SC/68C/EM/05

Sub-committees/working group name: EM

Ecological Roles and Impacts of Large Cetaceans in Marine Ecosystems

Joe Roman, Jeremy Kiszka, Heidi Pearson, Matt Savoca and Craig Smith

INTERNATIONAL
WHALING COMMISSION
75 years of science and stewardship 1946 – 2021

Ecological Roles and Impacts of Large Cetaceans in Marine Ecosystems

Credit: Dave Hurwitz / info@boatcompany.co.za

Prepared by Joe Roman, Jeremy Kiszka, Heidi Pearson, Matt Savoca, and Craig Smith

Working draft: Confidential
Do not distribute

Abstract

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. In this report we discuss the state of the science for the consumptive and nonconsumptive effects of whales, including their role as predators, prey, and influence on behavior-mediated impacts. Whale carcasses also provide nutrients and deep-sea habitat for hundreds of species, including more than 100 endemic animals, several of which rely on chemosynthetic bacteria. 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 and during long-distance migrations from high-latitude foraging areas to winter grounds, where several species calve and breed. Whales can also make physical changes in the oceans, through benthic and bubble-net feeding and swimming through the pycnocline. Population declines from commercial whaling likely affected all of these processes, and threats, from climate change and increased industrialization of the ocean, are expected to have an impact in individual whales, whale populations, and their ecological roles.

1. Background

In 2016, the International Whaling Commission (IWC) adopted a Resolution on Cetaceans and Their Contributions to Ecosystem Functioning (IWC/66/15 Rev3), introduced by the governments of Chile, Argentina, Brazil, Costa Rica, Dominican Republic, Mexico, and Uruguay. The resolution recognizes that cetaceans make significant contributions to ecosystem functioning and asked the Scientific Committee to examine the existing research on this contribution, develop a gap analysis regarding research, and to make a plan for remaining research needs. This document provides a review of the current knowledge of the ecosystem functioning of cetaceans with the aim of providing background for scientists and policymakers who will meet in 2021 to discuss these mechanisms, identify gaps in our understanding of these processes, and develop a research plan to enhance our understanding of the ecological function and ecosystem services provided by cetaceans.

Ecological Function

In recent years, there has been increased attention on the ecological roles of animals in aquatic and terrestrial systems. New research on the transport of resource subsidies by animals (Subalusky and Post 2019); the role of top-down-forcing in ecosystems and the impacts of trophic cascades on processes such as the dynamics of disease, wildfire, carbon sequestration, and biogeochemical cycles (Estes J. A. et al. 2011); and the emerging concept of zoogeochemistry, which explores the effects of animals on carbon and other biogeochemical cycles (Schmitz et al. 2018); along with advances in remote sensing and other technologies have greatly improved our understanding of animal ecology. As a consequence of these new studies and methodologies, the role of large-bodied predators in the functioning, resilience, and stability of marine and terrestrial ecosystems have become better understood and more widely researched (Heithaus et al. 2008, Ripple et al. 2014, Somaweera et al. 2020).

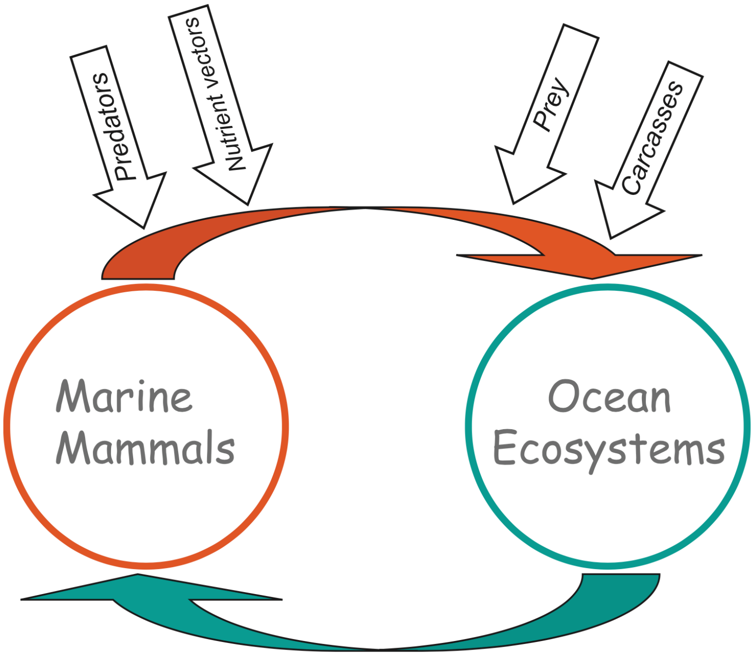


Figure 1. Four ecological pathways between marine mammals and their ecosystems, from Roman and Estes (2017). This image does not include physical processes, such as benthic and bubble-net feeding.

In this review, we focus on baleen and sperm whales. With their large size, abundance, and global migrations, great whales were dominant predators in the ocean, accounting for approximately 85% of the total marine mammal biomass before commercial whaling. Although studies of the ecological effects of great whales and other marine mammals often focus on predation, the return of these animals has uncovered potentially strong impacts on marine ecosystems, including the vertical and horizontal movement of nutrients and provision of detrital sources of energy and habitat in the deep sea (Fig. 1, Roman and Estes 2017). The potential influence of cetaceans on marine ecosystems is of interest because of the antiquity of cetacean evolution, the diversity of foraging modes employed by whales, and because cetaceans comprise far more consumer biomass than other marine mammal groups (Estes J.A. et al. 2006).

Cetaceans have a number of emergent properties that vary from the traits of other megafauna (Table 1). Their enormous size, small surface-area-to-volume ratio, high calcification, and high lipid content, for example, allows great-whale skeletons to provide chemo-autotrophically based habitats for decades at the deep-sea floor. This has profoundly influenced the functional roles of whales in providing habitat diversity, allowing evolution of novel species, and providing habitat and steppingstones for vent and seep species.

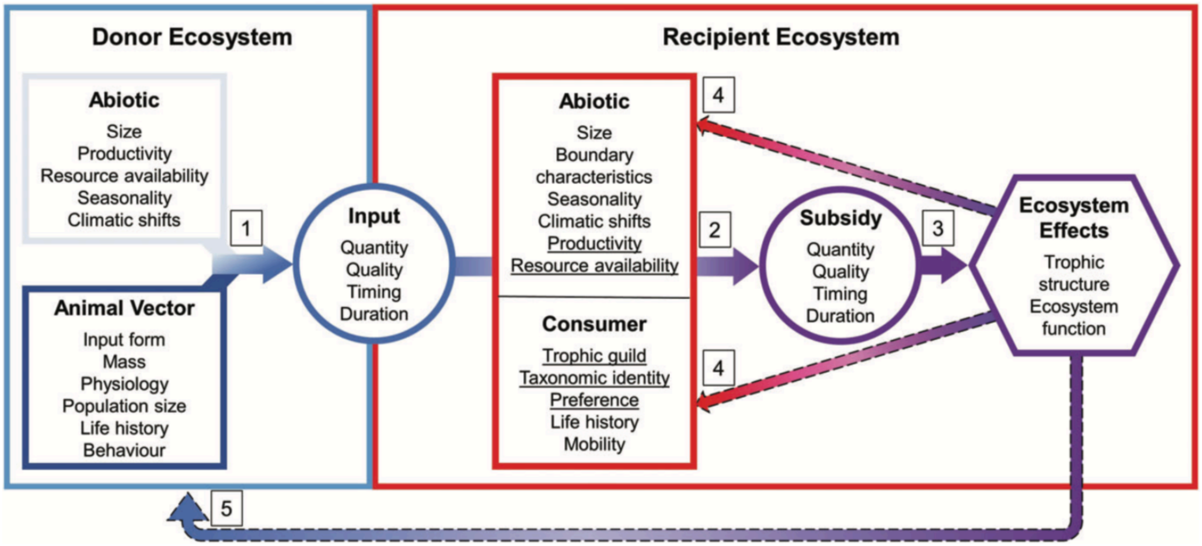


Fig. 2. Conceptual framework illustrating the influence of animal resource subsidies on ecosystem dynamics (from Subalusky and Post 2019). Animal vectors, including cetaceans and other marine mammals, can move resources from a donor ecosystem, such as a high-latitude foraging ground, to a recipient system such as a resting area or calving ground. The animal vector moves resources from one system to another, and the quality, quantity, timing, and duration of the resource input influences the subsidies provided to the recipient system.

Subalusky and Post (2019) note a few of the differences between ecosystem resource transfers that occur through passive processes, such as wind, atmospheric deposition, and riverine flow, and transfer of resources by animals (Fig. 2):

1. Animal resources are often rich in limiting nutrients.
2. Animals can move resources either more quickly along or against naturally established gradients.
3. Animals tend to aggregate in space and time, which can lead to “hot spots” and “hot moments” of biogeochemical cycling.

In the case of cetaceans, all three of these characteristics apply:

1. Whale feces, urine, and carcasses are rich in limiting nutrients such as nitrogen, iron, and phosphorous.
2. By feeding at depth and excreting at the surface, whales can move resources against typical ocean gradients such as the biological pump. They can also move enormous resources from the surface to the deep sea in the form of carcasses and from high-latitude, high-nutrient ecosystems to low-latitude oligotrophic systems.
3. Many feeding and breeding whales aggregate in hot spots and hot moments. Gray, humpback, and right whales, for example, forage in high-nutrient areas and populations of several species winter in relatively restricted areas with distinct time periods that are often associated with calving or breeding.

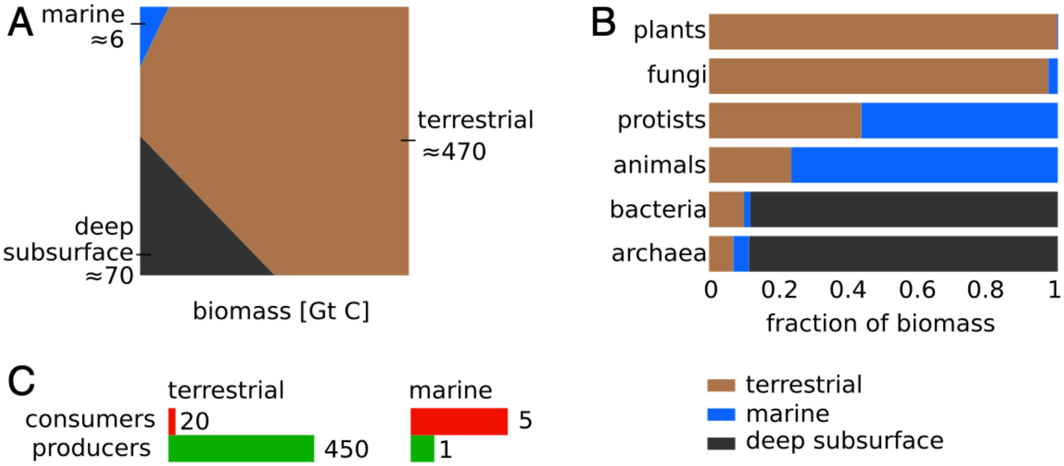


Fig. 3. Although marine biomass is smaller than terrestrial biomass (A), animals have a higher fraction of biomass in the ocean than on land (B). Plants are mainly terrestrial, animals are mainly marine, and bacteria and archaea dominant in the deep subsurface. Unlike terrestrial systems, there are more consumers than producers in marine systems; bars represent gigatons of carbon (C) (from Bar-On et al. 2018).

In addition to these ecological and organismic traits, it is important to note that although many of the studies of the role of animals in ecosystems have been conducted on land and in shallow coastal systems, marine biomass is dominated by animals, including vertebrates and invertebrates, and the amount of consumer biomass, as measured in carbon, far outweighs the biomass of producers—in steep contrast to terrestrial systems (Fig. 3, Bar-On et al. 2018). In this paper, we examine the effects of the largest animals in the ocean on marine ecosystems.

Table 1. Summary of selected traits of cetaceans and their related ecosystem functions and services. Several of these traits are adapted from Tavares et al. 2019.

