would lead to carbon sequestration comparable to other efforts to enhance biological carbon sequestration

A question was raised regarding if fish direct consumption of whale feces has been factored in the ecological models, since little evidence comes from direct observation in Abrolhos, Brazil to which Roman responded that it is unlikely to find feces there since whales are not feeding in that area. Potential whale sources of nutrients would be from calf feces, calf mortality, adult mortality, or via placentas. In addition, females distribute nitrogen through their urine which, according to models, can be quite substantial.

Smith commented that sea floor diversity includes species with a biphasic lifestyle that produce larvae that can disperse large distances and thus connect island metapopulations around hydrothermal vents and whale falls.

Pearson emphasized that whale feces do not sink like feces from fish or invertebrates. Rather, fecal matter is suspended in the water column due to its buoyancy allowing nutrients to leach out and be utilized by phytoplankton. She also indicated that one needs to be cognizant of shifting baselines in the new era of the Anthropocene where whale populations are greatly reduced from previous numbers. She raised the question: What could the potential contribution of whales be to carbon and nutrient cycles and other ecosystem functions if the populations were to recover?

Costa, in response to Wassmann et al.'s review, noted that two percent of global carbon flux as represented by whales can be considered a very large contribution and that whales are only one of the mega-vertebrates in the ocean. He provided examples of other scenarios where a small percentage in specific ecosystems can be important. For example, seagrass covers only two percent of the Mediterranean, but support 30-40 percent of the total value of commercial fisheries.

Wing added that while whale falls may only contribute two percent of carbon flux, if you calculated the flux of high energy lipids and labile organic matter the contribution of whale falls would be much higher. He stressed that when making connections between ecological systems, bioenergetics, and chemical cycling the units being used are important. He also drew attention to an apparent northern/southern hemisphere dichotomy when considering micronutrient limitation and explained that there are large parts of northern oceans that are micronutrient limited.

Table 1 gives an overview of selected traits of cetaceans and their related ecosystem functions and services, as compiled during the workshop.

3.2 Discussion on the general role of cetaceans in the ecosystem

Punt noted that the Commission may be particularly interested in priority areas relevant to this topic, based on the objectives of this workshop and suggested that a quantitative approach be used to identify priorities. He highlighted the Barents Sea as an example of a "data rich" area.

Kitakado referred to the second workshop and explained that the present workshop is meant to raise questions, formulate hypotheses, and identify the information gaps, and identify potential case studies.

Ritter noted the different views reflected in the reviews, and that they are in many cases a matter of scale; processes that might matter on a smaller spatial scale may not necessarily matter on a wider spatial scale. In whale hotspots, or during "hot moments," the significance of whales as ecosystem engineers will be very different compared to their overall, or global, contribution to ecosystem functioning. Punt suggested that the local versus global implications, i.e. the relative versus absolute effects, always must be elucidated. It was **agreed** that often it is not a question of whether whales play a role in ecosystem functioning but rather what role they play, which is largely dependent on the scale (from local to global).

Kitakado noted that, similar to temporal changes in cetacean ecosystem functioning between the pre- and post-whaling periods, there may also be spatial differences at the global compared to local scale including vertical and horizontal movement of nutrients. The question of whether this matters must be asked first when assessing the role of whales in ecosystem functioning as predators, consumers, prey, or ecosystem engineers. Butterworth cautioned against trying to cover these topics on a global scale, and instead recommended considering areas like the Southern Ocean, North Pacific, North Atlantic, or smaller areas within those, such as the Barents Sea or off New England. He also reminded the workshop that specific hypotheses had been discussed by the EM subcommittee some time ago (IWC, 2019 = SC report Annex L). Ritter encouraged participants to review those hypotheses to help inform workshop discussions.

4. WHALE FALLS

4.1 Presentation(s)

4.1.1 Craig Smith: Whale falls - ecosystem engineers, stepping stones, and oases of biodiversity at the deep-sea floor

There is substantial evidence that the carcasses of adult great whales at the deep-sea floor, or “whale falls,” provide important ecosystem functions, acting as ecosystem engineers to create new habitats, maintain novel biodiversity, and facilitate connectivity among chemosynthetic habitats (reviewed in Smith et al., 2015). Such ecosystem engineering is driven by key characteristics of great whale-carcasses, including (i) very large body size, (ii) high food quality, (iii) large, well calcified, lipid-rich skeletons, and (iv) high frequency of sinking to the relatively food-poor deep-sea floor. The carcasses of adult great whales pass through four overlapping stages of succession at the deep-sea floor in the NE Pacific. (1) A mobile-scavenger stage, during which up to 38 species are attracted. This stage can last for 4 to ~18 months. (2) The enrichment opportunist stage which results from a fallout of organic particles onto the seafloor and from persistence of organic material in the bones. It can last for 7 years, and is characterized by evolutionary novelties, including carpet worms, bone-eating *Osedax* worms, and a diversity of other polychaetes. (3) The sulfophilic stage results from anaerobic breakdown of bone lipids by sulfate reducing bacteria fueling chemoautotrophic bacteria on bones and inside clams, mussels, and vestimentiferan worms. Sulfophilic communities on adult skeletons are large (>30,000 macrofaunal individuals per carcass), species rich (100 – 200 species per carcass) and can persist for decades. Finally (4) a reef stage can occur during which the whale skeleton provides habitat for hard-substrate fauna. Modern deep-sea whale-fall communities have been observed on ~75 carcasses throughout the world ocean, and fossil communities have been recorded on ~50 fossil whale skeletons as old as 40 million years. Whale falls appear to have served as evolutionary stepping stones, with one characteristic taxon, *Osedax*, showing fossil evidence of adaptive radiation on whale falls, and another (the vent-seep mussel subfamily Bathymodiolinae) with a molecular phylogeny indicating use of whale falls to colonize the deep sea and then radiate in deep-sea vent and seep habitats. Even though whale falls are poorly sampled globally, there are >100 modern species known only from whale falls, indicating a substantial diversity of whale-fall specialists. Modern whale falls are abundant enough to support metapopulations of some whale-fall specialists, but metapopulation modeling indicates that whaling is likely to have driven, or currently be driving, some species to extinction from habitat loss (Smith et al., 2019).

A question was raised as to whether this modeling had accounted for a lack of uniformity of the distribution of whale carcasses across the habitat, given that dispersal distances are presumably uncertain. Smith responded that there are some assumptions in the model including that all larval production is a function of total metapopulation size, that the larvae are instantaneously well mixed across the region, and that the chemosynthetic ecosystem larvae have the potential to disperse for months. However, for larvae with smaller dispersal distances, that assumption is not as well supported. He advised that variable dispersal distances could be included into a metapopulation model. Punt suggested that linking such models with analyses conducted on global dispersal models may provide a more accurate view of larval dispersal. Smith indicated that adding fine scale heterogeneity of whale falls and general circulation models also could provide more information about transport vectors.

Roman noted that around South Georgia there may be many whale falls due to intensity of past commercial whaling there. Smith responded that finding specific sites would be difficult especially since in modern whaling most of the whale bones were removed to extract the valuable lipids. Additionally, any whale bones left from before industrial whaling would likely be gone by now as the lipid stores would have been depleted over the past 100+ years.

4.1.2 Heidi Pearson: Synthesis of the role of cetaceans in nutrient & carbon cycling

Cetaceans play important roles in marine ecosystems through their nutrient and carbon cycling functions. Whales release buoyant, nutrient-rich fecal plumes in surface waters that can stimulate phytoplankton growth, creating the essential foundation upon which marine life relies. Whale-mediated vertical flux of nutrients to the surface from below the mixed layer, and horizontal flux via migration from nutrient-rich feeding grounds to nutrient-poor breeding grounds, can be especially important in enhancing ecosystem functioning. Qualitative network modeling in a fjord system of Southeast Alaska indicates that increasing the abundance of whales and other top marine predators (pinnipeds and seabirds) leads to increased nutrient levels and primary production. Cetaceans also contribute to blue carbon, which refers to the natural processes through which the ocean traps carbon. Whale-stimulated primary production that is unconsumed may sink to depth, leading to carbon storage or sequestration. Through their large body sizes and long lifespans, cetaceans have the capacity to store carbon for decades to centuries. When carcasses sink to the seafloor, that lifetime of stored carbon can be sequestered for millennia. Five studies (Lavery et al. 2010, 2014; Pershing et al. 2010; Roman et al. 2014; Martin et al. 2016) have compared the change in carbon captured, stored, or sequestered by cetaceans between pre-exploitation and exploitation levels. Collectively, these studies reveal an estimated 96% decline in the amount of carbon captured, stored, or sequestered due to commercial whaling or fisheries bycatch. As many populations recover from commercial whaling, there is increasing potential for cetaceans to enhance nutrient and carbon cycling. While intriguing, understanding of these processes is still largely in its infancy, and they have been studied in relatively few species and regions (Martin et al., in press). However, there are ample opportunities to integrate data collection within current and future research programs to advance knowledge of the fine-scale mechanisms through which cetaceans may contribute towards nutrient and carbon cycling.

Wassmann suggested that caution be taken in describing “new” nutrients. He explained that when whales graze zooplankton (which have been grazing on phytoplankton) or fish (which graze zooplankton produced in the season), then defecate at the surface, these are not “new” nutrients but “recycled” nutrients.

Costa highlighted the fundamental assumption that whales defecate at the surface, but quantitative data on defecation rates are often missing. He noted that, in principle, this should be measurable with the help of new methodologies including rear-mounted cameras attached to whales. It was noted that these data could already exist with the deployment of CATS (Customized Animal Tracking System).

Butterworth noted that many presentations were comparing historical pre-exploitation whale numbers and current population estimates and stressed the importance that such calculations needed to be updated with the latest global abundance estimates available, ideally before the second workshop.

4.1.3 Andrew Pershing: Whales and Carbon

Pershing presented an overview of the calculations in his 2010 paper on carbon sequestration and storage by populations of great whales, including a discussion of the structure of marine communities (e.g. Pershing and Stamieszkin, 2020). One can think of open ocean food webs in two components--the short-lived, high turnover world of microbes and small zooplankton and the longer-lived (months-to-centuries) world of large zooplankton, fish, and whales. While carbon export in the ocean is dominated by the traditional biological pump (mostly microbial), humans do not actively intervene in processes at this scale. However, they do interact very strongly with the long-lived components through fishing, whaling, and conservation. As described in Pershing et al. (2010), whaling reduced the population of great whales and therefore reduced the amount of carbon exported to the deep sea through sinking whale carcasses. They estimated that rebuilding whale populations would export 200,000 tons C per year. While small relative to the size of the ocean’s biological pump, it is comparable to the scale of proposed interventions in the ocean carbon cycle such as iron fertilization.

Pershing emphasized a thread that runs through much of the work on the ecosystem impacts of cetaceans: whales' great size means that they are capable of unique things. In particular, he described how large size allows whales to store more carbon than smaller competitors. He presented calculations that the food that would support one 92 ton blue whale would support 7 minke whales or 1,800 Adelie penguins. However, the biomass of the minke whales would be half of that of the blue whale, and the penguins would only be 1/10th of the blue whale.

It was pointed out, as an example, that breaching humpback whales on their breeding grounds often release epibionts and ectoparasites into the ocean, and that such sloughed off organisms can potentially contribute to nutrient flows. Roman agreed that migratory whales are moving parasites and diatoms back and forth between high and low latitude areas via skin sloughing. Pershing responded that he had examined this issue and stressed that resulting numbers easily get dwarfed by, for example, the nutrient contribution of dead whales. He thinks such contributions could be more important in areas where whales are very active.

Savoca commented that there is information from tagged whales as to where they defecate. He explained that based on time budgets and digestive physiology, whales defecate more frequently close to the surface than at depth based on overall time budgets from tag data while foraging. He stressed that baleen whales primarily occupy the top 100-200 meters of the water column and, as such, they would primarily be contributing recycled nutrients not ‘new’ nutrients, whereas beaked and sperm whales would be raising new nutrients from well below the mixed layer.

Punt noted that quantitative ecosystem models are available from the Gulf of Alaska, including the southeast Alaska region. These models could complement qualitative models. Even where the data are poor, the qualitative models that Pearson had produced would be helpful particularly outside the US. Efforts could also be undertaken to try to extrapolate some of these qualitative models to other regions. Butterworth agreed that there may be many existing models but, depending on the assumptions about functional feeding relationships in the models, they can produce very different answers.

Questions arose as to when and where a whale is likely to die, such as whether southern hemisphere whales die uniformly during the year or whether they are more likely to die when on their feeding grounds or when they are migrating, fasting, or breeding? In consequence, how is the natural mortality rate differentiated between middle and very high latitudes? Answers to these questions may make a considerable difference in calculations of whale falls in certain areas. Ritter remarked that local or regional numbers of whale falls are also related to the “behaviour” of individual carcasses after death due to ocean currents, water temperature, and other factors.

Fisher asked if there could be whale fall hotspots associated with the location of current whaling activities; in Norway, for example, whales taken are flensed at sea and the carcasses are dumped. Tracks of the whaling vessels could help determine the approximate location of whale falls.

Smith added that for Eastern North Pacific (ENP) gray whales, mortality is relatively well known compared to many other populations of great whales. For other migrating whales, deaths are more likely along migration routes. Sperm whales do not undergo migration between feeding and breeding grounds, so their carcasses are more broadly distributed. He noted that it is important to consider spatial heterogeneity and migration but advised that the complexity of the migration cycle would need to be considered for each species and even for each population. Costa remarked that predation risk is also a major component. Many animals are going to die where the predation risk is greatest, which could result in a high risk locally in some regions compared to others. It was **agreed** that understanding where whales die is important.

Biuw suggested that, regarding the discussion on comparing different ocean regions, other processes to consider are horizontal advection, the flux of particulate matter, and the duration, concentration, and consistency of so-called hotspots and hot moments over time and how quickly they spread over large regions.

Butterworth drew attention to the relationship and overlap of the ASI and SH subcommittees of the SC. He suggested that the workshop co-chairs consider attending sessions of those subgroups to advise participants of the important issues being raised in this workshop. Ritter added that there are plans to link the EM and E subcommittees group because of an overlap of issues, and, given the general interest in the cetacean ecosystem functioning issue, there might be a joint session during the SC meeting.

The question of how long carbon may stay in the deep-sea was raised. It was noted that there are currents on the ocean floor leading to horizontal advection. The location of the whale fall – what ocean basin and where the whale falls within that area – will make a difference as to how long the carbon is expected to be sequestered. Also, the rate of biomass removal will vary by scavenger assemblage, and the time scale for nutrients returning to the surface is dependent on oceanographic factors. In general, carbon sequestration is considered to be more than 100 years. Even if nutrients from a whale fall move horizontally, the carbon will likely remain in the deep sea for more than 100 years virtually everywhere in the ocean unless in an upwelling zone. Generally, carbon stored in bones is likely sequestered for longer periods, whereas dissolved carbon could eventually be recycled.

5. NUTRIENT CIRCULATION & OCEAN FERTILIZATION

5.1 Presentations

5.1.1 Dan Costa: Marine mammal metabolism

The field metabolic rate (FMR) of marine mammals has often been assumed to be 2-3 times the predicted Basal Metabolic rate (BMR) of terrestrial mammals (e.g. Owen et al. 2017). However, BMR varies across taxa varies with diet, phylogeny, and lifestyle (McNab 2000). Some marine mammal taxa exhibit elevated BMR (otariids and delphinids), while others have lower rates (phocids and sirenians) (Costa and Maresh 2017). FMR estimates based on empirical data are only available for gray whales, carried out from empirical measurements of ventilation volume, oxygen extraction per ventilation, and the ventilation rate (e.g. Sumich, et al 2013). Measurements of the lung volume of dead minke whales were combined with ventilatory data to estimate their FMR and foraging humpback whales. Empirical measurements of ventilatory mechanics for cetaceans have been reviewed in Fahlman et al. (2020). Annual energy budgets have been developed for blue, gray, humpback, pilot, minke, sperm, and beaked whales (New et al 2013; Braithwaite, et al 2015; Christiansen et al. 2014; Villegas-Amtmann et al. 2017; Farmer et al. 2018; Pirotta et al. 2021). Urinary nitrogen output of fasting while lactating cetaceans can be estimated from capital breeding northern elephant seals. Estimates of prey intake have been reported for five mysticetes and nine odontocete cetaceans (Goldbogen et al. 2019). Data on the arrival and departure times of individual whales and their migratory path are crucial to refining bioenergetics models and predictions of nutrient flux. A critical assumption to models of material flux is where marine mammals defecate and could be addressed using rear-mounted cameras. Measurements of the composition of prey and feces concerning energy, macro, and micronutrients (N, Fe, Ph, and Mn) should be conducted. Assimilation efficiency can be assessed from measurements of an unassimilated element such as Manganese concentration in the prey and feces. This method has been validated in fur seals (Fadely, et al. 1990) and used to measure assimilation efficiency in minke whales consuming North Atlantic krill, *Thysanoessa sp*. (93% range 87-93) (Martensson et al. 1994).

In discussion, Costa noted that knowledge about ventilation rates could be increased by video recordings,acoustic data, or using ventilation flow meters, which has been done on gray whale calves in breeding lagoons. Other estimates can be derived from examining lung volume from dead whales. Prey consumption and nitrogen content can be measured by collecting feces and examining manganese as a tracer for assimilation efficiency or to increase the quality of estimates of prey intake and feces output.