Trait	**Description**	**Functions**	**Services**	**Example**	**Reference**
Body size and soft-tissue lipid content	Mass, % 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 habitats at seafloor, nutrient cycling, carbon sequestration	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)
Bone lipid content	Percent and total mass of lipids in skeleton	Provision of persistent organic or sulfide-rich habitat at seafloor	Promotion of habitat heterogeneity (including organic-rich and chemoautotrophic habitats), biodiversity at the deep-sea floor, evolution of novel whale-fall species, ecological and evolutionary	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)

			steppingstones for vent and seep faunas		
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)
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)
Epidermal molt	Killer whales and other migratory species travel thousands of kilometers each year for skin molt migration	Routine skin maintenance, feeding/molting hypothesis	Nutrient transport, microbial connectivity	Southern Hemisphere killer whales and other whales that migrate from polar latitudes to tropical waters	(Pitman et al. 2019)
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)
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)
Migration	Distance traveled per day, month, or year. Populations show range of movements from resident species (Gulf of Mexico whale) to highly migratory (North Pacific gray whales, many humpback whale populations)	Nutrient transport, dispersal of microbes and other organisms, deep-sea whale-fall communities	Resource subsidies from high nutrient foraging areas to more oligotraphic winter or calving areas, provision of whale-fall communites along migratory pathways.	Nutrient dispersion, enhanced productivity, whale fall communities	(Doughty et al. 2016, Roman et al. 2014)
Mortality rate	Number of deaths per unit of time	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 steppingstones for	(Smith et al., 2014, 2015, 2017, 2019, Taylor et al. 2007)

				hydrothermal vent and cold seep animals; nutrient supply for condors, polar bears, and sharks	
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), biodiversity at the deep-sea floor, evolution of novel whale-fall species, ecological and evolutionary steppingstones 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)

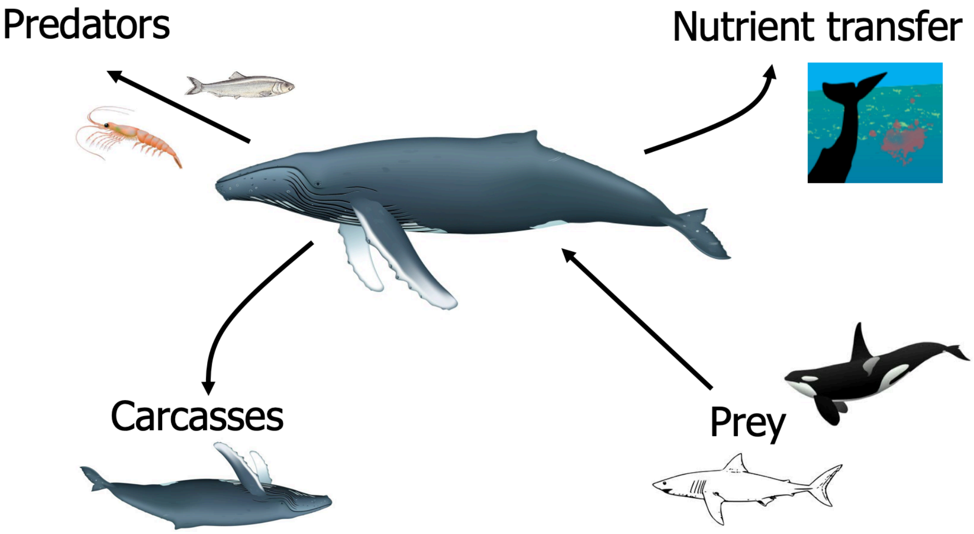


Fig 4. The functional role of baleen whales in marine ecosystems include direct predation and indirect food-web interactions, whales as vectors of nutrient and material flux, whales as prey, and whale falls or carcasses.

2. Cetaceans as Consumers: Consumptive Effects

This section is currently in review and has been removed from the report. New information on the consumptive effects of large cetaceans will be available soon.

3. Whales as Prey: Consumptive Effects

The large size, abundance, and high energy density of great whales make them a valuable nutritional resource for humans and a few other animals, such as sharks and killer whales. Killer whales have been observed attacking and consuming great whales, which were possibly an important prey resource before commercial whaling (Pitman et al. 2001). Recent observations of humpbacks mobbing mammal-eating killer whales indicate that large rorquals can defend their calves and other marine mammals against potential predators (Pitman et al. 2017).

One leading hypothesis for the seasonal migration of large whales from high to low latitude waters is to reduce the risk of predation of calves to killer whales. Species that are considered to have fight strategies, such as humpback, gray, and right whales, tend to migrate to shallow coastal areas. Fast-moving flight species, such as fin and blue whales have streamlined bodies and calve in pelagic habitats, where they can undertake prolonged escape sprints (Ford and Reeves 2008). Such tendencies have impacts on the behavior and distribution of many baleen whales (see also Section 5).

One highly charged debate involves the extent to which orcas feed on baleen whales and the consequences of industrial whaling to ocean ecosystems. Approximately 10% of the estimated 50,000 killer whales worldwide appear to feed exclusively on marine mammals (Forney and

Wade 2006, Reeves et al. 2006). The decline of great whale populations during industrial whaling, and the sudden elimination of harvested carcasses as a food resource for killer whales at the end of the industrial-whaling era, might have caused transient orcas to expand their diets to smaller marine mammals, resulting in some population declines (Springer et al. 2003). After the commercial overexploitation of great whales, killer whales either declined in abundance or expanded their diet to include other prey species (Estes JA et al. 2009). In the North Pacific Ocean, killer whales might have started to feed more extensively on other marine mammals, such as harbor seals, Steller sea lions, and sea otters, with an impact on their population size (Springer et al. 2008, Springer et al. 2003). The loss of sea otters released herbivorous sea urchins—the otter's preferred prey—from limitation by predation, causing an increase in their rate of herbivory and a decline of coastal kelp forests (Estes JA et al. 1998). Based on evidence from the Aleutian Islands and elsewhere in the North Pacific, kelp forest declines led to reductions in primary productivity, coastal fish populations, and marine sequestration of carbon (Markell 2011, Reisewitz et al. 2006, Wilmers et al. 2012). The follow-on effects of pinniped declines have not been as well studied, though there is some indication that there was an ecosystem shift from crustacean to finfish dominance in some systems (Estes JA et al. 2013).

Although there are numerous records of killer whales attacking great whales and their calves, and living whales commonly have rake marks on their flukes from failed attacks, the importance of consumer-prey interactions for these species remains contentious. Some of the leading challenges include: 1. killer whales only rarely attack or eat great whales, 2. the multispecies collapse was not sequential, 3. declines may have been caused by nutritional depletion, 4. the timing of the collapses is not consistent with the timing of whale depletions, 5. the geographical patterns of the key species are not consistent with the spatial extent of the multispecies collapses.

For criticism of the sequential-collapse hypothesis, see especially DeMaster et al. (2006), Mizroch and Rice (2006), Trites et al. (2007), and Wade et al. (2007). DeMaster et al. hypothesized that the declines in pinniped populations are perhaps best understood by considering multiple factors including bottom–up forcing, such as nutritional stress in the western Steller sea lion population, and top–down forcing, including predation by killer whales, mortality from commercial fishing, and directed harvests. Their second hypothesis is a modification of the top–down forcing mechanism, suggesting that killer whale predation on one or more of the pinniped populations and the sea otter population was mediated via the recovery of the eastern North Pacific population of the gray whale. Wade et al. contended that the data do not show sequential changes in whale, pinniped, and sea otter populations and that the spatial patterns were complex and inconsistent with the prey-switching patterns put forward by Springer and colleagues. Springer et al. addressed several of these issues in an article in *Marine Mammal Science* in 2008. Although the debate in the peer-reviewed literature has calmed, opinions remain divided on this hypothesis.

4. Physical Ecosystem Engineering

Foraging whales can influence the ocean's local physical environment through processes such as benthic and bubble-net feeding and swimming through the pycnocline (Roman et al. 2014). The plowing of meter-wide gouges in the Bering Sea floor by gray whales feeding on amphipods can affect benthic topography for centuries (Nelson and Johnson 1987). This bottom-feeding behavior also moves substantial amounts of sediment and nutrients into the water column, enhancing nutrient recycling and bringing some benthic crustaceans to the ocean surface, an activity that provides food for surface-feeding seabirds (Alter S. E. et al. 2007).

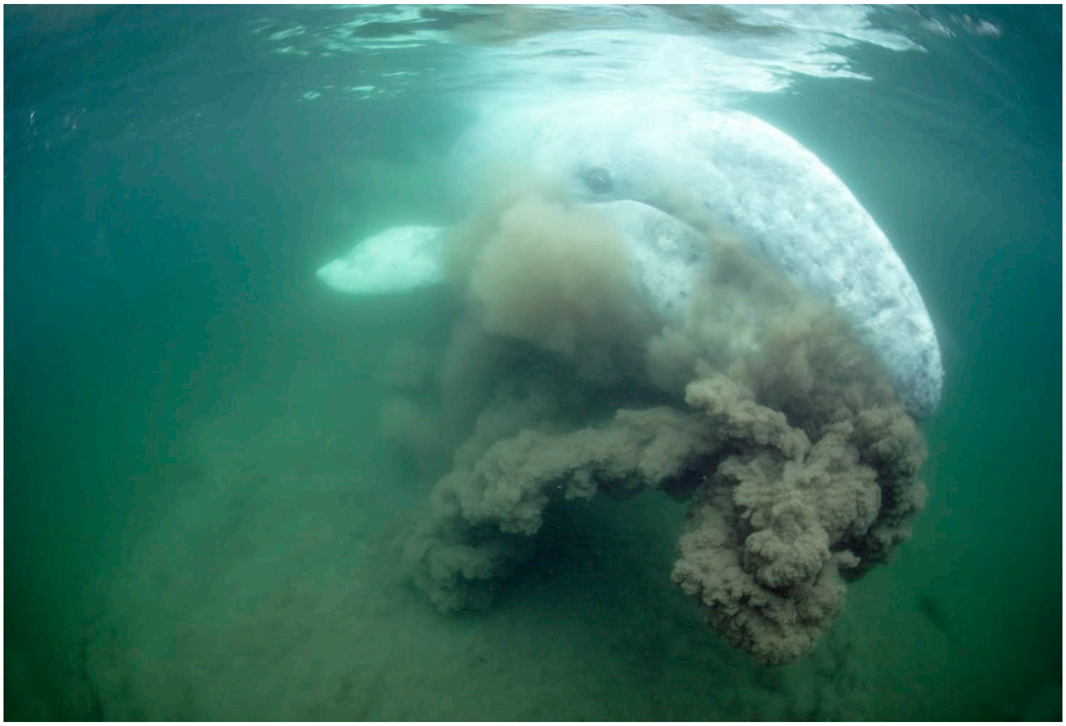


Fig. 5. Gray whale feeding on benthic invertebrates (photo courtesy of F. Nicklin).

Gray whales create elliptical pits in bottom sediments during suction feeding, typically about 10 cm deep and up to $5m^2$ in area (Oliver et al. 1984). These elongated depressions usually appear in short chains or in parallel splayed arrays (Jones et al. 2012, Oliver and Slattery 1985). These feeding pits can draw 2–30 times more scavengers and other invertebrates compared to adjacent sediments (Trites 2018). When the whales drive amphipods and other benthic prey to the surface, they can be are consumed by seabirds and diving ducks (see Seabird Facilitation in section 6 below).

Fig. 6. Humpback whale bubble net feeding is a form of ecological engineering that is short lived. Bubble nets formed beneath the thermocline are likely to increase diffusivity between the photic and aphotic zone. Note also the attraction of seabirds to the feeding whales. (Photo pending.)

Humpback whales also intentionally disturb the sand and shell-hash (a mix of mud, sand, and broken shells) sea bottom to flush sand-lance prey from their burrows (Hain *et al.* 1995). North Atlantic right whales in the Bay of Fundy are frequently observed with mud on their heads and bodies while feeding, indicating that they play a role in bioturbation, a function that has come close to vanishing with the near extinction of these whales (Roman et al. 2016, Hamilton and Kraus 2019).

Whereas the effects of disturbance on benthic areas can be relatively straightforward to detect and monitor, determining the influence of whales in the pelagic system, especially in regard to biogenic mixing and the pycnocline, has been more elusive. Humpback whales create spiral flow features using underwater exhalations to concentrate their prey; these “bubble nets” may be the most ephemeral of engineered physical constructs (Hastings *et al.* 2007).

Diving and surfacing whales can enhance the upward transport of nutrient-rich deep water as they pass through density gradients during feeding sessions (Dewar *et al.* 2006). In a preprint, Lavery et al. (2012) estimated that sperm whales off Hawaii increased diapycnal diffusivity by 10^{-6} m^2 $s^{-1,}$ which results in the flux of 10^5 kg of nitrogen into the euphotic zone each year. Although a relatively modest amount of nitrogen, sperm whale foraging occurs throughout the day and for much of the year, so this mixing could provide the nutrients necessary to enable phytoplankton growth and survival in the absence of other seasonal and daily inputs.

5. Behavioral drivers of the ecological function of cetaceans

Research on the effects of cetaceans on marine ecosystems has largely focused on their role as predators (Estes JA et al. 1998, Gerber et al. 2009, Morissette et al. 2010) and more recently through their roles in the translocation and recycling of nutrients within and across habitats (see Roman et al. 2014 for a review). Yet the ecological role of organisms in communities also include a number of nonfeeding, behavior-mediated mechanisms, such as the transmission of risk effects and behavioral facilitation (Heithaus et al. 2008, Kiszka JJ et al. 2015, Wirsing et al. 2008). Here we provide an overview of several behavioral drivers that help shape foraging tactics, habitat use, and food selection. We also discuss how they could affect the ecological roles of cetaceans in marine ecosystems.

Risk effects

Although nonconsumptive effects are known to have a strong impact on community dynamics, very few studies have investigated how predation risk initiated and experienced by cetaceans affect community dynamics (Heithaus et al. 2008, Wirsing et al. 2008, Kiszka et al. 2015). A large number of species, both in terrestrial and aquatic ecosystems (Lima and Dill 1990), invest in anti-predator behaviors to reduce the probability of being killed by a predator, even when predator-inflicted mortalities are rare (Creel and Christianson 2008, Heithaus et al. 2008). Risk effects can result in the loss of foraging and reproductive opportunities and affect individual fitness and population dynamics (Creel and Christianson 2008, Lima and Dill 1990, Mukherjee et al. 2014). Since risk effects can potentially be experienced by most individuals within a population relative to direct predation, their impact on prey species could exceed the impact of direct predation (Creel 2011, Schmitz et al. 2010, Werner and Peacor 2003). Such risk effects can have major impacts on populations and communities and in turn they can affect the roles and importance of species in ecosystems.

Anti-predator responses to predation risk have been described in a number of cetacean species (both large and small), ranging from acute (short-term) reactions (e.g., flight responses; Ford and Reeves 2008, Jefferson et al. 1991) to shifts in habitat use (Heithaus and Dill 2002, Norris et al. 1994), diving behavior (Allen et al. 2014, de Soto et al. 2020), and group dynamics, including group size (Gygax 2002) and the formation of mixed-species groups to increase vigilance (Kiszka J. J. et al. 2011, Perrin et al. 1973). Shifts in distribution and habitat use have a range of spatial and temporal scales, from diel to seasonal. Killer whales (*Orcinus orca*) might have dramatically affected the evolution and behavior of a number of cetacean species, particularly large whales (Corkeron and Connor 1999). Humpback (*Megaptera novaeangliae*) and gray whales (*Eschrichtius robustus*) undertake, at a substantial energetic cost, one of the longest mammalian migrations between nutrient-rich high latitudes to oligotrophic tropical and subtropical waters (Dawbin 1966, Swartz et al. 2006, Whitehead and Moore 1982). Some authors have suggested that the high predation risk from killer whales in high latitudes may have driven these species to embark in such migrations (Clapham 2017, Corkeron and Connor 1999, Pitman et al. 2019). Costly movements and trade-offs to reduce predation risk have been described in other cetacean species, particularly delphinids (e.g., Srinivasan et al. 2010). Since they are mostly mesopredators, many small cetacean species are at risk from killer whales and a range of other predators (large delphinids, sharks), and can adopt a range of tactics to reduce risk (see Heithaus 2001 for a review). Insular spinner (*Stenella longirostris*) and Dusky dolphins (*Lagenorhynchus obscurus*) undertake diel movements between their offshore and productive foraging habitats to their shallow and safer inshore resting grounds to reduce predation (Heithaus 2001, Norris and Dohl 1980, Srinivasan and Markowitz 2010).

Fig. 7. Right whale surface active group in the Bay of Fundy. Such groups can persist for hours, with frequent observations of feces at the surface (courtesy New England Aquarium).

Perceived risk from human activities

The Risk Disturbance Hypothesis suggests that animals should respond to human disturbance in a way that is similar to their response to natural predators (Frid and Dill 2002). Due to their long lifespan, cetaceans are expected to invest in behaviors that will reduce their exposure to disturbance. Anthropogenic noise and vessel traffic, for example, can affect the behavior of cetaceans, their movements, behavioral budgets, habitat use, and relative abundance (Bejder et al. 2006, Pirotta et al. 2015, Senigaglia et al. 2016, Williams et al. 2006). Although population-level consequences of disturbance are increasingly understood in a number of cetacean species, nothing is known on how behavioral disruptions might affect the ecological roles and importance of cetaceans.

Foraging facilitation

Cetaceans are effective marine predators known to form multispecies aggregations with a range of other species, primarily epipelagic predators such as seabirds, sharks, and large teleosts such as tunas (Veit and Harrison 2017). The foraging of seabirds in close proximity to cetaceans is one of the most commonly documented forms of behavioral, or foraging, facilitation (Kiszka et al. 2015), and only seabirds seem to benefit from these associations. This foraging been observed in a variety of ecosystems, from productive polar regions to the oligotrophic waters of tropical oceans (Evans 1982, Pitman and Balance 1992, Veit and Harrison 2017). In most if not all associations, cetaceans drive prey to the surface, making it available to species that have limited diving or sensory abilities and improving their foraging success (Grebmeier and Harrison 1992). Although some species, particularly Procellariformes in oligotrophic waters, are thought to be highly dependent on cetaceans for foraging, we have a limited understanding of the importance of cetaceans in enhancing foraging success in other seabirds.

Behavior as a driver of nutrient movements

Cetaceans may be important in mediating the translocation and recycling of nutrients within and across habitats and ecosystems (Kanwisher and Ridgway 1983, Roman et al. 2014, Schmitz et al. 2010). Predation risk from killer whales and large sharks can have a major influence on the movements of cetaceans, which can in turn affect the cetacean-mediated flows of nutrients, both horizontally and vertically. High predation risk from killer whales in high latitudes may have shaped migratory patterns of several baleen whale species (Corkeron and Connor 1999), which could play a major role in translocation nutrients from nutrient-rich foraging grounds to tropical and subtropical oligotrophic waters (Roman et al. 2014, Roman et al. in prep). Similarly, diel movements of small cetaceans, such as spinner dolphins, dusky dolphins, and others, between habitats and microhabitats might have major consequences on the deposition of nutrients in recipient habitats in inshore waters (coral reefs, seagrass beds and other coastal ecosystems (Heithaus and Dill 2002).

Behavior can potentially have a strong effect on the ecological roles and importance of cetaceans. North Atlantic right whales, for example, are frequently observed in surface active groups on their feeding grounds (Fig. 7). These groups can persist for hours, with large amounts of high-nutrient feces observed in the waters surrounding the focal female and males (Roman et al. 2016). The importance of cetaceans as behavioral facilitators is poorly understood, particularly for a number of other predators that might greatly depend on them.

As human disturbances are increasing across a range of marine ecosystems, changes in cetacean behaviors could also alter the function these species play. We encourage the scientific community to incorporate behavior as a potential driver of the ecological function of cetaceans in marine ecosystems.

Individual behavior

Cetaceans, like many other animal species, exhibit a wide range of behaviors, in feeding, migrating, and other aspects of their lives. One potentially fruitful area of study is to examine how diversity among individual whales within a single population can drive function at the ecosystem scale. Allgeier et al. (2020) have shown that nutrient supply from individual fish differs from the population average more than 80% of the time; accounting for this individual variation nearly doubles estimates of nutrients supplied to the ecosystem. Such trait variation among individuals, where individual dominance in ecological processes is akin to “superspreaders” in epidemiology (Eames and Keeling 2003), has largely been overlooked in traditional approaches to conservation management and ecosystem function (Allgeier et al. 2020). To our knowledge, such variation has not been examined in individual whales in the context of ecosystem function, but it is likely to be a promising if challenging aspect in ecosystem functioning. One advantage that whale biologists have in this regard is that for many species individual whales are tracked via photo identification and other methods. A disadvantage is that except for a few species, such as bottlenose dolphins, captive or exclusion studies are not practical for cetaceans.

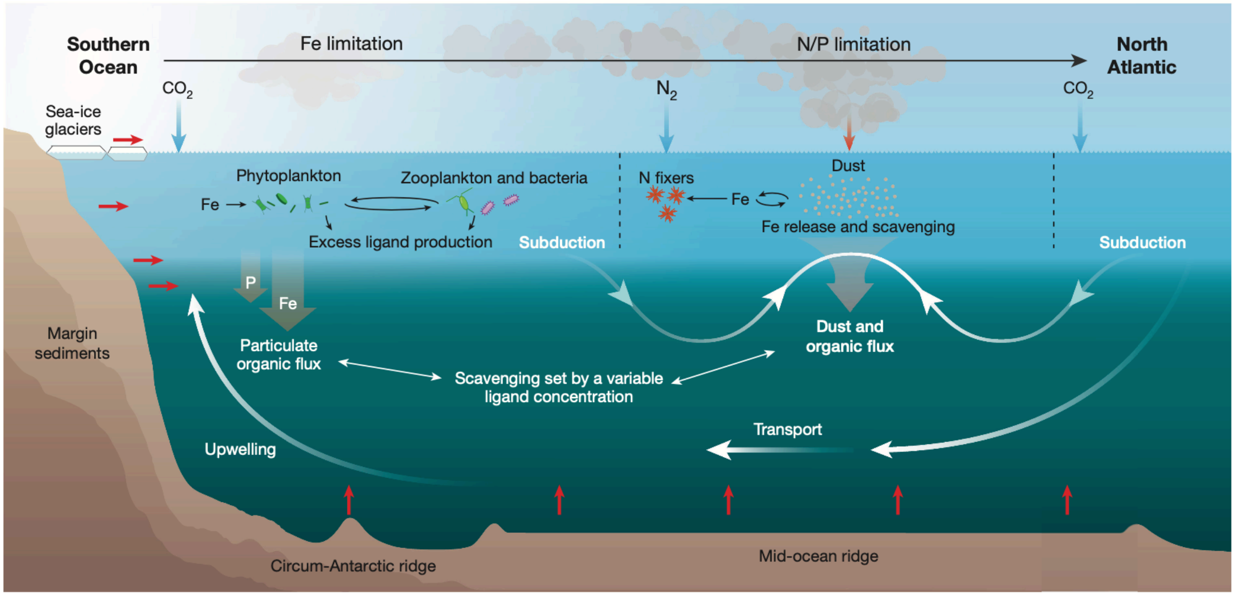


Fig. 8. Major processes in the ocean iron and nitrogen cycles. Iron is the limiting nutrient in the Southern Hemisphere. In the North Atlantic and parts of the North Pacific, nitrogen and phosphorous tend to be the limiting agents (image from Tagliabue et al. 2017). Whale feces have high concentrations of all three elements.

6. Cetaceans as Vectors of Nutrients and Sources of Nutrients

Whales facilitate the transfer of nutrients by nutrient recycling in the surface layer, releasing fecal plumes and urine near the ocean surface after feeding at depth, and by moving them from productive, high-latitude feeding areas to less productive low-latitude calving areas (Roman et al., 2014). They can also contribute mechanical energy to the ocean when they dive to feed, mixing that can be especially important in stratified conditions or when there is little wind (Dewar et al. 2006).

Whale Pump

Cetaceans primarily feed at depth during short dives followed by extended surface periods when defecation can occur. Evidence for this upward movement of nutrients includes several lines of evidence, as reviewed by Roman and McCarthy (2010), including attachment to the surface for respiration, reduced metabolism at depth, physiological response to hydrostatic pressure, a decrease in glomular filtration rate and urine flow during forced diving studies, and observations of buoyant fecal plumes at the surface (Katona and Whitehead 1988, Kooyman et al. 1981, Ortiz 2001). As early as 1983, Kanwisher and Ridgway (1983) noted that cetaceans could play an analogous role to upwelling by lifting nutrients from deep waters and releasing fecal material “that tends to disperse rather than sink when it is released.” Whale foraging dives are typically characterized by rapid descents and ascents to reduce transit time to prey aggregations (Croll et al. 2001), and high metabolic rates in gray seals while motionless at the surface support the idea that marine mammals process food during extended surface intervals following deep-water foraging (Sparling et al. 2007). Even if defecation and excretion occurred randomly, it would on average occur higher in the water column than where these animals feed, since they are unlikely to dive deeper than foraging efforts require.

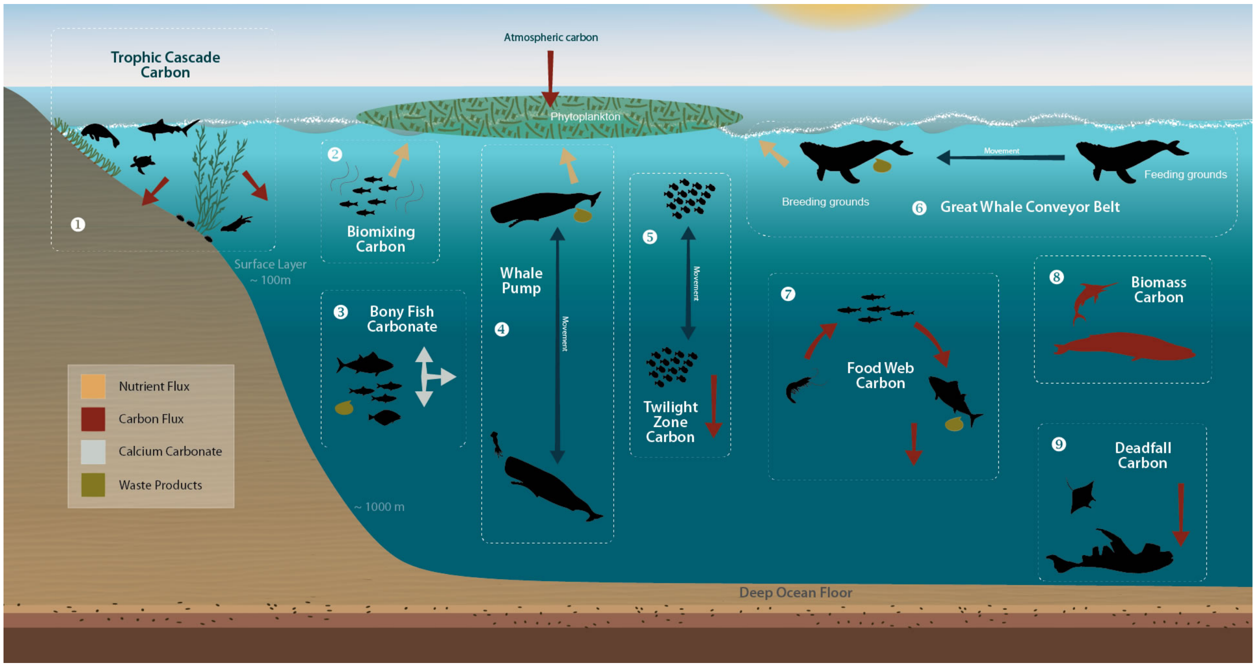


Fig 9. Like other marine organisms, whales can play an important role in the nutrient and carbon cycle in coastal and oceanic ecosystems (courtesy GRID-Arendal 2018).