5.1.2 Jeremy Kiszka: Dolphins mediate the translocation and recycling of oceanic nutrient subsidies to coral reefs

Cetaceans have the potential to consume considerable portions of total production in a system owing to their large body sizes, relatively high trophic levels, potentially high abundances, and high metabolic rates. In addition to their ecosystem roles as predators, cetaceans may also be important vectors of nutrient transport within or between habitats or ecosystems. Cetacean-mediated nutrients can enhance primary production and increase the population sizes of lower trophic level organisms beyond what in-situ nutrient availability could support. The importance of two abundant tropical dolphins (*Stenella longirostris* and *S. attenuata*) around an Indian Ocean coral island in mediating the transport and recycling of nutrients in a nitrogen-limited coral reef ecosystem was investigated. Both species forage primarily at night on offshore epi- and mesopelagic prey and rest, travel, and socialize along the outer slopes of the barrier reef. Based on field estimates of dolphin abundance combined with data on metabolic and excretion rates, it was estimated that these two species excrete 55,240 kg N yr-1 along the barrier reef. The relative contribution of dolphin excretions and local organic matter sources to reef species was investigated using a Bayesian stable isotope mixing model based on particulate organic matter (POM), seagrass, and dolphin samples collected from the lagoon, reefs, and the open-ocean. Concentration-dependent percent contributions of each source were calculated for several fish species occurring in seagrass, inner reef, and outer reef habitats. Model results suggest that dolphin-derived nitrogen contributes to 10-45% of the available production in the reef food web, and the primary route appears to be via nitrogen uptake by benthic producers. These results are an order of magnitude higher than those published for other predators such as sharks on similar reef systems. Because dolphins bring offshore nitrogen to the oligotrophic reef systems, these fluxes may be critical to supporting the productivity of coral reef communities.

In discussion, it was noted that small cetaceans, like large whales, also contribute to both the horizontal and vertical transport of nutrients. It would also be interesting to study the relative contribution of marine mammals as compared to other taxa such as sea birds, pelagic fish, and reef sharks, both in terms of quantity and where nutrients might be delivered.

Costa highlighted that dolphins, by feeding on vertically migrating prey over a large horizontal space and then moving inshore to rest and socialize, effectively create a point source. Nutrients are accrued from a large area and presumably released into the smaller areas offering another example of cetacean-mediated movement of nutrients in the environment.

Ritter & Vrooman suggested that there is a strong need for more studies into the ecosystem functions of small cetaceans, especially their roles in linking offshore and inshore habitats. They noted that numbers (rather than size) may matter for dolphins given their larger population sizes.

Questions arose concerning “dolphin falls.” Smith advised that studies have compared dolphin carcasses on the sea floor with gray whale falls and that gray whales, because of their larger body size, bones, and lipid content, persist for decades, whereas dolphin carcasses are consumed much more quickly. In terms of nutrient fluxes and food availability on the seafloor, the impacts may be well a function of dolphin population sizes. Nevertheless, body size affects nutrient turn-over and movement.

5.1.3 Steve Wing: Ecological function of large marine vertebrates in marine ecosystems

Micronutrient limitation highlights the essential role of bioavailable iron in the carbon cycle. The resulting High-Nutrient Low-Chlorophyll (HNLC) conditions are dramatically punctuated by high productivity hotspots surrounding islands and frontal systems, including the marginal sea ice zones where great whales aggregated historically. Lithogenic sources of iron become insoluble at pH > 4 and only small amounts of the direct supply of iron are available for uptake by bacteria and primary producers. A likely explanation for these observed patterns is that iron is extensively recycled and remineralised in marine food webs, where bioavailable iron is bioaccumulated resulting in high concentrations in the excreta of seabirds; marine mammals, including Mysticetes and Odontocetes; and large fishes. There is evidence that iron can be recycled in the marine food web at least seven times before it is sequestered in nutrient sinks in the system.

The extensive recycling of biogenic iron highlights the essential role of animals in nutrient cycles leading to widespread incorporation of biological vector activity from large marine vertebrates in biogeochemical models of nutrient cycles in these systems. Euphausiids are vital in this transaction, dominating secondary productivity in southern waters and enabling access to lithogenic iron through benthic foraging, specialized gut bacteria, and long gut-passage times. Surface swarms are extensively consumed by baleen whales, seals, and penguins in the Southern Ocean and provide a mechanism for biological transport of iron to the euphotic zone. Odontocetes and Mysticetes play a vital role in the maintenance of intact biogeochemical processes in marine ecosystems through their influence on the diversity and patterns in the flux of organic matter and nutrients through food webs (Estes et al. 2011). Evidence for important changes in the composition and size distribution of pelagic primary producers in Antarctic and subantarctic iron-limited waters indicate that biologically mediated iron recycling may influence and enhance channels for organic matter uptake by primary consumers such as copepods and euphausiids. This result may have important consequences for the non-linear relationship between biological nutrient recycling and fluxes of organic matter and nutrients through complex marine food webs. Through providing connections across marine food webs that result in both integrations of multiple channels for organic matter as well as broad connectivity within food webs, these large marine vertebrates contribute to the resilience and stability of food web networks. By providing ecosystem connectivity that crosses major ecotones, oceanographic regions and water masses, large marine vertebrates can connect major bioregions.

In discussion, Wing added that there is evidence for strong bioaccumulation of some of these elements, particularly micronutrients.

5.2 Discussion & Identification of data gaps

Sousa-Lima and Ritter referenced studies measuring or estimating the detectability of strandings of small and large cetaceans using floating/drifting simulations. There seems to be a need for more studies on small cetaceans, in addition to large cetaceans, regarding their ecosystem functions in general.

Punt stressed that coral reef systems could provide an opportunity to develop dynamic models allowing for quantification of fall feedback loops and nutrient deposition, as well as providing an opportunity for targeted sampling, which allows parameterization of some of the models.

Butterworth made a cross-reference to de la Mare's work on individual based models (IBM) (de la Mare 2018) and the use of rules for cetacean behavior at the individual level, which translates into emergent properties at the population level. He suggested that linkages should be used at the upcoming SC meeting. Kitakado, as convenor of Ecosystem Modelling (EM) Working Group, explained that the SC currently uses IBMs to understand reproduction rates, particularly with relation to MSYR, and that considering the use of de la Mare's model regarding ecosystem functioning should be discussed in the EM Subcommittee.

Costa referred to a number of bioenergetic models developed in the last five years (e.g., on blue and gray whales) which examine population processes (e.g. refs). Biuw remarked that there is need to also monitor what types of models are being developed outside the IWC, particularly regarding population consequences of disturbance (PCOD, Pirotta et al. 2018).

Comments were made that first cetacean calf survival rates are usually lower than those for succeeding offspring, due to the heavy contaminant load they receive via nursing. There was a general increased interest in the cumulative consequences of multiple stressors on cetaceans. It was **agreed** that studying human-induced changes, including climate change, and their impact on cetaceans' ecosystem functioning is important.

Roman expressed the view that the issue of whale falls and carbon sequestration are equally important. He asked several questions regarding nutrient movement, such as: what is the expected response to the increased stratification of the ocean considering that this is what many models now seem to predict (e.g., for the North Pacific and Southern Ocean)? Also: how do cetaceans react to such changes? Further: what may the role be of air breathing vertebrates as stratification increases? Potentially, animals diving below the thermocline on a regular basis may help to break down the increased stratification or move nutrients up and down. Wing explained that both large animals diving below the thermocline as well as large animals feeding on vertically migrating organisms have to be considered in this context. Even surface feeders can be accessing nutrients raised from below the thermocline. Some models of the biological pump are changed considerably in terms of carbon or nutrient flux as soon as they include vertical migration. Hence, these are potentially vital processes that whales and seabirds are facilitating.

6. CETACEANS AS PREDATORS

6.1 Presentations

6.1.1 Viv Tulloch: Using ecosystem models to understand impacts of threats to cetacean - past, present and future

Tulloch provided an overview of her quantitative ecosystem modelling research on cetaceans (Tulloch et al. 2018, 2019; SC67A/EM/12). The research uses a Model of Intermediate Complexity for Ecosystem Assessments (MICE) to hindcast abundances of five baleen whales (blue, fin, humpback, Antarctic minke, southern right), and forecast population numbers, linking whale and krill dynamics with future ocean temperature, primary productivity, and sea ice change across the whole Southern Hemisphere, from 1890 to 2100. The models use the most up-to-date IWC catch data, and are fitted to krill and whale abundance data from surveys. The climate–biological coupled ecosystem model predicts declines under climate change, even local extinctions by 2100, for Pacific populations of blue, fin, and southern right whales, and Atlantic/Indian Ocean fin and humpback whales (Tulloch et al. 2019). Future directions for this model include expanding the spatial scale to the Northern Hemisphere, and inclusion of additional key predators such as pinnipeds. A new ecosystem model is currently being developed for killer whales, seals, salmon and herring for the North American west-coast to provide a quantitative framework for understanding ecosystem dynamics and evaluating impacts of current and future human activities to inform management. Finally, the amount of historical and future carbon sequestered by the five baleen whale species listed above was quantified for the Southern Hemisphere, via two sequestration pathways: direct (via carcasses sinking) and indirect (via feces fertilization). Carbon sink was estimated to have declined from 270,000 t C.yr-1 to 50,000t C.yr-1 due to whaling, and increases in future sequestration were projected to be 130,000 t C.yr-1 by 2100 given climate change impacts on whale numbers, which is reduced from the potential 230,000tC.yr-1 without climate change impacts (Dufort et al., in review).