Even in cases where whales feed nearer to the surface, they can play a crucial part in biogeochemical cycling processes through the consumption of nutrient-rich krill, or other zooplankton, and subsequent defecation. Ratnarajah et al. (2014) measured the concentration of iron, cadmium, manganese, cobalt, copper, zinc, phosphorus and carbon in baleen whale feces and muscle and krill tissue using mass spectrometry. Metal concentrations in krill tissue were between 20,000 and 4.8 million times higher than typical Southern Ocean seawater concentrations, and whale fecal matter was between 276,000 and 10 million times higher. They concluded that krill can act as a reservoir of essential trace elements in surface waters of the Southern Ocean, and whales can release these stored elements through feeding and defecation.

To date, field measurements and models have been conducted in the Southern Ocean, North Atlantic, and North Pacific for several nutrients found in whale feces, with a focus on iron, nitrogen, and phosphorous, three elements that are often limiting agents in the modern ocean (Fig. 8, Tagliabue et al. 2017). High concentrations of all of these elements have been found in whale feces (e.g., Lavery et al. 2010, Ratnarajah et al. 2014, Roman and McCarthy 2010, Roman et al. 2016). The influence on marine ecosystems will vary in space and time (see for example, Fig. 9), and this very patchiness is often central to the concept of ecosystem engineering (Hastings et al. 2007). Characteristics that are likely to enhance the effect of the whale pump include: aggregated feeding areas (hot spots), stratified water column, feeding below or along the thermocline, the retention of nutrients in a particular area, and limited temporal feeding (hot moments).

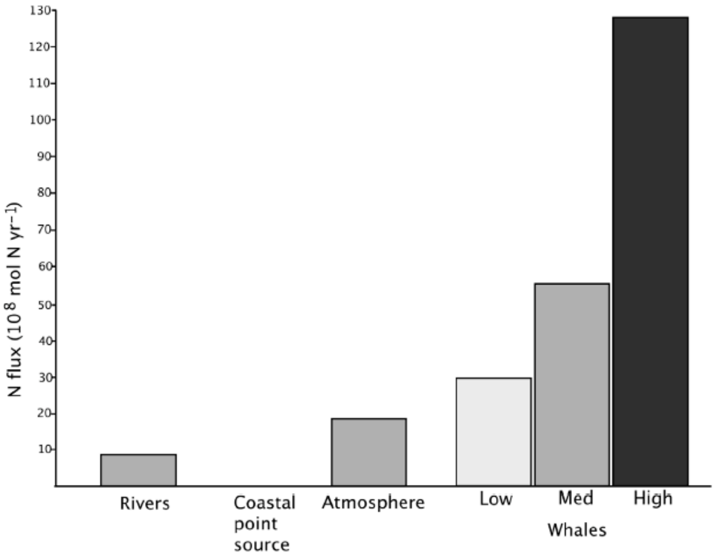


Fig. 10. The flux of nitrogen in the Gulf of Maine before commercial hunting. Historical numbers are based on a range of estimated for pre-exploitation estimates (see Roman and McCarthy 2010). Sources that are not expected to be influenced by anthropogenic change, such as offshore transport from Scotian Shelf water, are not included in this graph.

Nitrogen

To date, studies of the whale pump in the nitrogen cycle have largely been restricted to the Northern Hemisphere (e.g., Roman and McCarthy 2010, Roman et al. 2016, Rhodes-Reese et al. in prep). Analysis of NH^{4+} concentrations in fecal plumes of humpback whales on Stellwagen Bank in the Gulf of Maine, northwest Atlantic found elevated concentrations of 0.4 to 55.5 µmol kg^{-1}. Reference water samples in the area had concentrations below 0.1 µmol kg^{-1}, which is typical for stratified, nutrient-limited summer waters. Later samples collected from fin, sei and right whales all showed elevated levels of NH^{4+}, with right whales feeding on copepods showing the highest levels of NH^{4+}, up to 793 µmol kg^{-1}. In total, whales and seals may be responsible for replenishing 2.361^4 metric tons of N per year in the Gulf of Maine's euphotic zone, more than the input of all rivers combined. Historically, with more abundant whales and other air-breathing vertebrates, and fewer anthropogenic impacts, whales and other large animals likely played a large role in the nitrogen cycle in areas where they feed, breed, and along migratory pathways.

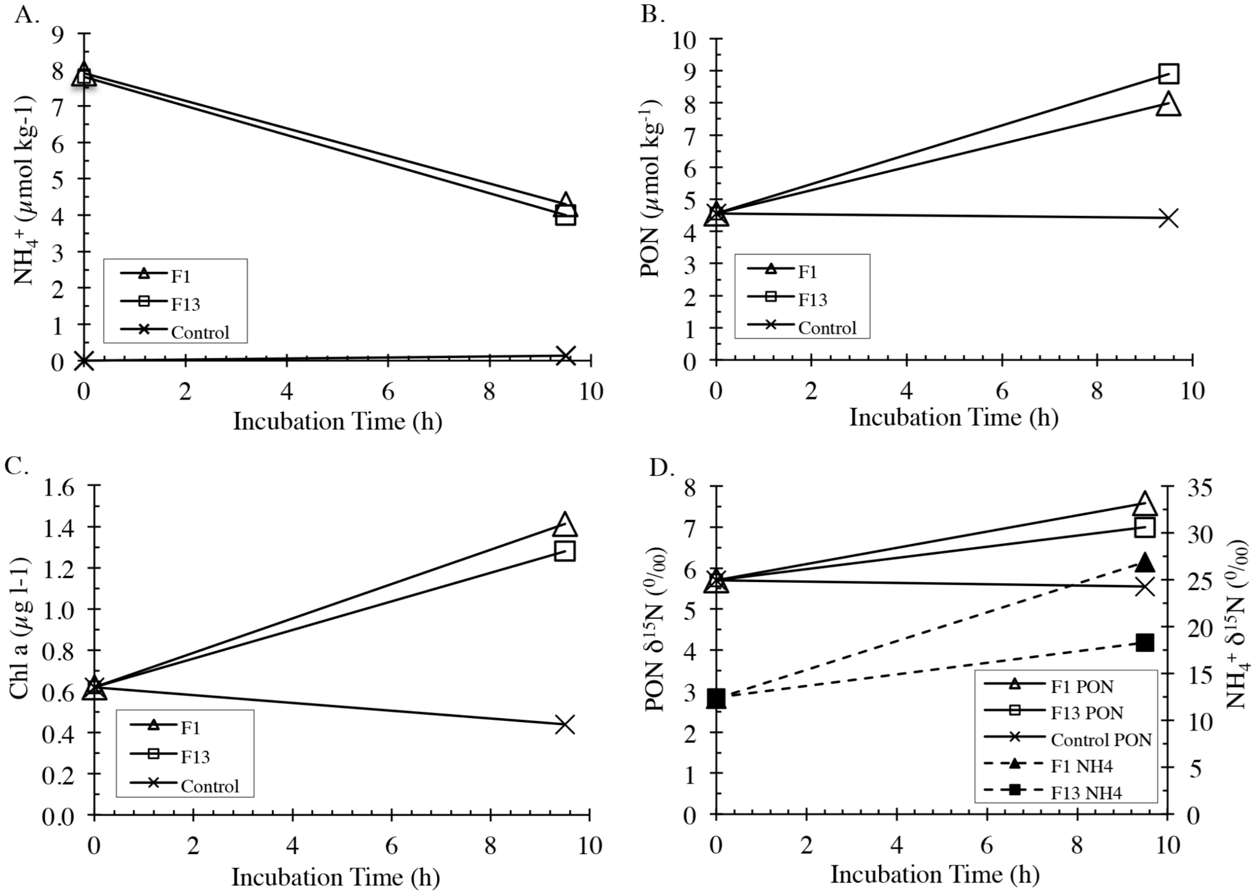


Fig. 11. Phytoplankton uptake experiment using natural $^{15}NH_4^+$ tracer obtained from right whale fecal matter suspension filtrates. Change in NH_4^+ concentration over incubation time (a); change in PON (b); change in Chl *a* (c), changes in $\delta^{15}N$ for NH_4^+ and PON (d). Preliminary evidence indicates that whale feces enhance primary productivity on a mesocosm scale. (From Roman et al. 2016).

Iron

Iron availability controls primary productivity in large areas of the Southern Ocean (Martin John H et al. 1990, Ratnarajah L. et al. 2018). Biomagnification within marine food webs can lead to high concentrations of iron in the diet of seabirds and marine mammals (Wing et al. 2014). Several studies have demonstrated that the feces of baleen and sperm whales have high concentrations of iron and other metals (Lavery et al. 2010, Nicol et al. 2010). Ratnarajah et al. (2014), for example, found metal concentrations in krill tissue that were between 20,000 and 4.8 million times higher than typical Southern Ocean seawater concentrations, whereas baleen whale fecal matter was between 276,000 and 10 million times higher.

Fig. 12. Blue whale fecal plume off the Australian coast (Ian Weise, pending permissions).

Sperm whales feed on deep-living prey and defecate at the surface, transporting allochthonous iron into the euphotic zone and raising the nutrient standing stock of surface waters (Lavery et al. 2010). This nutrient contribution can enhance new production, increasing net uptake of CO_2 from the atmosphere and carbon export to the deep ocean (Lavery et al. 2010), though the amount of carbon that is stored, sequestered, or released back into the surface waters remains an area of active debate. In contrast, whales that feed near the surface may not contribute to new production or carbon export to depth because they are not adding new iron to the surface waters (Lavery et al. 2014). These surface-feeding whales, however, can aid in the retention of autochthonous, or recycled, iron, promoting regenerated production. A model developed by Lavery et al. (2014) for the Southern Ocean suggests that blue whales defecate 3×10^6 kg of iron yr^{-1}, which could stimulate primary production that is equivalent to that required to support the prey consumed by these whales. This finding suggests that surplus-yield models should include iron defecation and presumable other nutrients: in the case of blue whales such a model indicated that they do not make marine resources unavailable to fisheries, but rather they can promote Southern Ocean productivity.

To date, there have been more than a dozen mesoscale iron fertilization experiments conducted worldwide, demonstrating phytoplankton iron limitation in the equatorial and subarctic Pacific Ocean and the Southern Ocean, with results that include phytoplankton blooms large enough to be seen from space (Tagliabue et al. 2017). And although the response of phytoplankton to dried feces has been conducted in lab studies (Ratnarajah et al. 2014), mesoscale scale responses to whale feces have not been performed to our knowledge. There is some indication that the iron in feces is more likely to be utilized through the microbial loop than through phytoplankton (Ratnarajah pers. comm), a potential pathway that requires further study.

At least one study has suggested that only at high values for parameters such as population estimates (past and present) and consumption rate would whales have an impact on the Southern Ocean (Ratnarajah Lavenia et al. 2016). Recent research (see section 2) suggests that consumption rates for baleen whales are likely much higher than were traditionally considered. We also have new estimates for the foraging and breeding areas of whales, which are much smaller than the entire Southern Ocean basin, which would indicate that whales likely play important roles in iron transport in particular hot spots and hot moments (Fig. 14).

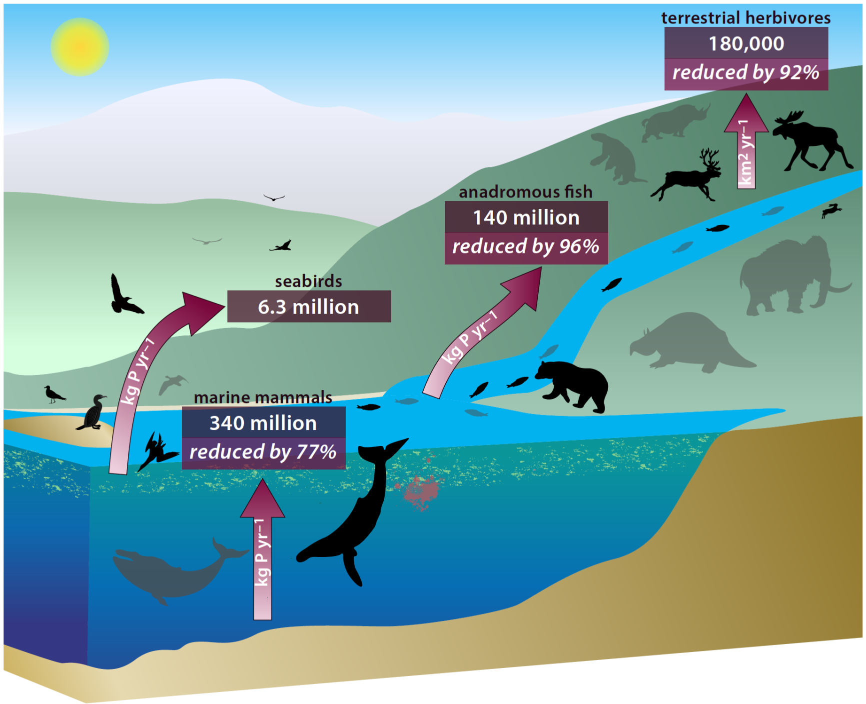


Fig. 13. Potential interlinked system of moving and recycling phosphorus. The diagram shows a potential route of nutrient transport of the planet in the past. Grey animals represent extinct or reduced population densities of animals. (From Doughty et al. 2016).