Kitakado commented that these results are important to understand the temporal change in ecosystem functioning and to understand the interannual changes of the distribution of cetaceans. The substantial depletion of large whales in Antarctica has important implications for understanding ecosystem functioning in that area.

Punt emphasized the value of including nutrient cycling in the analysis at the population level and to begin to examine whether whales can be integrated as drivers of lower-level trophic models. That could lead to a full feedback loop where whales impact nutrients, which potentially impact krill, which then impact whales. This could start to address the key question of what is the ecosystem functioning at the regional level. Tulloch responded that her models did include one-way interactions from nutrient, phytoplankton, zooplankton, detritus (NPZD model to krill and whales, but agreed that integrating two-way interactions with an NPZD model would be of great value.

In the Antarctic Peninsula fjords, recent huge aggregations of krill and feeding humpback whales have been observed, and questions arose as to whether such inshore movement of krill aggregations were captured in modelling and whether this is potentially important. Tulloch responded that spatial variability of krill population dynamics is an analysis gap, and agreed that it would be worthwhile to consider reducing the spatial scale of the model to capture those variabilities in population dynamics and their spatial scale.

6.1.2 Matt Savoca: Improving estimates of rorqual whale nutrient recycling with high-resolution measurements of predator and prey

Savoca's work with a team of international collaborators, estimated engulfment capacity (from allometric equations relating measured length to buccal cavity volume), measured lunge-feeding rates via biologgers, and measured fine-scale prey density using active acoustics to generate high-resolution estimates of daily prey consumption by rorqual whales. Extensive measurements on blue (Eastern North Pacific), fin (Eastern North Pacific, Western North Atlantic), humpback (Eastern North Pacific, Western North Atlantic, Western Antarctic Peninsula), and Antarctic minke whale (Western Antarctic Peninsula) were obtained. Results suggest that prior estimates of daily prey consumption – most frequently generated with metabolic models – systematically underestimate prey consumption by these species. The implications of these new prey consumption and nutrient recycling estimates on ecosystem models have regional and global importance. Future work on this topic should focus on improving temporal resolution of both predator and prey measurements, connecting ingested prey to egested nutrients, and linking these recycled nutrients to local and regional effects on primary productivity and carbon storage.

When asked about nighttime feeding at shallow depths (generally an unusual occurrence), Savoca explained that there appears to be a correlation between the moon phase and blue whale feeding at night. The mechanism that may be driving this behavior raises interesting questions as to whether the whales need to see the prey swarms or whether the swarms get denser during full moon nights. Other research revealed that there is a density threshold whereby if the prey is not sufficiently dense then whales would lose energy foraging, so they do not forage. He noted evidence of feeding for 48 hours continuously and commented that the physiology required to do that is hard to imagine.

Questions regarding the upper limit for feeding and how fast whales digest remain. While large whales are predicted to have a very low basal metabolic rate due to their large size, it could be that they exhibit extreme fluctuations in their field metabolic rate. When they are feeding, gestating, or lactating they have intense metabolic demands. In response, they may be able to raise their metabolic rate so that this ranges from very slow (associated with slow digestions and slow gut passage rates) to high (particularly when engaged in intense foraging which would expedite food digestion and a more rapid gut passage time).

6.1.3 Bob Pitman: Killer whale predation in Antarctica – diversity and ecological impacts

In Antarctic waters, killer whales are large, common, and diverse apex predators with high energetic demands. Five different killer whale ecotypes have been described based on differences in morphology, habitat, prey preferences, and foraging behavior, etc. (i.e., types A, B1, B2, C, and D). When these forms occur sympatrically, they do not intermingle or interbreed, suggesting that there could be species-level divergences. Photo-identification studies show that an estimated 1.000 killer whales inhabit the Antarctic Peninsula area: 149 type A (whale- and seal-eaters occupying open water, numbers increasing); 102 type B1 (ice-seal specialists, heavy pack-ice, numbers decreasing), and 740 type B2 (probably mainly fish-eaters, open water/light pack-ice, numbers stable). The varying status of these ecotypes seems to reflect recent declines in the amount of sea ice in the Peninsula area due to global warming. In McMurdo Sound, 352 individual type C killer whales (fish-eaters, fast-ice, stable) were identified, of which 70 are considered part of a 'resident' population. Almost nothing is known about type D killer whales except they are open-ocean forms most commonly found along the Circumpolar Front. Through their differences in prey, these killer whales mediate a range of pressures on their respective prey species. The next steps to determine the ecological impact of killer whale predation in Antarctica and to predict potential changes in their status due to a rapidly warming environment will include quantification of the number and species of prey taken by each of these different ecotypes.

When asked how the research feeds into the killer whale predation hypothesis related to the migratory behavior of baleen whales, Pitman referred to a recently published paper (Pitman et al. 2019) postulating that killer whales defer normal skin molt while in freezing Antarctic waters (as indicated by the accumulation of diatoms on their skin) in order to conserve body heat, but then they must engage in long distance migration to warm, low-latitude waters so they can molt. Most large whales acquire similar accumulation of diatoms and it is suggested that they might migrate for the same reason.

Pearson expressed interest in the potential nutrient flux of killer whales resulting from their movement to low latitudes through sloughed skin and asked if it can be assumed that the entire epidermal layer is sloughed. This aspect can potentially be included in consideration of the great whale conveyor belt even though killer whales are not large whales. Pitman explained that it is possible to follow humpback whales off western Australia based on their skin trail and that they breach frequently to get rid of the skin. It is thought that they lose all of their skin but that only a small layer is sloughed. The sloughed skin is eaten by, for example, silver gulls. He added that it should be possible to weigh bits of molted skin and extrapolate to the estimated 70 square meters of skin of a large whale and thus calculate the biomass of skin loss during migration.

When asked to provide more information about the behavioral response of humpback whales to killer whales, Pitman explained that baleen whale responses fall into two categories – flight or fight. Fight species, such as humpbacks, bowhead, and gray whales, when attacked by killer whales, try to fight them off and they also tend to cooperate in doing so. Balaenoptera whales (excluding humpbacks) are flight species using their speed to escape from killer whales. For these whales it is safest for the mother to give birth in the mid-ocean and raise the calf to a size that can outrun killer whales. Hence, these balaenopterid whales are going to “cold spots" since those areas are devoid of killer whales. If large whales are going to be migrating to the tropics for molting, then accumulating sufficient calories to afford to stay there for a few months and to have a calf, probably provides increased safety from killer whales.

6.2 Discussion & Identification of data gaps

Punt emphasized that the greatly varying percentages given for consumption rates have dramatic implications for ecosystem modeling and should be studied further. Savoca replied that their best estimates for prey were made on a daily basis and that high resolution measurements throughout the entire feeding season would help solving that problem.

Savoca highlighted that actual numbers of krill are probably greater than the projections for krill populations in the Southern Ocean and that the whales are feeding on large quantities of krill. Whales are keeping nutrients in the system via recycling and, therefore, they operate in a more circular manner. Models need to take the associated inputs and outputs into account.

Costa noted that not all prey species are equivalent in terms of energy content. Models therefore must take account not only of consumption rates but also prey quality (e.g., lipid richness which may vary widely between prey species). Moreover, the timing of how long animals spend feeding is also very important. He added that in the development of a simple bioenergetics model for gray whales it makes a difference if the animal is feeding for 24 hours or for 12 hours per day, and how long an individual stays in a feeding ground. There is also a need for data on diurnal feeding patterns.

Savoca emphasized that better fine-scale measurements are definitely needed, including the energy density of different prey species throughout the course of the year. Biuw added that the functional response is important to take into consideration in the context of foraging activity in relation to prey density. Studies focusing on areas where it is known that prey is densely congregated may provide biased estimates because the whales may not experience that same prey density throughout the feeding season.

Costa explained that with models using stochastic dynamic programming (SDP), variance and uncertainty are high because assimilation efficiency is hard to measure. He advised that when modeling beaked whales, it turned out that small changes in assimilation efficiency have profound implications for the energy budget and whether a whale produces a calf (New et al., 2013). Today, the only data available are on minke whales feeding on krill, which has an appreciably different energy content compared to fish.

It was **agreed** that determining the number of days for which whales are feeding per year/season, as well as consumption rates across species, is of great importance. Likewise, studies on metabolic rates, assimilation efficiency, and the energy content of prey are important subjects for future research.

7. OTHER ECOSYSTEM FUNCTIONS

7.1 Identification of other ecosystem functions of cetaceans

Nothing was raised under this agenda item.

7.2 Discussion & Identification of data gaps

Nothing was raised under this agenda item.

8. OTHER MATTERS

8.1 Terminology

It was noted that some terms relating to ecosystem functioning have multiple or different meanings depending on context, including legal documents. Therefore, a glossary of terms was suggested which would define how such terms had been used for the purpose of this workshop (see ANNEX D).