Phosphorous

To date, only limited field studies have been conducted on the phosphorus content of baleen whale feces (e.g., Roman et al. 2016). Initial studies show high levels of phosphorus in whale feces, consistent with examinations of other marine species, such as seabirds and pinnipeds. High release rates of PO_4^{3-}, much as with NH^{4+}, indicate that both nutrients are quickly released into seawater, and could readily be taken up by phytoplankton (see the very limited study in Fig. 11). A global model conducted by Doughty et al. (2016) examines the worldwide distribution of phosphorous by megafauna including cetaceans, seabirds, anadromous fish, scavengers and terrestrial herbivores (Fig. 13). Before commercial exploitation, deep-diving marine mammals transported about 340 million kg of phosphorous per year to surface waters, where it was presumably available to phytoplankton of coastal systems. Movements by seabirds and anadromous fish also provide important transfer of nutrients from the sea to land, totaling ~150 million kg of P per year in the past, a transfer that has declined to less than 4% of this value as a result of the decimation of seabird colonies and anadromous fish populations. The restoration of these historic pathways could help address concerns about exhausting phosphorus supplies, distributing phosphorous away from areas of excessive nutrient loading to areas that are currently nutrient limited (Doughty et al. 2016, Steffen et al. 2015).

Questions of Scale

In our view, one of the core uncertainties in examining whale nutrient ecology centers around scale. Are whales assessed on the level of global marine production paradigms, or is the relationship best studied through the concept of patch dynamics, which asserts that the concentration of a resource is an important aspect of its impact on a community? In their discussion of whale falls, Butman et al. (1996) suggested that patches are increasingly recognized in all ecosystems as a fundamental mechanism for enhancing biological diversity by enhancing the diversity of the physical environment. This may be true for whale nutrient transfer as well—with some areas of the ocean being influenced by whale nutrient transfer and others being relatively untouched. In what areas are whales likely to be important? A few characteristics likely include

1. high abundance of whales (present or historical)
2. nutrient-limited systems that are typically stratified
3. physical characteristics that enhance nutrient retention
4. seasonal changes in nutrient transfer

As Schmitz et al. (2018) noted for animals in general: “Considerations of animal movement will require highly resolved spatially explicit understanding of landscape features, including topography, climate, and the spatial arrangement of habitat patches and habitat connectivity within and among ecosystems across landscapes.” The same holds true for marine systems, which remain less well understood, with spatially explicit needs for understanding oceanographic features, retention, stratification, patchiness, and connectivity between marine ecosystems.

Of Forage Fish and Zooplankton

The consistency, buoyancy, and dispersion of fecal matter vary depending on diet. In the Southern Hemisphere, much of the work has been conducted on krill-eating whales, such as blue whales, and deep-diving species, such as sperm whales. In the Northern Hemisphere, fecal plumes have been collected from humpback, fin, and right whales. In the Gulf of Maine study area, right whale diets are comprised largely of *Calanus* copepods, and humpbacks and fin whales feed on forage fish or krill (Roman and McCarthy 2010). When whales are feeding on crustaceans, the feces is typically positively buoyant, brightly colored, clumped, and relatively easy to see and collect (Roman personal observations). When they feed on sand lance, herring, or other forage fish, it is typically darker in color, with some reflection form the scales, and is more neutrally buoyant suspended and dispersing just below the water surface.

Seabird Facilitation

In addition to the upward movement of nutrients through mechanical mixing and excretion, cetaceans can drive deep-dwelling prey species to the surface, where they become available to seabirds and other near-surface predators (Kiszka JJ et al. 2015). Seabird-cetacean associations have been observed in many species: including humpback, minke, fin, and pilot whales; common dolphins; porpoises; and other cetaceans with gannets, kittiwakes, and other seabirds that appear to be attracted to surface feeding (Evans 1982). Gray whales bring amphipods and other benthic prey to the surface, where they are consumed by fulmars, kittiwakes, and phalaropes (Grebmeier and Harrison 1992). Surf scoters (*Melanitta perspicillata*) and other diving ducks also likely benefit from the foraging activities of gray whales in the spring (Anderson and Lovvorn 2008).

Nutrient co-limitation

One intriguing new development that could be relevant for examining the nutrient ecology of fecal plumes was a 2017 study published on nutrient co-limitation in *Nature*. Browning et al. (2017) find extensive regions of the South Atlantic gyre in which the addition of nitrogen or iron individually resulted in no significant phytoplankton growth over 48 hours. Yet the addition of both nitrogen and iron increased concentrations of chlorophyll *a* by up to approximately 40-fold, leading to diatom proliferation and reduced community diversity. Their results suggest that nitrogen–iron co-limitation is pervasive in the ocean. Since both nutrients have been found at high levels in whale feces, comparable experiments in oligotrophic and productive feeding grounds could be valuable additions to the nutrient-vector literature for baleen whales. Their experimental design included nutrient-amendment experiments conducted with triplicate biological replicates, which allowed for statistical testing while remaining logistically feasible (Browning et al. 2017). Such experiments could be fruitful to examine the impacts of whale feces on ocean systems.

Migration: Great Whale Conveyor Belt

Animal body mass and mobility can influence the timing and duration of nutrient inputs, in addition to the scale of connection between donor and recipient systems (Subalusky and Post 2019). Whale mass, population size, and mobility are characteristics that make them of special interest in animal resource subsidy studies.

Most baleen whales are capital breeders, often feeding in high-latitude productive waters and breeding in lower latitude warmer waters. As the largest animals ever to have lived, with the longest migration of any mammal, they likely play an important role in nutrient subsidies (Roman et al. 2014). Although many whales do not feed on their wintering grounds, they are an important source of nutrient input into these generally oligotrophic areas. The equator-ward transport of nutrients can be in the form of whale carcasses, placentas, and sloughing skin. In addition to this biomass, whales typically fast on their winter breeding grounds but continue to metabolize reserves, releasing nitrogen in the form of urea into typically oligotrophic tropical or subtropical waters. Roman et al. (2014 and in prep) assumed that nitrogen is limiting on the calving grounds, so any excretion of nitrogen will be quickly assimilated by phytoplankton. Assuming Redfield ratio of 106:16 mols of C:N, this means that every ton of nitrogen released on the calving grounds leads to 5.68 tons of new carbon fixed. A first order estimate for Southern Ocean blue whales indicated that before commercial whaling began, blue whales would have transported ~24 000 tons N yr^{-1} from the N-rich Southern Ocean to the comparatively nutrient-poor lower-latitude oceans, potentially allowing phytoplankton to fix an additional 140 000 tons −1 C yr (Roman et al. 2014).

These subsidies can support phytoplankton, scavengers, benthic macroinvertebrates, and fish populations. The impact of this great whale conveyor belt was greatly reduced during the age of commercial whaling. Whale-fall habitats declined in range (through serial depletion), size (through selecting for the largest species and individuals), and number (through overharvest) (Smith et al. 2019). Before whaling, great whales may have increased primary productivity significantly in lower-latitude breeding areas. Recovering species, such as humpbacks and southern right whales, may help restore this ecological function in the global oceans.

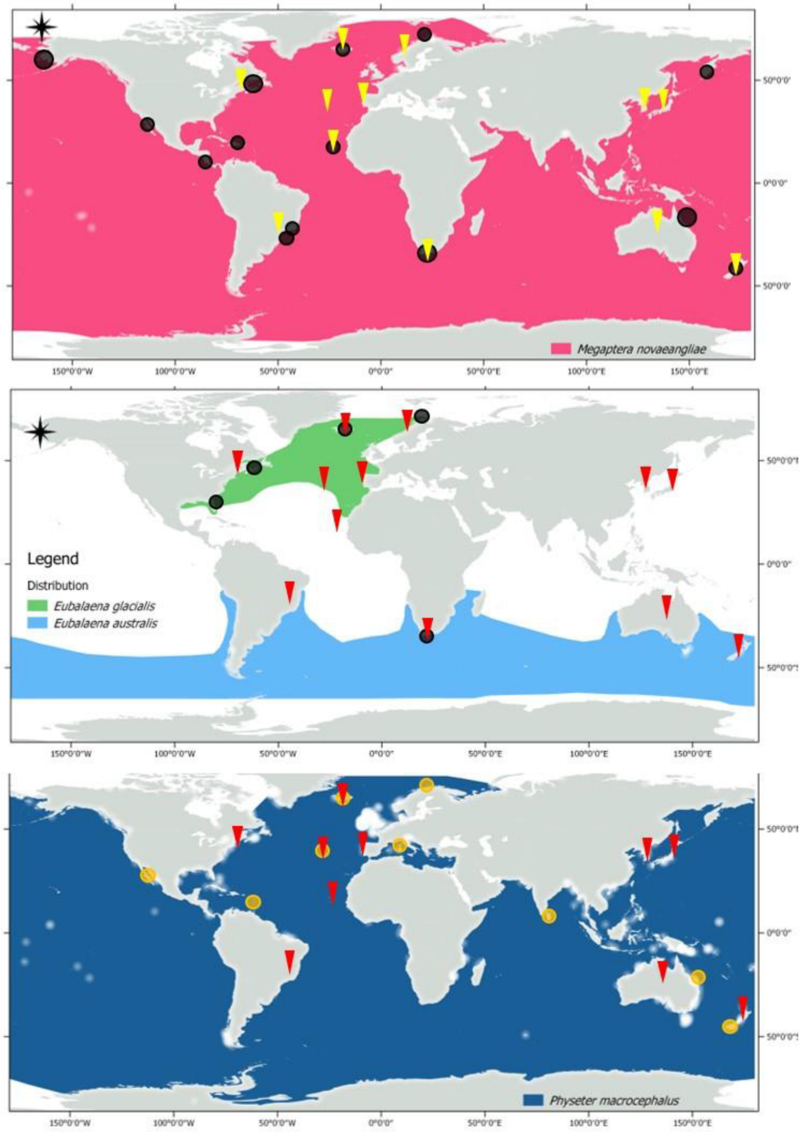


Fig. 14. Worldwide distribution of humpback whales, North Atlantic and southern right whales, and sperm whales based on shape file distributions from the IUCN (http://www.iucnredlist.org/technical-documents/red-list-training/iucnspatialresources). The circles represent current whale-watching hotspots (from Mazzoldi et al. 2019).

In their consideration of key questions in marine megafauna, Hays et al. (2016) noted that the key to understanding ecological roles are analyses of spatiotemporal patterns of abundance and behaviors (e.g., foraging and resting), which are driven by movement decisions. “Yet,” they noted, “there has been little use of movement data in this context.” Previous attempts to look at nutrient movement by whales and other marine mammals employed IUCN distribution data based on shape files that often overestimated the range of cetaceans, obscuring the patchiness of whale distribution and diluting the impact of nutrient distribution (see, for example, Fig. 14). To develop a better understanding of habitat and season usage, we developed seasonal global distribution maps for gray whales, humpbacks, and right whales based on spatial data for foraging and feeding grounds derived from publicly available databases including Whaling History (whalinghistory.org), OBIS-SEAMAP, and Global Biodiversity Information Facility (Fig. 15, Roman et al. in prep).

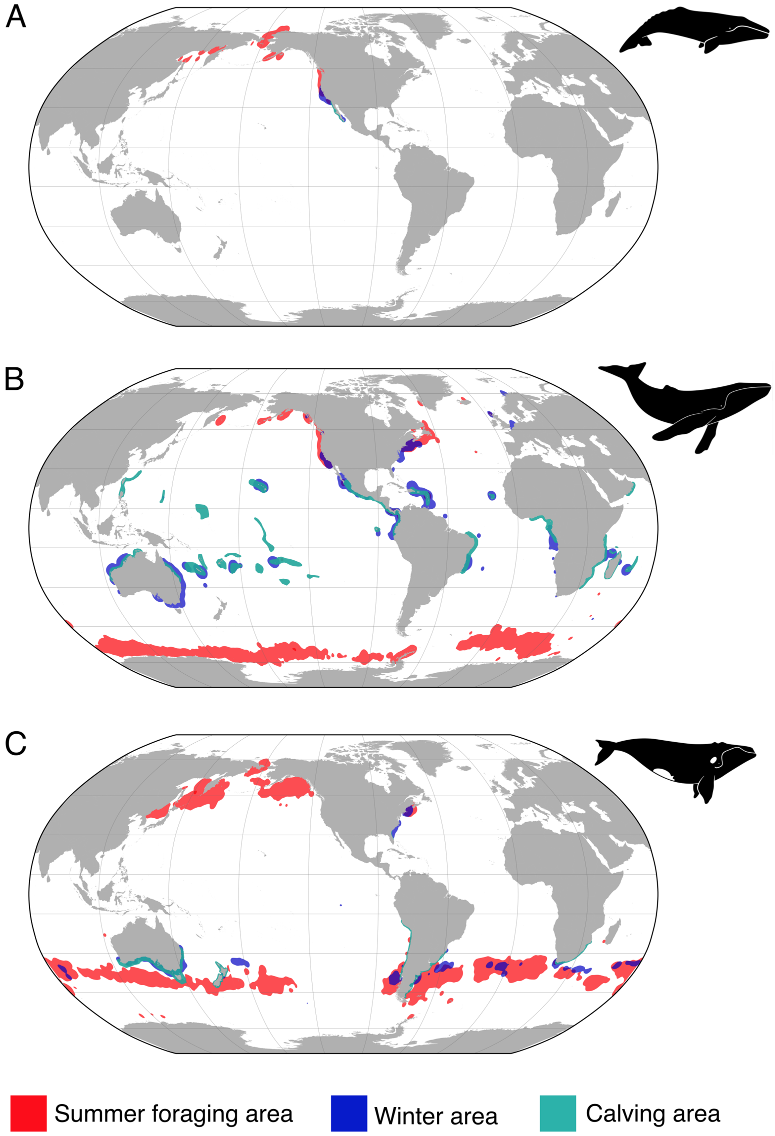


Fig. 15. Global distribution of gray whales (A), humpbacks (B), and right whales (C). The movement of nutrients from high latitude feeding grounds to low latitude winter and calving grounds is an important nutrient subsidy. Maps combine nineteenth-century whaling data with contemporary sightings (Roman et al. in prep).