8.2 Methods for determining ecosystem functioning

8.2.1 Doug Butterworth: Ecosystem based fisheries management

Carruthers and Hilborn (2021) was developed to inform specific discussions in the North Atlantic Fisheries Organisation, but covered issues of wider relevance, particularly regarding the application of models involving trophic functioning to the provision of scientific advice to bodies with responsibilities for marine population regulation. This is a component of Ecosystem Based Fisheries Management (EBFM) and has a bearing on some potential outcomes from the workshop. There were two relevant messages from the paper. First, at both national and international levels, there have been few tactical applications of the outputs from ecosystem models, including trophic functioning, used to provide input in management decisions over the past two decades, despite considerable research efforts on the topic. The reason suggested was the general difficulty of achieving reliable predictions from such models, given their complexities and their often numerous possible and defensible formulations which led to rather different implications. The second message emphasized the need for such models, when used to advise on possible tactical decisions, to meet basic standards for correct implementation, reproducibility, objectivity and performance. In particular, those models needed to be fit to data (such as time series of population abundance indices) to allow for empirical validation, and to provide a basis for comparison of and choices amongst alternative models.

Following brief discussion, it was **agreed** that guidance was needed from a higher level regarding in which forum management implications associated with ecosystem functioning are best addressed.

8.2.2 Other

It was noted that the ToR explicitly requested the workshop to address methodological approaches on the study of how cetaceans affect ecosystem functioning. To that end, Table 2 gives an according overview of research needs including suggested research which also had been touched upon in the various workshop presentations. Table 2 will also aid in the preparation and conduct of the second workshop on ecosystem functioning. The focus shall be on questions that can be quantified (i.e. questions that relate to testing of hypotheses versus merely generating hypotheses) including those that can potentially be answered before the second workshop.

8.3 Role of scientists, organizations, and stakeholders

It was noted that interest in the issue of ecosystem functioning of cetaceans, particularly in the context of climate change, has gained momentum over the past two years and will likely increase. Discussions about "blue carbon" and nature-based solutions (NBS) are of interest to stakeholders, especially ENGOs and decision-makers. Ritter drew attention to one argument which he has repeatedly heard from decision-makers which is that, given the current climate emergency, even the smallest contribution to carbon sequestration, for example by cetaceans, may possibly make a difference.

The role of science in this context was discussed. While it is clear that cetaceans contribute to carbon storage and sequestration, it is also clear that the science is incomplete. Decision-makers need to be provided with accurate information, but scientists have to be careful in portraying what is known. Likewise, there is a responsibility to inform the public based on the best available science, including any uncertainties. It was suggested that the best set of population trends, numbers, and biomass be provided by the IWC Secretariat and that such information be available on the IWC website. These data would then be available to researchers including those who are conducting studies and making calculations relevant to the role of cetaceans in ecosystem functioning. The workshop noted that some of this information is already provided on the website in a process coordinated through the ASI Sub-committee.

In summary it was **agreed** that large vertebrates are an integral part of a well-functioning marine ecosystem and that they provide a potentially long list of ecosystem functions and services to humans (compare Table 1). While the workshop did not address such wider issues in greater detail, there are scientific components relevant to such matters that could be reviewed if the Commission requested that from the SC. The network of people participating in this workshop would be well placed to comment on such matters.

Galletti reminded workshop participants that IWC resolution 2016-03 led to this gap analysis workshop. The resolution also contains a request to examine the economic and social value of the contributions of cetaceans to ecosystem functioning to society which will be the focus of a workshop conducted under IWC Conservation Committee (CC) later in 2021. That workshop will be greatly informed by the discussions of this workshop.

9. WORK PLAN AND PRIORITY RECOMMENDATIONS

Kitakado proposed using a series of tables to capture the outcomes of the workshop and to provide a roadmap for intersessional work in preparation for the next workshop. Such tables would be intended to provide an overview and a balanced representation of what is known and to identify knowledge gaps. The tables could also include references to relevant studies, and capture questions and hypotheses identified during the workshop discussions. This proposal received support. The importance of specifying the work that can be undertaken between this workshop and the second workshop, including updates to some of the calculations, was stressed. Kitakado provided a summary of the content of a set of such tables (see Tables 1-3) and highlighted their value in summarizing the discussions about data and knowledge gaps.

To assist in the preparation for the second SC workshop on ecosystem functioning, the co-Chairs proposed a series of general questions or hypotheses along with sub-items, which focus on what could be achieved within the one year of the intersessional period, including the development or modifications of models (see Table 3).

Table 3. A list of general questions, hypotheses, and tasks to be accomplished or considered for a second workshop.

1) Development or modification of existing ecosystem models for the basis of subsequent items
● What are the appropriate consumption rates to use in analyses. Comparison of alternative methods of assessing consumption rates (according to time on the feeding grounds and prey composition) ● (Metapopulation) models for the abundance, over time and space, of enrichment and reducing habitats at the deep-sea floor created by whale falls, and extinction risks to whale-fall specialists ● Extension of existing ecosystem models to explicitly include nutrient flux due to cetaceans ● Summary of the current status of (end-to-end) ecosystem models globally in terms of (a) their inclusion of cetaceans and (b) the extent to which the inputs in (2) below are included - and what would be needed to make (a) and (b) happen ● Models to address processes across ecosystem boundaries (marine to terrestrial and vice versa, transcending large marine ecosystems, etc.).
2) Inputs needed for a robust assessment of the contribution of cetaceans in "ocean fertilization", "carbon cycle and sequestration", "delivery of nutrient and energy", and "habitat provision" (contribution relative to species other than cetaceans, consumption, metabolism, biodiversity, habitat including deep sea floor)
● Species-specific horizontal (migratory) movement ● Identification of provider-beneficiary relationships (species interactions) ● Species-specific diving behaviour ● Schema for developing and parameterizing energy budgets, best practices and validation.) ● Review of status of bioenergetic modelling and associate gaps and uncertainties, including rate at which animals utilize materials ● Energy and nutrient content of prey and feces ● Nutrient content in seawater ● Phytoplankton uptake rates of cetacean-derived nutrients ● Cetacean mortality sources and rates, and carcass disposition, in space and time (e.g., along migration routes, in calving grounds, feeding grounds, whaling grounds, etc.) for representative species ● Phytoplankton carbon flux to depth, and horizontal advection into and out of systems from models ● Extent of co-limitation of nutrients and whale feces (N and Fe in particular but could be broader) ● Addressing issues related to the timing of biological events (blooms etc) in relation to cetacean presence and activity within a system
3) Quantification of spatial difference in ecosystem functioning of cetaceans, with focusing on link with environments and regional ecosystem characteristics? (historical trends in different places…)

- Case studies desirable in the following areas: Southern Ocean, South Pacific, Eastern North Pacific, North Atlantic including Barents Sea, Gulf of Maine, other oceans/seas that are nutrient limited.
- Contrast areas where cetaceans utilize different forage species and functional groups (e.g., krill, fish, benthic invertebrates, etc. and contrast ecosystem models of northern hemisphere versus southern hemisphere baleen whales)

4) Quantification of temporal changes in ecosystem functioning of cetaceans, with focus on difference between pre-whaling and current populations and identification of information and knowledge gaps [review of trends of abundance of cetaceans =liaise with ASI-G, contrast regions (SO, NA) with different intensity of human-induced mortality and extent of depletion or restoration]

- Contrast areas with well characterized changes in the abundance of cetaceans (e.g., the Southern Ocean) with areas of relatively intact or restored cetacean populations. Consider, if possible, areas with relatively few other anthropogenic stressors to isolate the ecological effects of changes in cetacean abundance.
- Development of (temporal/regional) scenarios regarding human-caused impacts of cetacean abundance and feeding (minimally) to allow quantification of the effects on cetacean ecosystem function
- How has the decline of whale populations influenced alternate channels for sequestration of nutrients in the Southern Ocean? Forensic analysis of ecosystem components from pre and post whaling periods.
- How has the decline of whales affected habitat availability and biodiversity of whale-fall fauna, including whale-fall specialists?
- How have the trophic positions of the cetacean community changed since pre-whaling days, in terms of niche overlap, species packing, and individual specialization as indicators of resource limitation? Surplus-yield models should include the effect of iron and other nutrients in whale feces..

5) Qualitative assessment of the future roles and ecosystem functioning of cetaceans, with a focus on implications of global changes

- Develop a synthesis framework to communicate the likely consequences of ecosystem functioning (get a graphic artist/ communications specialist?) with a focus on relative likelihood (c.f. IPCC)
- Can we estimate what effect various alternative cetacean management strategies would have on ecosystem functioning and mitigating climate change? Over what time scale, and over what spatial scale, would such strategies have the desired effects? How large are these relative to actions that affect other ecosystem components and physical/biological processes?
- How do multiple ecosystem stressors combine to enhance/reduce the ecosystem impacts of cetaceans?

6) Different contributions to ecosystem functioning over different cetacean species/functional groups (small versus large, mysticetes versus odontocetes, etc.)

- Which of the ecosystem functions or services are limited to large whales, and which also apply to smaller cetaceans? What further research is needed to investigate the ecosystem services of small cetaceans?
- Do cetaceans make a unique contribution to marine ecosystems (i.e., one that would be lost in their absence)?