Efforts are currently in progress to determine the movement of nitrogen and other nutrients across ocean basins, based on current and past whale population sizes, and determine the influence on these nutrient subsidies on primary productivity as well as scavenging communities.

Fig. 16. A killer whale in Antarctica with diatoms visible on its skin (courtesy C. Coulson)

Epidermal Molting

In addition to the movement of nutrients via carcasses, placentas, and urine, there has been increased attention in the role of epidermal molting as a driver of long-distance migration in whales (Fig. 16). Whales slough epithelium throughout their lives, but Pitman et al. (2019) suggest that cetaceans may need to migrate to warmer waters to molt their skin, a feeding/molting hypothesis. Such movements could also help control the effects of pathogenic bacteria (Hooper et al. 2018). The relationship between diatom growth, skin molting, and migration has been observed since the 1920s and 30s, when A. G. Bennet and T. John Hart noted that diatoms could aid in the understanding of the nutrition and migration of fin and blue whales (Bennett 1920, Hart 1935). In the Antarctic, thin and clean whales were assumed to be recent arrivals that had been fasting in the tropics. After a month or so, the whales began to accumulate a conspicuous yellow diatom film that covered the whole body.

To date, we are not aware of any estimates of the contribution of this skin sloughing to the nutrient ecology of breeding grounds, but observations indicate that seabirds and likely fish consume the molt opportunistically. Silver gulls have been observed converging on breaching humpback whales and feeding on sloughed skin during whales' migration off Ningaloo in western Australia (Pitman pers. comm.) It seems reasonable that humpback breaching enhances sloughing.

We believe this could be a fruitful line of research, especially given the large surface area of baleen whales—humpback whales have a surface area of approximately 70 square meters). In addition to the epidermis, whales almost certainly transport bacteria and diatoms between their summer foraging and winter molting grounds. An analysis of this movement, and its potential ecological consequences, could prove fruitful in coming years.

Fig. 17. Tiger shark swimming over the carcass of a humpback calf on Ningaloo Reef, western Australia (courtesy Jess Leask).

Sharks

Whale carcasses on the calving ground can attract scavengers. Tiger sharks and other large sharks have been observed feeding on whale carcasses on the coasts of Brazil and the Ningaloo Reef in Western Australia (Bornatowski et al. 2012, Fig. 17). On Abrolhos Bank in Bahia, Brazil, large sharks fed on 22% of humpback whales carcasses, and shark bites are occasionally observed on living whales (Bornatowski et al. 2012). In these two areas, tiger sharks reproduce nearshore during the whales' breeding season.

7. Whale Falls

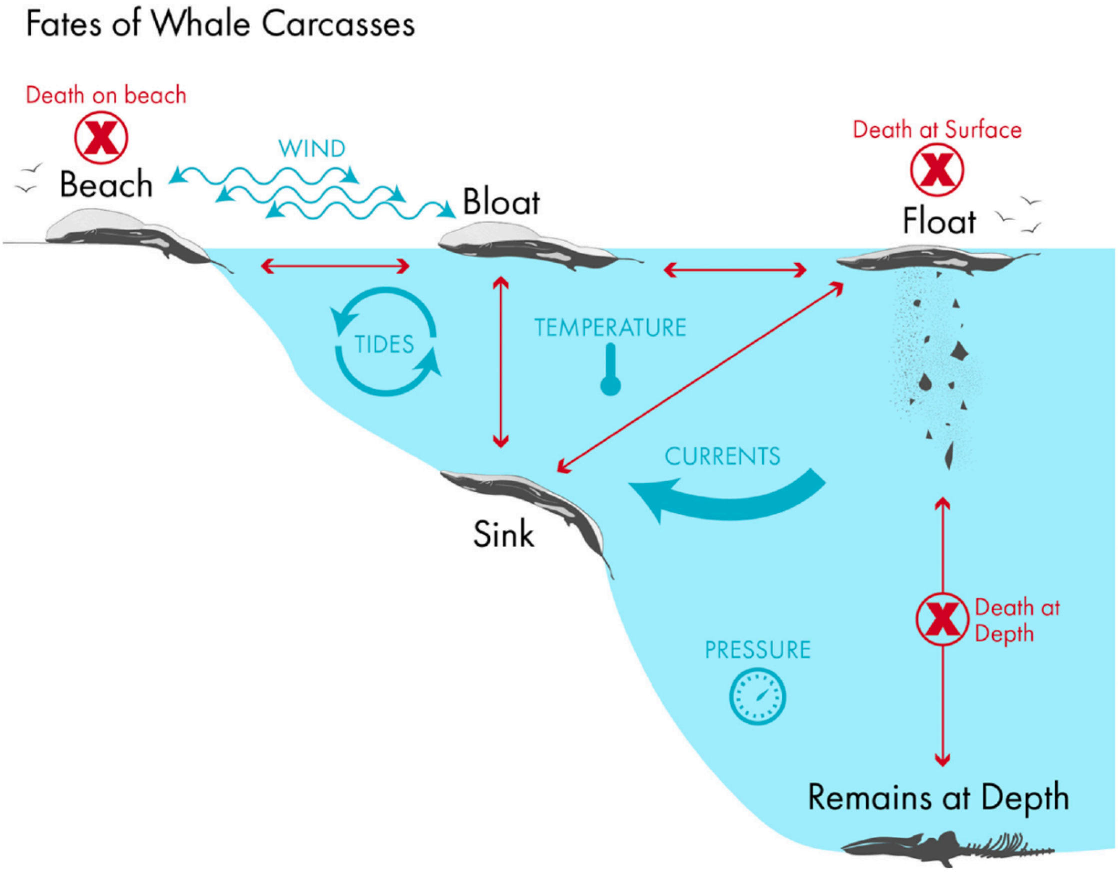


Fig. 18. The fates of whale carcasses depend on many factors such as where the whale dies and the winds, tides, and currents (Moore et al. 2020).

Dead whales are the largest, most food-rich detrital particles in the ocean, often containing more than 10^6 g of organic carbon in energy-rich lipids and proteins (Smith C. R. 2006). Whale carcasses can wash ashore, stay in shallow coastal waters, or sink into deep waters, where they support numerous species, at least 100 of which are considered whale fall specialists (Figs. 18 and 19, Moore et al. 2020, Smith C. et al. 2019). In the deep sea, the food-rich conditions and widespread occurrence of whale falls have led to ecological and evolutionary opportunities on the deep-sea floor, in a manner similar to that of hydrothermal vents and cold seeps (Smith C. R. 2006).

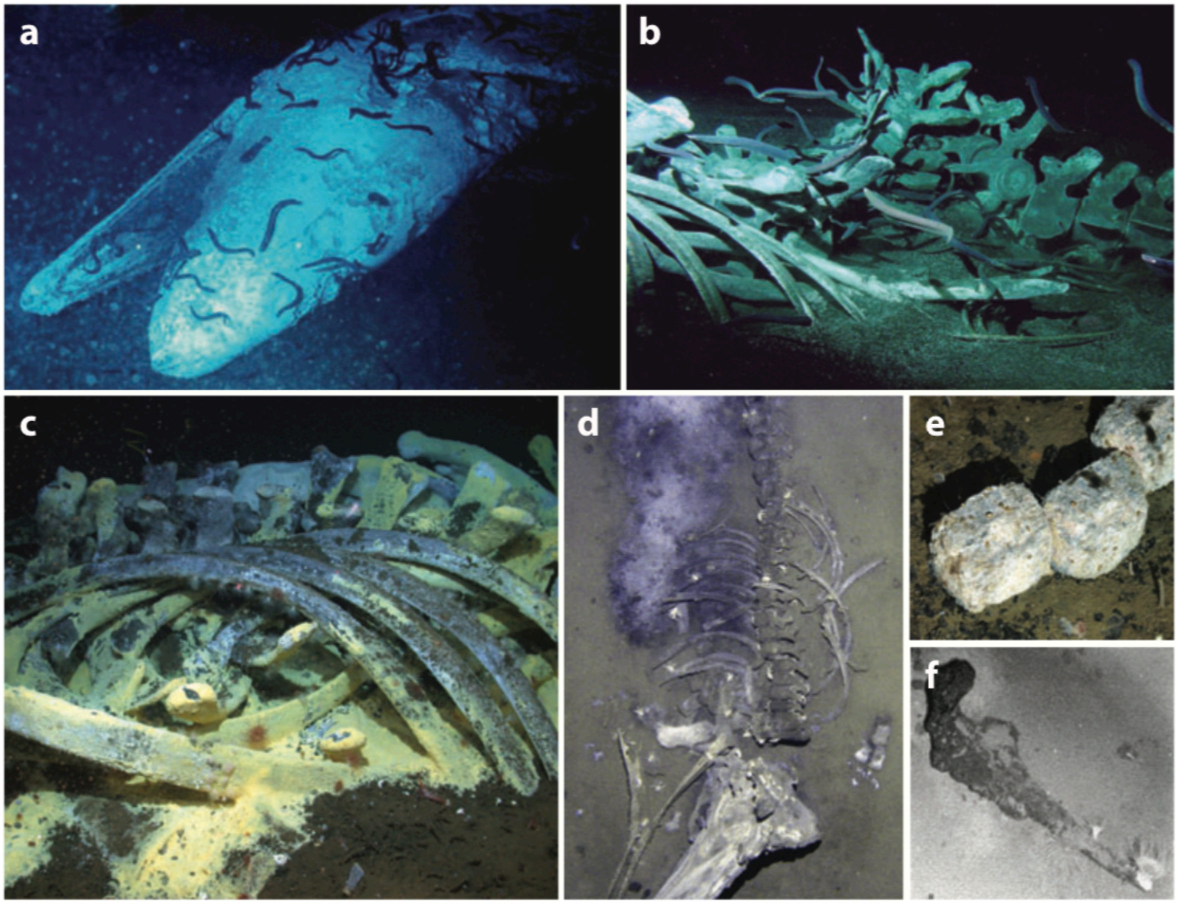


Fig. 20. Stages of ecological succession observed at modern whale falls from Smith et al. (2015). (*a*) The mobile-scavenger stage on an implanted gray whale carcass. (*b*) The enrichment-opportunist stage on the same carcass. (*c*) The sulfophilic stage on the implanted carcass. (*d*) The sulfophilic stage at a natural mysticete whale fall in central Pacific. (*e*) The sulfophilic stage at a natural whale fall in the South Sandwich Arc in the Southern Ocean at 1,444 m. (*f*) The reef stage on a manganese-encrusted whale bone in the Clarion-Clipperton Zone at 4,800 m.

Whaling and Whale Fall Communities

The ongoing loss of global megafauna as a result of human activity has had drastic effects on mutualistic species, with strong consequences for biodiversity, ecosystem integrity, ecological function, and ecosystem services (Galetti et al. 2018, Schweiger and Svenning 2018). Hundreds of deep-sea species rely in part or completely on the carcasses of great whales, and the ecological consequences of centuries of whaling are likely widespread and long-lasting for many of these animals. In fact, it is possible that the earliest extinctions in the ocean occurred in these deep-sea hotspots (Smith 2006, Roman et al. 2014, Smith et al. 2019).

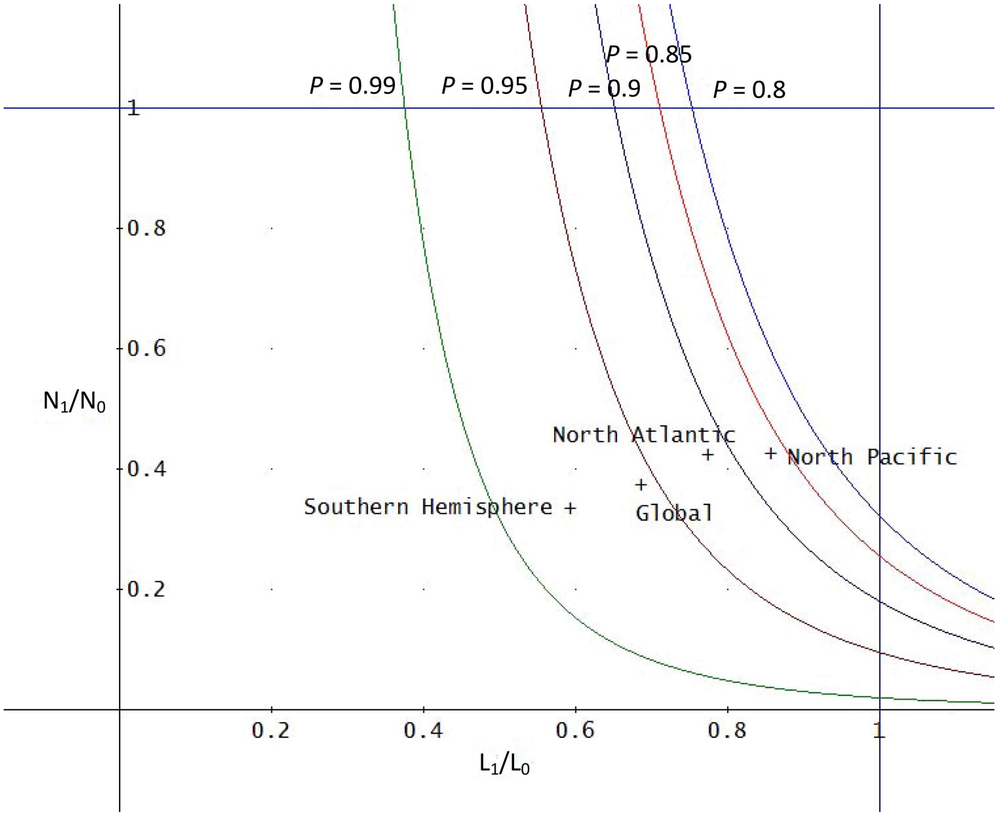


Figure 21. Level curves showing the pre-whaling occupancy rate ($P0$) of whale falls required for the post-whaling survival by a whale-fall specialist. $P0$ is plotted in terms of the relative decline in mean whale length ($L1/L0$) versus the relative decline in whale abundance ($N1/N0$) resulting from whaling. For example, if a $L1/L0$ versus $N1/N0$ point falls on the green curve marked $P0 = 0.99$, then a whale-fall specialist would need to have occupied at least 99% of the available whale-fall sites prior to whaling to avoid extinction. $P0$ is initially much more sensitive to changes in whale length than to changes in whale abundance (Smith et al. 2019).