In discussion, the following general aspects were deemed essential for the further development of the issue of ecosystem functioning: a) whether existing models are available or if new models need to be developed; b) the feasibility of using existing technologies to improve existing models; c) what species and regions should receive particular attention; d) the importance of comparing and contrasting areas with different characteristics and functionalities; e) the impact of multiple stressors including direct and indirect forms of human-induced mortality on cetaceans and the impacts on ecosystem functioning of those stressors; f) nutrient limitations and co-limitations; and g) the need to request assistance from the ASI subcommittee regarding up-to-date abundance and trend data.

The workshop **recommended** that the general questions given in Table 3 together with sub-items represent the best ways forward to proceed with the work on understanding cetacean ecosystem functioning in the short term.

The intent is to continue to review and amend Tables 1-3 during the intersessional period. The EM subcommittee, and members of the SC in general, also could provide such input and information for these Tables.

10. ADOPTION OF REPORT

The report was adopted on 04 May, 2021, 2100 h.

ANNEX A: Workshop Agenda

1st IWC-CMS Workshop on Cetacean Ecosystem Functioning

AGENDA

5. INTRODUCTORY ITEMS

- **5.1 Welcoming remarks**
- **5.2 Election of Chairs**
- **5.3 Appointment of rapporteurs**
- **5.4 Adoption of Agenda**
- **5.5 Review of documents**

6. REVIEW OF THE TERMS OF REFERENCE

7. BACKGROUND ON CETACEAN ECOSYSTEM FUNCTIONING

3.1 Reviews of existing knowledge

- **3.1.1 Keynote review I: Cetacean ecosystem functions (Joe Roman)**
- **3.1.2 Keynote review II: A critical evaluation of whales as ecosystem engineers (Wassmann et al.)**

3.2 Discussion on the general role of cetaceans in the ecosystem

8. WHALE FALLS

4.1 Presentation(s)

- **4.1.1** Craig Smith: **Whale falls - ecosystem engineers, stepping stones and oases of biodiversity at the deep sea floor**
- **4.1.2** Heidi Pearson: **Synthesis of the role of cetaceans in nutrient & carbon cycling**
- **4.1.3** Andrew Pershing: **Whales & Carbon**

4.2 Discussion / Identification of data gaps and needs for research and analysis

9. NUTRIENT CIRCULATION & OCEAN FERTILIZATION

5.1 Presentations

- **5.1.1** Dan Costa: **Marine mammal metabolism (provisional title)**
- **5.1.2** Jeremy Kiszka: **Dolphins mediate the translocation and recycling of oceanic nutrient subsidies to coral reefs**
- **5.1.3** Steve Wing: **Large vertebrates in marine ecosystems**

5.2 Discussion / Identification of data gaps and needs for research and analysis

6. CETACEANS AS PREDATORS

6.1 Presentation(s)

- **6.1.1** Viv Tulloch**: Using ecosystem models to understand impacts of threats to cetacean - past, present and future**

6.1.2 Matt Savoca: **Improving estimates of rorqual whale nutrient recycling with high-resolution measurements of predator and prey**

6.1.3 Bob Pitman: **Killer whale predation in Antarctica - diversity and ecological impacts**

6.2 Discussion / Identification of data gaps and needs for research and analysis

7. OTHER ECOSYSTEM FUNCTIONS

7.1 Identification of other ecosystem functions of cetaceans

7.2 Discussion / Identification of data gaps and needs for research and analysis

8. OTHER MATTERS

8.1 Terminology

8.2 Methods for determining ecosystem functioning

8.2.1 Doug Butterworth: **Ecosystem based fisheries management**

8.2.2 Other

8.3 Role of scientists, organizations, and stakeholders

9. WORK PLAN AND PRIORITY RECOMMENDATIONS

10. ADOPTION OF REPORT

ANNEX B:

Terms of Reference

1. The workshop will review existing scientific information through
   1a) Receive a review relevant scientific studies, on the contribution of cetaceans to ecosystem functioning (will be accomplished in advance of the workshop/meeting through contract, results to be presented at workshop/meeting)
   1b) Receive presentations from selected experts on their research into how cetaceans affect ecosystem functions;
2. An assessment of what can realistically and reliably be quantified currently
3. Identification of potential geographical areas and species/taxa on which to focus
4. Identify knowledge gaps as well as data gaps in our understanding of cetaceans and their impact and role in ecosystem functioning;
5. Develop a prioritized list of recommendations for scientific research to fill identified knowledge gaps, including studies on methodological approaches to study how cetaceans affect ecosystem functioning.

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

ANNEX C

Tables 1, 2 and 4

Table 1. Summary of selected traits of cetaceans and their related ecosystem functions and services

Colour code: RED = nutrient transfer and circulation, GREEN = feeding-related traits, BLUE = provision of habitat, contribution to biodiversity, and blue carbon

Trait	Description	Functions	Services	Example	Reference(s)
Nutrient transfer and circulation					
Body size and latitude	Cetaceans in tropical systems are dominated odontocetes (mostly smaller species: beaked whales, blackfish, delphinids), which largely replace mysticetes	Energy conversion by feeding on individual prey in a more oligotrophic environment vs engulfing swarms.	Vertical transport of nutrients - either by relatively shallow divers that feed nocturnally on diel migrating prey or deep divers. Smaller but more numerous whale falls	Small cetaceans nearly absent from Antarctic waters	Baird et al. 2001, 2008; Shaff and Baird 2021; Doughty et al. 2016?
Capital breeding	Stored energy used for reproduction and survival	Long-distance migration, winter calving and fasting	Transport of nutrients from highly productive foraging grounds to nutrient poor, low latitude feeding grounds, in the form of carcasses, placentas, skin sloughing, feces, and urine	Coastal species such as gray whales, humpbacks, and rights, best exhibit these traditional baleen migrations	Roman et al. 2014; Acevedo et al. 2017

Epidermal molt	Killer whales and other migratory species travel thousands of kilometers each year for skin molt migration. Also some behaviors such as breaching (e.g. humpback whales) remove skin but also ectoparasites and epibionts.	Routine skin maintenance, feeding/molting hypothesis	Nutrient transport, microbial connectivity, food for scavengers and detritivores	Southern Hemisphere killer whales and other whales that migrate from polar latitudes to tropical waters	Pitman et al. 2019; Whitehead 1985
Life span	Time in years	Nutrient storage	Nutrient cycling and maintenance of trophic interactions and ecosystem resilience and stability	Baleen whales are among the longest living mammals; foraging, migration, and whale fall communities are all affected by this trait	Keane et al. 2015; Taylor et al. 2007; Jones et al. 2009
Migration	Distance traveled per day, month, or year. Populations show range of movements from resident species (Gulf of California fin whale) to highly migratory (North Pacific gray whales, many humpback whale populations) For migratory species, length of stay in breeding or feeding areas	Nutrient transport, dispersal of microbes and other organisms, deep-sea whale-fall communities	Resource subsidies from high nutrient foraging areas to more oligotrophic winter or calving areas, provision of whale-fall communities along migratory pathways	Nutrient dispersion, enhanced productivity, whale fall communities	Doughty et al. 2016; Roman et al. 2014; Stevick et al 2004; Rasmussen et al. 2007; Avila et al. 2020

Mortality rate	Number of deaths per unit of time in a particular area	Nutrient transport, carcass succession and decomposition in deep sea, coast lines, and breeding areas	Biodiversity promotion in the deep sea, maintenance of gene flow and genetic diversity,	Whale fall communities throughout the deep sea; ecological and evolutionary stepping stones for hydrothermal vent and cold seep animals; nutrient supply for condors, polar bears, sharks and gulls	Smith et al., 2014; 2015, 2017, 2019; Taylor et al. 2007; Marón et al. 2015
Prey for predators	Cetaceans as prey to killer whales and sharks, including 50 cm cookiecutter sharks	Providing prey for a range of predators	Killer whales and large sharks are a source of carcasses for scavengers and detritivores. For small sharks: a source of nutrient movement from surface layers to mid-water communities	Killer whale predation on large and small cetaceans; nearly all cetaceans in low latitudes have cookiecutter shark bite wounds.	Jefferson et al. 1991; Pitman et al. 2001, Barrett-Lennard et al. 2011, Wenzel and López Suárez 2012, Pitman et al. 2015
Whale pump	Nutrients moved from aphotic zone to the surface	Similar to that of the biological pump, nutrient transfer from depth to surface and across migration routes	Nutrient cycling and promotion of biological diversity, particularly nitrogen, phosphorus and iron	Field studies and models have been conducted in the Southern Ocean, North Atlantic, and North Pacific Focus on iron, nitrogen, and phosphorus.	Nicol et al. 2010, Roman & McCarthy 2010, Roman et al. (2016)
Body size and soft-tissue lipid content	Mass, percent weight	Organic and inorganic nutrient storage and transport through growth, migration, mortality, and sinking	Transport of organic matter and inorganic nutrients from productive upper ocean to food-poor deep sea, provision of food to deep-sea, shallow-water and terrestrial scavengers, formation of reducing	Whale-fall communities at deep-sea floor in multiple stages of succession	Smith and Baco 2003; Smith et al. 2014, 2015, 2017, 2019; Pershing et al. 2010

			habitats at seafloor, nutrient cycling, carbon sequestration		
Bone lipid content	Percent and total mass of lipids in skeleton	Provision of persistent organic and sulfide-rich habitat at seafloor	Promotion of habitat heterogeneity (including organic-rich and chemoautotrophic habitats) and biodiversity at the deep-sea floor, evolution of novel whale-fall species, ecological and evolutionary stepping stones for hydrothermal vent and methane seep faunas	Whale-fall communities at deep-sea floor in organic-enrichment and sulphophilic stages	Smith and Baco 2003; Higgs et al. 2010; Smith et al., 2015
Iron content in feces	Percent of iron content in whale feces, stimulation of primary and secondary productivity (krill) in feeding grounds	Provision of iron-rich sources to support and enhance phytoplankton and zooplankton growth	Nutrient enrichment of feeding grounds, stimulation of productivity throughout the wider marine ecosystem	Blue, fin, humpback, and sperm whales in Southern Ocean	Lavery et al 2014; Roman et al. 2014; Nicol et al 2010;
Macronutrients in whale feces	Amount of nitrogen (NH4+) and phosphorous (PO43-) in whale feces	Stimulation of phytoplankton growth	The growth rate of phytoplankton from areas of whale populations	North Atlantic right whales stimulate the growth of phytoplankton species	Roman and McCarthy 2010; Roman et al. 2016,
Social and reproductive behavior	Group size	Nutrient provision	Concentration of nutrients via hot spots and hot moments	Fecal plumes from right whale breeding aggregations concentrate nutrients in surface waters	Roman et al. 2016, Roman et al. in review
Feeding-related traits					

Consumption rate	Amount of prey or milk ingested per unit of time	Trophic dynamics and cascades, nutrient storage and transfer	Ecosystem resilience and stability	Baleen whales on foraging grounds, deep-diving species in the aphotic zone	Savoca et al. in review; Pauly et al. 1998; Goldbogen et al. 2019; Costa & Maresh 2017
Diel feeding patterns	Most feeding occurs at night and tracks deep scattering layer - mostly in the tropics	Allows animals to feed on vertically migrating midwater prey.	Vertical transport of nutrients from midwater to the surface	E.g., pantropical spotted dolphin, beaked whales (Ziphius Mesoplodon), rough-toothed dolphins,	Baird et al. 2001; Baird et al. 2008; Shaff and Baird 2021;
Excretion rate	Amount of excreted material per unit of time (g/day)	Nutrient storage, vertical nutrient subsidies, and community shaping by altering primary productivity	Nutrient cycling, enhanced primary productivity, carbon storage and sequestration	Iron in sperm whale feces in Southern Hemisphere, nitrogen in baleen whales in North Atlantic	Lavery et al. 2010; Roman and McCarthy 2010
Feeding distance	Distance between the breeding location and foraging area	Nutrient storage, movement of nutrients from areas of high productivity to areas that are typically in lower latitudes and often lower productivity	Nutrient cycling and promotion of biological diversity	Whales have the longest migration of any mammals, traditional migration of baleen whales	Corkeron and Connor 1999; Geijer et al. 2016; Acevedo et al. 2017; Horton et al. 2017 Front Mar Sci
Diving behaviour	(Maximum) dive depths	Diving for foraging	Displacements more deeply, more movement of nutrients in the water column	Beaked whales and sperm whales dive deeper than any other animal	Würsig et al. 2018; Encyclopedia of marine mammals

Trophic Level	Trophic level of species in relation to prey consumption	Diet composition and trophic level ranges	Some nutrients are bio-accumulated in the food web. Cetaceans also exert top down controls on food webs	Predators, including smaller species, often have higher micronutrient concentrations in faeces	Pauly et al. 1998
Surplus killing	Killing either more or much larger prey than can be consumed	Food source for deep and shallow water organisms and terrestrial scavengers	Can provide large amounts food (tons) for benthic scavengers and detritivores	Killer whales feeding on gray whales in Alaska, minke whales in Antarctica, and blue whales in Western Australia.	Barrett-Lennard et al. 2011, Pitman et al. 2015, Pitman et al. in review
Cetaceans as 'beaters' of live prey for seabirds	Feeding/traveling whales and dolphins opportunistically providing live prey for seabirds	Seabirds catch prey that would not normally be available to them	The prey is dispersed as guano at sea and at colonies	Seabirds feeding with bubble-net feeding humpbacks and in association with dolphin schools	Au and Pitman 1986,Obst & Hunt 1990; Anderson & Lovvorn 2008, Veit and Harrison 2017
Cetaceans providing carrion for scavenging seabirds	Large, predatory odontocetes break up large prey and scraps are scavenged by seabirds	Seabirds feeding on prey normally too large for them	The prey is dispersed as guano at sea and at colonies	Seabirds picking up scraps from feeding mammal-eating killer whales, or other odontocetes	Pitman and Ballance 1992, Ridoux 1987
Provision of habitat, contribution to biodiversity & "blue carbon"					

Skeleton size and calcification	Mass and surface area/volume ratio of largest vertebrae, skull, and long bones	Provision of persistent organic or sulfide-rich habitat at seafloor, provision of hard substrate in soft-sediment habitats	Promotion of habitat heterogeneity (including organic-rich and chemoautotrophic habitats) and biodiversity at the deep-sea floor, evolution of novel whale-fall species, ecological and evolutionary stepping stones for vent and seep faunas	Whale-fall communities at deep-sea floor in organic-enrichment, sulphophilic, and reef successional stages	Smith and Baco 2003; Rouse et al. 2004, 2018; Smith et al., 2014, 2015, 2017, 2019
Carcass sinking to deep-sea floor	Nutrient food source for deep ocean fauna	Food source for many specialised deep-sea species, not found elsewhere. Many different stages, and last for decades on the sea-floor.	Physically modify and create new habitats. A number of stages supporting different species including 102 species 'whale fall specialists' that are not found elsewhere and need a whale fall to complete life cycles.	Whale-fall communities at deep-sea floor in multiple stages of succession	Schuller et al. 2004; Smith and Baco 2003; Smith et al. 2014, 2015, 2017, 2019
Body Mass	"Size matters", with high metabolic efficiency, larger animals store more carbon compared to smaller ones	Storing carbon, preventing it from being released into the atmosphere	Contribution to blue carbon as a "nature based solution" (NBS)	Same food (krill) that supports one 92-ton blue whale also supports • 7 minke whales • 1800 penguins but, the total biomass would be less (1/2 or 1/10), extra carbon would go to atmosphere	Pershing & Stamieszkin 2020; Pershing et al.. 2010; Roman et al. 2014
Reproduction rate	Number of calves per year	Reproduction	More offspring more biomass for the ecosystem	In general, small cetaceans have more calves per year than large ones	De Magalhaes & Costa 2009

Table 2. Ecological Functions of Cetaceans: Research and Development Needs

Colour code: RED = nutrient transfer & circulation, GREEN = Feeding-related traits, BLUE = provision of habitat, contribution to biodiversity & "Blue carbon"

Recommended Research	**Gap Filled (Questions answered)**
Nutrient transfer & circulation	
Effect of nitrogen, iron, and phosphorus in primary productivity (vertical)	Furthers understanding of nutrient cycling in foraging areas of cetaceans and other air-breathing vertebrates
Nutrient transport from high to low latitudes (horizontal)	Furthers understanding of global nutrient subsidies by cetaceans and other capital breeders
Great whale conveyor – placenta, urea, fecal, sloughed skin, and carcass samples. Water samples	Furthers understanding of which nutrients, and how different whale species transports across which oceans
Impacts of the addition of nitrogen, iron, and phosphorus on concentrations of phytoplankton growth, compared to these nutrients individually	Is phytoplankton growth higher where there is additional of nutrients, compared to one or other alone.
Impacts of other limiting (co-)factors of phytoplankton growth (e.g. manganese, saccharides, cobalamin (B12)	Increases understanding how limiting factors act synergistically to enhance phytoplankton growth
Bubble feeding enhancing the upward transport of nutrient-rich deep water and surface gas exchange	Furthers understanding of the biological pump - Humpback whales create spiral flow features using underwater exhalations to concentrate their prey, this will stir up and push nutrients to the surface.
Physical engineering of the sea floor by cetaceans. The nutrients stirred up during bottom feeding how they remain suspended in the water column, and how they support other marine life	Furthers understanding of the whale pump and how it supports marine ecosystems. E.g., whale pits created by gray whales, and the increased number of invertebrates supported by the stirring up of these sediments.