During whaling in the age of sail, there was probably a rise in whale carcasses, as whales were hunted for their blubber, and most of the carcasses sank at sea (Smith 2006). But as whale populations dwindled and the largest whales were rendered in their entirety aboard factory ships, whale fall communities were deprived of habitat, deep-sea oases in a dark, low-nutrient environment. These communities are now paying an extinction debt, where they may survive in remnant whale-fall habitats, but it is not clear if all whale-fall species will persist long enough to see the return of abundant populations and large-bodied whales (Smith 2006).

A recent model based on Levins metapopulation equation demonstrated that the persistence of metapopulations of whale-fall specialists is linearly related to the abundance of whales and extremely sensitive (to the fourth power) to the mean size of whales (Smith C. et al. 2019). The largest whales (both within and between species) are disproportionately important in maintaining the novel biodiversity of whale-fall communities and in providing ecological and evolutionary stepping- stones for hydrothermal-vent and cold-seep faunas (Fig. 21, Smith et al., 2015, 2017, 2019).

Fig. 22. Polar bears feeding on a bowhead whale carcass on Wrangell Island, Russia. More the 180 bears were seen feeding on the carcass in 2017. Courtesy Olga Belonovich/Heritage Expeditions.

Smith et al. (2019) developed a metapopulation model for whale-fall specialists. They found that the loss of the largest whales caused the highest risks to these deep-sea species (Fig 21). The reduction of these habitats probably had the greatest impact on the diversity of whale-fall specialists in areas where whales have been hunted for centuries, allowing extinctions to proceed to completion. Species that did not occupy at least 80% of carcasses prior to whaling are likely to go extinct after intense commercial whaling, assuming whale populations have been reduced by 66% and mean whale body size reduced by 10% (Roman et al. 2014). If populations were reduced by 90%, the number of extinctions is higher. Species with low whale occupancy rates prior to whaling are at highest risk of extinction.

Just as the communities of the deep sea lost the nutrient-rich islands they relied on when whales were removed from the ocean, scavengers along the coastlines also lost important resources, as whales and other marine mammals declined. Bald eagles, grizzly bears, ravens and other scavengers feed on whale skin and soft tissue; wolves feed on the organs; and polar bears, in the absence of sea ice, rely on stranded whales (Fig. 22, Laidre et al. 2018, Smith C. R. 2006). The California and Andean condors once depended on whales and other marine mammals that washed up on the beach. Before the nineteenth century, blue whales were common, as were seals and sea lions. After marine mammal populations were depleted in the nineteenth and twentieth centuries off the west coast of South America, condors shifted from blue whales and fur seals to a diet dependent on guanacos, small wild camelids related to llamas. Many now feed on sheep, horses, and cows, if they can find them (Lambertucci et al. 2018). In California, the dietary shift from marine to terrestrial carcasses may have further endangered the California condor by reducing available resources and increasing the risk of poisoning from lead ammunition in wild game lost or abandoned by hunters (Finkelstein et al. 2012).

8. Cetaceans' Role in the Carbon Cycle

Cetaceans have potential to aid in carbon storage (carbon removed from the atmosphere for <100 years) and sequestration (carbon removed from the atmosphere for ≥100s of years; Passow and Carlson 2012). At least five pathways have been identified through which cetaceans may aid in carbon storage or sequestration. These five pathways can be divided into two main categories: biomass and nutrient cycling.

Biomass

Cetaceans can directly store carbon in their bodies throughout their lifetime (living biomass carbon). Cetaceans that are larger and longer lived store more carbon for longer periods of time. Bycatch and whaling represent losses of stored carbon that would otherwise be trapped in cetacean bodies. Bycatch of 3.4 million pantropical spotted (*Stenella attenuata*) and spinner (*S. longirostris*) dolphins from the tuna purse-seine fishery in the Eastern Tropical Pacific over a 48-year period resulted in an estimated loss of 5.5 x 10^4 mt of stored C (Table 5, Martin S. L. et al. 2016). Global industrial whaling during the twentieth century resulted in an estimated loss of 1.7 x 10^7 mt of stored C (Fig. 23, Pershing et al. 2010).

Whale falls, or cetacean carcasses that sink to the deep seafloor (>1,000 m), can sequester carbon for hundreds to thousands of years ("deadfall carbon"; Lutz and Martin 2014). If carcass-derived carbon becomes buried in deep-sea sediments, that carbon can be sequestered for potentially millions of years (Ducklow et al. 2001). Based on the 2001 global population abundance estimate of eight whale taxa, an estimated 2.9 x 10^4 mt C/yr was sequestered via whale falls; this is an order of magnitude less than that sequestered by pre-whaling populations (Table 5).

Nutrient cycling

Cetaceans can indirectly increase carbon storage and sequestration by increasing availability of limiting nutrients, such as N, P, and Fe, in surface waters, which can stimulate phytoplankton production (see Section 6 and Nicol et al. 2010; Ratnarajah et al. 2014, 2016; Roman and McCarthy 2010; Roman et al. 2014, 2016; Smith et al. 2013). This enhanced production can occur via release of nutrient-rich by-products, such as feces, urine, placentas, or sloughed skin, across vertical or horizontal gradients, or via swimming behavior. Allochthonous, or imported, nutrient input from depths beneath the mixed layer can stimulate new primary production, which is quantitatively equivalent to carbon export to the deep ocean, or carbon sequestration. In contrast, autochthonous, or recycled, nutrient input from depths within the mixed layer stimulates total primary production and carbon storage (Ducklow et al. 2001, Dugdale and Goering 1967, Eppley and Peterson 1979, Lavery et al. 2010). There are three recognized mechanisms through which cetaceans can contribute toward allochthonous or autochthonous nutrient input.

1. The whale pump: cetaceans release buoyant, nutrient-rich fecal plumes in surface waters. Cetaceans can aid in carbon sequestration by releasing allochthonous nutrients into the euphotic zone derived from feeding below the mixed layer. Cetaceans can also aid in carbon storage by releasing autochthonous nutrients into the euphotic zone derived from feeding within the mixed layer. Based on modern population abundance estimates of Southern Ocean sperm and blue whales, an estimated 4 x 10^5 mt C/yr was sequestered and 2.8 x 10^6 mt C/yr was stored, respectively, via the whale pump. These estimates are

an order of magnitude lower than prewhaling populations of sperm whales and two orders of magnitude of blue whales (Table 5).

2. Through the “great whale conveyor belt,” migratory whales transport nutrients from high-latitude feeding grounds to low-latitude breeding grounds via urine, placentas, and sloughed skin. These can be considered allochthonous nutrient inputs that may ultimately lead to carbon sequestration because nutrients are released at locations 1000’s of km distant from their origin. Nitrogen released by the modern-day population of Southern Ocean blue whales on their calving grounds is estimated to result in sequestration of 5.1 x 10^2 mt C/yr, which is nearly three orders of magnitude less than the pre-whaling C sequestration estimate (Table 5, Roman et al. 2014).

3. Finally, cetaceans may increase allochthonous nutrient input to the euphotic zone by physically enhancing upward nutrient flux (“biomixing carbon”; Lutz and Martin 2014). This may occur via turbulence associated with cetacean dives (Dewar et al. 2006) or bubbles that cross the thermocline, for example in humpback whale bubble-net feeding (Jurasz and Jurasz 1979, Roman et al. 2014).

Future Research Directions

While the aforementioned studies have established a solid foundation regarding the role of cetaceans in the carbon cycle, understanding of these mechanisms is still in its infancy. Empirical investigations and additional study sites are needed to enhance, support, or refute hypotheses regarding if and how cetaceans can contribute to carbon storage and/or sequestration. There are several avenues for future research.

Provided sound data on life history and population structure are available, it is possible to quantify the amount of carbon stored via living biomass carbon and sequestered via deadfall carbon. However, to date, only 12 species have been examined. Further, the most robust quantification currently available (Pershing et al. 2010) was based on global population estimates from 2001; thus, it is important to update this analysis using current population estimates and enhanced understanding of preexploitation and future numbers wherever available. A better understanding of the stoichiometry of whale carcasses would also be beneficial.

There is a strong need for empirical data to test the nutrient-cycling hypotheses. While a solid foundation has been established based on modeling (e.g., Lavery et al. 2010, 2014; Roman et al. 2014), it is unknown how closely these results approximate reality. Further quantification of cetacean diving behavior is needed to determine what proportion of foraging dives occur above vs. below the mixed layer and thus contribute to autochthonous vs. allochthonous nutrient cycling. It is also important to determine how bioavailable fecal plume nutrients are to phytoplankton and the impact of the microbial loop on phytoplankton nutrient uptake (Ratnarajah 2018). Finally, it is critical to estimate the proportion of carbon derived from primary productivity that sinks below the mixed layer and becomes sequestered.

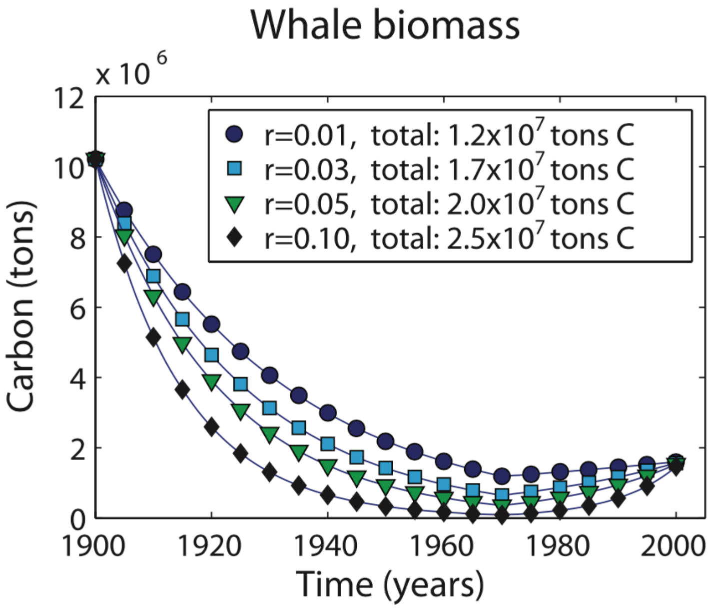


Fig. 23. Biomass of eight species of large whales. Each line represents a different biomass accumulation rate (from Pershing et al. 2010).

Finally, the role of cetaceans in the carbon cycle has only been examined for a handful of species in limited areas. Fewer than 15 cetacean species have been studied out of a global total of 89, and quantitative data are only available for two regions: the Southern Ocean and the Eastern Tropical Pacific. Particularly with respect to the nutrient cycling hypotheses, one must be careful not to generalize or extrapolate findings based on one region as cetacean diet, foraging behavior, limiting nutrients, and phytoplankton species can vary widely between regions.

Table 5. Estimated amount of carbon stored or sequestered in pre-exploitation and modern populations. C values are gross and do not account for the amount of C respired by cetaceans. Exploitation refers to bycatch for dolphins and industrial whaling for all other cetaceans.