High resolution, long-term studies of implanted great whale carcasses at deep-sea observatories (e.g., Ocean Networks Canada)	Increases understanding of nutrient cycling, community succession, and functional roles of bacteria/ archaea, Osedax and sulfophilic biota at deep-sea whale falls, and elucidates the role of whale bones as dispersal stepping stones for vent and seep biota, especially across ocean basins.
Whale pump – dive depth, thermocline depth, fecal samples, and water samples to determine micro- and macro-nutrient content	Fills in gaps of how different species move nutrients from different depths throughout the water column
Fecal samples, and water samples to determine micro- and macro-nutrient content	Furthers understanding of how whales contribute to island hotspots in the iron limited Southern Ocean and of enhancement of productivity & nutrient circulation in hot-spots and during hot moments
Determining cetacean dive depths in relation to thermocline	Increases knowledge of how consumption by cetaceans interacts with vertically migrating zooplankton and mesopelagic fish communities, both in terms of vertical organic matter and nutrient fluxes? And how grazing and defecation by cetaceans contributes to nutrient cycling and primary production?
Comparison of pre- and post-whaling population numbers	Need to understand how the decline of whale populations influenced alternate channels for sequestration of nutrients in the Southern Ocean, ho nutrient transfer and circulation has changed over time (pre/post whaling), to determine the movement of nitrogen and other nutrients across ocean basins (based on current and past whale population sizes), and to predict the future role or function of whales in ecosystems
Studies on bio-availability of micronutrients	Furthers understanding if iron in feces is more likely to be utilized through the microbial loop than through phytoplankton
Quantification of cetacean diving behavior	What proportion of foraging dives occur above vs. below the mixed layer and thus contribute to autochthonous vs. allochthonous nutrient cycling
Fecal samples of small cetaceans; Behavioural studies (e.g., niche occupancy of dolphins)	To determine the contribution of dolphins to the movement of nutrients, both horizontal and vertical, and across ecosystems

Lab studies to determine how phytoplankton and bacterial communities respond, both in terms of production and composition, to nutrient delivery by cetaceans of different species	To understand the effects of whale-mediated nutrients on the abundance and composition of phytoplankton and microbial communities? Consequences for organic matter and nutrient routing in food webs?
Comparative studies between marine vertebrates in different geographical areas	To estimate the relative contribution of cetaceans vs. other organisms/processes for vertical and horizontal nutrient transport, specifically comparing different regions with contrasting physical forcing regimes
Studies on seasonal timing of whale migrations and local/regional plankton blooms	To estimate the effects of match or mismatch between spring phytoplankton blooms and seasonal variations in cetacean feeding/defecation rates in modifying the contribution of cetaceans to nutrient cycling
Provision of habitat, contribution to biodiversity & “blue carbon”	
Comparative and controlled studies on whale falls in different oceans. Includes controlled placement of whale bones (standard size, standard deployment time) in different regions to explore location effects	Do ecosystem functions of whale falls (nutrient cycling, community succession, decomposition of bones by bacteria/archaea versus Osedax) vary across ocean basins with different whaling histories? How does biodiversity on whale falls vary between areas with heavily depleted great-whale populations (Southern Ocean, North Atlantic) versus areas where some populations have recovered (Northeast Pacific?) Determining the role of whale falls as novel habitats promoting evolution of biodiversity; test of the hypothesis that whaling has caused species extinctions at the deep-sea floor
Comparative and modelling studies of individual whale falls, and/or controlled placement of lipid-rich whale bones, near vents/seeps and on abyssal plains	Do whale falls provide dispersal stepping stones for vent/ seep species across abyssal plains?
Studies on the composition of sloughed skin from cetaceans	Does skin sloughing contribute to the nutrient ecology of breeding grounds?
Water samples from residence versus molting areas (Orcas and humpbacks)	Do whales transport bacteria and diatoms between their summer foraging and winter molting grounds?

Comparative studies on biomass carbon – abundance, age/sex structure, longevity	Furthers understanding of the populations of different species, the carbon they remove from the environment.
Comparative studies on whale falls/ deadfall carbon – Abundance, age/sex structure, mortality rates. Different species in different conditions.	Further understanding of where whales die, and end up falling, the age of carcasses, and the role of different environments on species and scale of decomposition
Whale falls studies in current whaling areas. (In some areas, whale carcasses are dumped at sea during whaling operations after the required parts are removed.	These carcasses could be studied to understand successions on whale falls.
Studies on the impact of disturbance on energetics of cetaceans	How do behavioral disruptions affect the ecological roles and importance of cetaceans?
Determine how cetaceans have direct and indirect influences on fluxes of materials in marine food webs	The implications of climate change for ecological function and ecosystem services—including wildlife populations, fisheries, and carbon sequestration—are unclear. How has the decline of whale populations influenced alternate channels for sequestration of nutrients in the Southern Ocean?
Finer spatial resolution ecosystem models	To determine spatial variability in krill/whale population dynamics - and/or alternate scenarios of krill distribution and prey shifting to better predict finer-scale whale trends in abundance
Highly resolved spatially explicit understanding of landscape features, including topography, oceanographic features, stratification, patchiness, and connectivity, and habitat connectivity within and among ecosystems	To determine spatial scales with regard to cetaceans' roles in ecosystem functioning
Inclusions of other krill predators (e.g., seabirds, seals, fish, penguins, jellyfish, squid) in ecosystem models to better understand the roles of different predators in whale ecosystems, in terms of competition for and consumption of prey	To better predict relative role or function of cetaceans in ecosystems, trends in abundance, and predict changes to ecosystem function over time

Comparative ecosystem models that evaluate role of cetaceans in ecosystem and future abundance trends between Northern Hemisphere and Southern Hemisphere, that include climate change	To better predict future role or function of cetaceans in ecosystems, in relation to trends in abundance, and to predict changes to cetacean ecosystem function over time
Feeding-related traits	
Physiological and tagging studies on defecation rates of cetaceans, including localization of defecation	How often do cetaceans defecate? Do cetaceans always defecate at the surface?
Measuring field metabolic rates of mysticetes (e.g., oxygen extraction, breathing rates)	To quantify cetaceans spatial and temporal contribution local ecosystems via prey consumption
Use of tags with integrated echosounders to map the prey field in the immediate vicinity of the whale	To enhance precision on what prey is likely to be ingested by foraging whales
Behavioural and tagging studies to determine feeding rates (hours/days/year) of whales Comparative studies of cetaceans in non-krill dominated systems, such as the NE Atlantic and Barents Sea	How many days per day/season/year do different species spent intensively feeding?
Research to improve the data resolution at different stages within a feeding season	Furthers insights into feeding rates and feeding efficiency across species
Comparative and behavioural studies on feeding success of seabirds with/without cetacean presence	Furthers understanding of the importance of cetaceans in enhancing foraging success in other seabirds
Examine how diversity among individual whales within a single population can drive function at the ecosystem scale	Furthers understanding ecosystem function diversity and variation between individual whales

Table 4: Draft template for an overview summary of cetacean ecosystem functions and their relevance to geographic areas and temporal/spatial development, including rating of relevance: H=High, M=Medium, L=Low, U=Unknown.

(This table is to be completed at the second workshop)

	General description	**Temporal change in general (Pre-whaling and current)**	**Spatial difference in general**	**Southern Ocean**	**North Atlantic**	**North Pacific**	**South Pacific?**	**Barents Sea?**	**Alaska?**	**Tropics ?**
As predators	Consumption effects	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L
As prey	Consumptive effects	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L
Whale falls	Nutrient and energy delivery (e.g., carbon supply); modeling of whale-fall habitat abundance in different regions	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L
Cetacean strandings	Energy and nutrients	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L
Nutrient cycling	Productivity, growth & health	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L

Whale pump	Nutrient transport (vertical)	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L
Whale conveyor belt	Nutrient translocation (horizontal)	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L
Carbon sequestration	Taking Carbon out of the system	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L
Benthic-pelagic coupling		H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L
Bubble nets	Mixing water with consequences for nutrient cycling	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L	H/M/ L

ANNEX D

Glossary

During workshop discussions, several terms related to cetacean ecosystem functioning were used. For the purpose of this workshop, these terms are defined as follows.

Term	**Definition**
Blue Carbon	The carbon naturally captured, stored, and sequestered in coastal and marine ecosystems.
Carbon Capture or Carbon Fixation	The process through which photosynthetic organisms take up dissolved inorganic carbon and convert it to organic carbon.
Carbon Cycle	The flow of carbon in various forms, such as carbon dioxide (CO2), carbon in biomass, and carbon dissolved in the ocean as carbonate and bicarbonate, through the atmosphere, hydrosphere, biosphere, and lithosphere.
Carbon Sequestration	The long-term (> 100 years) storage of carbon in plants, soils, geologic formations, and the ocean.
Ecological Function	The role of organisms within an ecological system. Such functions can include processes that sustain an ecosystem and provide services to humans or other organisms.
Ecosystem Function	The physical, chemical, and biological processes that transform and translocate energy or materials in an ecosystem.
Ecosystem Services	The direct and indirect benefits that people obtain from nature—--from food to climate regulation to nonuse values such as existence values.
Whale Fall	A sunken carcass of a whale at the seafloor. In the deep sea, whale falls may provide oases of food availability for scavengers, and create specialized habitats for a diversity of species dependent on organic enrichment, or on sulfide emitted during anaerobic decomposition of the whale bones and soft tissues.
Whale Pump	The process by which whales carry nutrients from the depths where they feed back to the surface via their feces. (The same concept can be applied to other cetaceans and large marine vertebrates who feed at depth and defecate in surface waters).

ANNEX E

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