Mechanism	Species	Region	Pre-exploitation C estimate (*N*)	Modern C estimate (*N*, year)	C stored or sequestered	Reference
Living biomass carbon	Pantropical spotted dolphin (*Stenella attenuata*)	Eastern Tropical Pacific	5.9 x 10^{4} mt C (3.6 x 10^{6})	1.4 x 10^{4} mt C (8.6 x 10^{5}, 2006)	Stored	Martin et al. 2016
Living biomass carbon	Spinner dolphin (*S. longirostris*)	Eastern Tropical Pacific	2.4 x 10^{4} mt C (1.8 x 10^{6})	1.4 x 10^{4} mt C (1.1 x 10^{6}, 2006)	Stored	Martin et al. 2016
Living biomass carbon	8 baleen whale taxa[1]	Global	2.0 x 10^{7} mt C (2.6 x 10^{6})	3.1 x 10^{6} mt C (8.8 x 10^{5}, 2001)	Stored	Pershing et al. 2010
Deadfall carbon	8 baleen whale taxa[1]	Global	1.9 x 10^{5} mt C/yr (2.6 x 10^{6})	2.9 x 10^{4} mt C/yr (8.8 x 10^{5}, 2001) 1900	Sequestered	Pershing et al. 2010
Whale pump	Sperm whale (*Physeter macrocephalus*)	Southern Ocean	2.4 x 10^{6} mt C/yr (1.2 x 10^{4})	4 x 10^{5} mt C/yr (1.2 x 10^{3}, 2001)	Sequestered	Lavery et al. 2010
Whale pump	Blue whale (*Balaenoptera musculus*)	Southern Ocean	1.3 x 10^{8} mt C/yr (2.4 x 10^{5})	2.8 x 10^{6} mt C/yr (5.2 x 10^{3}, 2012)	Stored	Lavery et al. 2014
Great whale conveyor belt	Blue whale	Southern Ocean	1.4 x 10^{5} mt C/yr (3.4 x 10^{5})	5.1 x 10^{2} mt C/yr (4.7 x 10^{3}, 2001)	Sequestered	Roman et al. 2014

[1] *Balaenoptera acutorostrata, B. bonaerensis, B. borealis, B. brydei, B. musculus, B. physalus, Balaena mysticetus, Eschrichtius robustus, Eubalaena spp., Megaptera novaeangliae*

9. Whale Recovery and Climate Limitations

Climate change is likely to have an impact on ocean food webs by affecting their foundations, including primary-producer communities and habitats (Trebilco et al. 2020). The implications of these changes for ecological function and ecosystem services—including wildlife populations, fisheries, and carbon sequestration—are unclear, as are the implications for policy and management.

Many whale researchers have noticed shifts in the habitats of their study species. The endangered North Atlantic right whale, for example, relied on a summer foraging ground in the Bay of Fundy, off eastern Canada, at least since the 1980s. In recent years, it has shifted its range to the Gulf of Saint Lawrence, presumably because of shifts in its primary prey, the copepod *Calanus finmarchicus*. The shift put them at greater risk to fisheries entanglements and ship strikes, with high mortality rates in 2017 and 2019, and a disruption in reproduction.

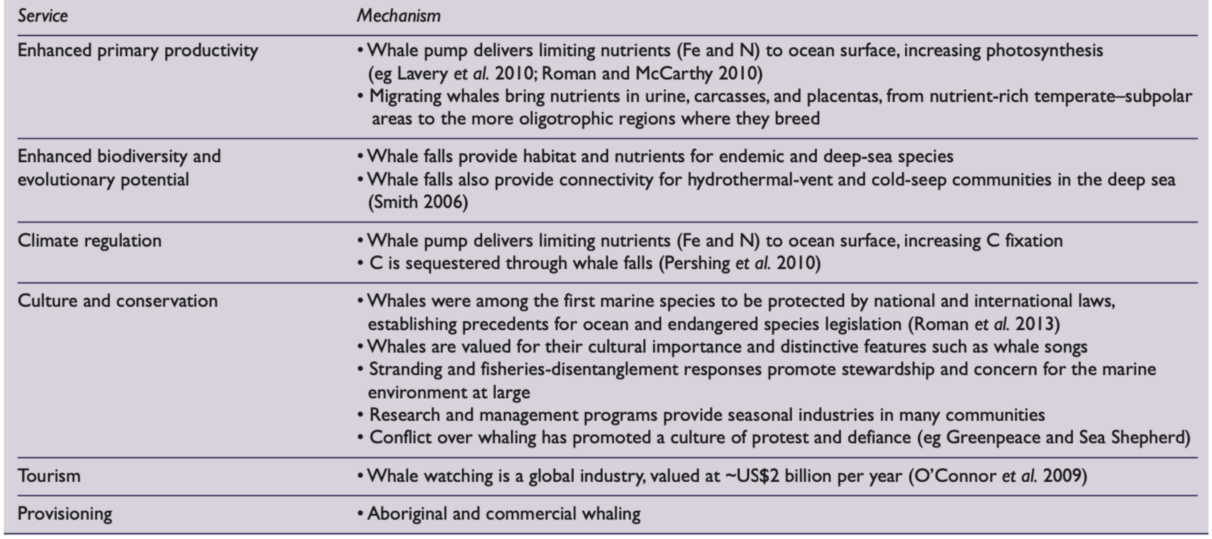
Human use of the oceans is also expected to change, especially in high latitudes, as a result of climate change. Alter et al. (2010) have noted that the decline in Arctic sea ice is likely to result in increases in shipping, oil and gas exploration, and fishing, exacerbating acoustic disturbance, ship strikes, bycatch, and prey depletion for Arctic cetaceans. Climate change could also result in increased hunting pressure on near-shore dolphins and whales in lower latitudes as the availability of other marine resources diminishes.

Since protection efforts have been established in the United States, Europe, much of the Southern Hemisphere, and elsewhere, many populations of marine mammals have increased since lows in the mid to late twentieth century (e.g. Roman et al. 2013, Roman et al. 2015, Tulloch et al. 2019). Despite these recoveries, the influence of future climate change on cetacean recovery remains unknown. Climate-biological models predict negative future impacts of climate change on krill and all whale species, including local extinctions in the Southern Ocean by 2100 (Tulloch et al. 2019). The consequences of climate perturbations are likely to result in changes in the ecological functions of cetaceans and other marine mammals.

10. Ecosystem Services

The ecological function of whales produces a variety of services, which extends from direct use value, such as whaling and whale watching, to enhanced productivity and biodiversity, and cultural and spiritual values (Table 7). Although beyond the scope of this workshop and review, a better understanding of the ecological function of whales is essential to valuing ecosystem services, the likely focus of later workshops.

Table 6. Selected ecosystem services provided by whales (from Roman et al. 2014).



Service	*Mechanism*
Enhanced primary productivity	• Whale pump delivers limiting nutrients (Fe and N) to ocean surface, increasing photosynthesis (eg Lavery *et al.* 2010; Roman and McCarthy 2010) • Migrating whales bring nutrients in urine, carcasses, and placentas, from nutrient-rich temperate–subpolar areas to the more oligotrophic regions where they breed
Enhanced biodiversity and evolutionary potential	• Whale falls provide habitat and nutrients for endemic and deep-sea species • Whale falls also provide connectivity for hydrothermal-vent and cold-seep communities in the deep sea (Smith 2006)
Climate regulation	• Whale pump delivers limiting nutrients (Fe and N) to ocean surface, increasing C fixation • C is sequestered through whale falls (Pershing *et al.* 2010)
Culture and conservation	• Whales were among the first marine species to be protected by national and international laws, establishing precedents for ocean and endangered species legislation (Roman *et al.* 2013) • Whales are valued for their cultural importance and distinctive features such as whale songs • Stranding and fisheries-disentanglement responses promote stewardship and concern for the marine environment at large • Research and management programs provide seasonal industries in many communities • Conflict over whaling has promoted a culture of protest and defiance (eg Greenpeace and Sea Shepherd)
Tourism	• Whale watching is a global industry, valued at ~US$2 billion per year (O'Connor *et al.* 2009)
Provisioning	• Aboriginal and commercial whaling

11. Gap Analysis: Selected Questions

During the workshop, we will 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 function and ecosystem modelling of such impacts. It is anticipated that studies related to cetaceans as consumers, cetaceans as vectors and sources of nutrients, carbon sequestration, and whales as prey could be especially ripe for fieldwork and model development. The questions at the end of selected sections above represent gaps that have been identified by the authors and are not representative of the views of the workshop. We anticipate that those will come forward during and following the meeting. To start this dialogue, we have constructed two tables.

Table 1 is a summary of selected traits of cetaceans and their related ecosystem functions and services. Contributors to the workshop are encouraged to add additional traits, along with gaps in our understanding, for the final report.

Table 6 puts forth several research and development needs for the ecological function of cetaceans, including an expected timeline. At this point, it has only a preliminary list of recommended research, and it is anticipated that a table developed by workshop participants could help move this research forward.

Table 7. Research and development needs for the ecological function of cetaceans.

Research and Development Needs Ecological Function of Cetaceans		
Recommended Research	**Gap Filled**	**Timeframe (yr)**
Effect of nitrogen and iron in primary productivity (vertical)	Furthers understanding of nutrient cycling in foraging areas of cetaceans and other air-breathing vertebrates	5 years
Nutrient transport from high to low latitudes (horizontal)	Furthers understanding of global nutrient subsidies by whales and other capital breeders	5 years
Role of whales in the carbon cycle	Furthers understanding of the role of large animals in the carbon cycle, including storage and sequestration	5 years
Comparison of biodiversity of whale-fall communities between areas with recovered versus heavily depleted great whale populations	Elucidates 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	5 years
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	10 years
Controlled whale-bone implantations across ocean basins	Elucidates the role of whale bones as dispersal steppingstones for vent and seep biotas, especially across ocean basins	5 years

12. References

Allen AN, Schanze JJ, Solow R, Tyack PL. 2014. Analysis of a Blainville's beaked whale's movement response to playback of killer whale vocalizations. Marine Mammal Science 30:154-168.

Allgeier JE, Cline TJ, Walsworth TE, Wathen G, Layman CA, Schindler DE. 2020. Individual behavior drives ecosystem function and the impacts of harvest. Science Advances 6:eaax8329.

Alter SE, Rynes E, Palumbi SR. 2007. DNA evidence for historic population size and past ecosystem impacts of gray whales. Proc. Natl. Acad. Sci. U.S.A. 104:15162-15167.

Alter SE, Simmonds MP, Brandon JR. 2010. Forecasting the consequences of climate-driven shifts in human behavior on cetaceans. Marine Policy 34:943-954.

Anderson EM, Lovvorn JR. 2008. Gray whales may increase feeding opportunities for avian benthivores. Marine Ecology Progress Series 360:291-296.

Bar-On Y, Phillips R, Milo R. 2018. The biomass distribution on Earth. Proceedings of the National Academy of Sciences 115:6506-6511.

Bejder L, Samuels A, Whitehead H, Gales N, Mann J, Connor R, Heithaus M, WATSON-CAPPS J, Flaherty C, Krützen M. 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology 20:1791-1798.

Bennett A. 1920. On the occurrence of diatoms on the skin of whales. Proceedings of the Royal Society of London. Series B, Containing Papers of a Biological Character 91:352-357.

Bornatowski H, Wedekin LL, Heithaus MR, Marcondes MCC, Rossi-Santos MR. 2012. Shark scavenging and predation on cetaceans at Abrolhos Bank, eastern Brazil. Journal of the Marine Biological Association of the United Kingdom 92:1767-1772.

Browning TJ, Achterberg EP, Rapp I, Engel A, Bertrand EM, Tagliabue A, Moore CM. 2017. Nutrient co-limitation at the boundary of an oceanic gyre. Nature 551:242-246.

Butman CA, Carlton JT, Palumbi SR. 1996. Whales don't fall like snow: Reply to Jelmert. Conservation Biology 10:655-656.

Clapham PJ. 2017. When it's right to be wrong. Marine Mammal Science 33:966-967.

Corkeron PJ, Connor RC. 1999. Why do baleen whales migrate? Marine Mammal Science 15:1228-1245.

Creel S. 2011. Toward a predictive theory of risk effects: hypotheses for prey attributes and compensatory mortality. Ecology 92:2190-2195.

Creel S, Christianson D. 2008. Relationships between direct predation and risk effects. Trends in Ecology & Evolution 23:194-201.

Croll DA, Acevedo-Gutierrez A, Tershy BR, Urban-Ramirez J. 2001. The diving behavior of blue and fin whales: is dive duration shorter than expected based on oxygen stores? Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology 129:797-809.

Dawbin WH. 1966. The seasonal migratory cycle of humpback whales. Whales, dolphins and porpoises:145-170.

de Soto NA, Visser F, Tyack PL, Alcazar J, Ruxton G, Arranz P, Madsen PT, Johnson M. 2020. Fear of killer whales drives extreme synchrony in deep-diving beaked whales. Scientific Reports 10:1-9.

DeMaster DP, Trites AW, Clapham P, Mizroch S, Wade P, Small RJ, Ver Hoef J. 2006. The sequential megafaunal collapse hypothesis: testing with existing data. Progress in Oceanography 68:329-342.

Dewar WK, Bingham RJ, Iverson RL, Nowacek DP, St. Laurent LC, Wiebe PH. 2006. Does the marine biosphere mix the ocean? Journal of Marine Research 64:541-561.

Doughty CE, Roman J, Faurby S, Wolf A, Haque A, Bakker ES, Malhi Y, Dunning JB, Svenning JC. 2016. Global nutrient transport in a world of giants. Proceedings of the National Academy of Sciences of the United States of America 113:868-873.

Ducklow HW, Steinberg DK, Buesseler KO. 2001. Upper ocean carbon export and the biological pump. Oceanography 14:50–58.

Dugdale R, Goering J. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity 1. Limnology and Oceanography 12:196-206.

Eames KT, Keeling MJ. 2003. Contact tracing and disease control. Proceedings of the Royal Society of London. Series B: Biological Sciences 270:2565-2571.

Eppley RW, Peterson BJ. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282:677-680.

Estes J, Doak D, Springer A, Williams T. 2009. Causes and consequences of marine mammal population declines in southwest Alaska: a food-web perspective. Philosophical Transactions of the Royal Society B. 364:1647-1658.

Estes J, Steneck R, Lindberg D. 2013. Exploring the consequences of species interactions through the assembly and disassembly of food webs: A Pacific/Atlantic comparison. Bulletin of Marine Science 89:11-29.

Estes J, Tinker MT, Williams TM, Doak DF. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282:473-476.

Estes JA, DeMaster DP, Brownell RLJ, Doak DF, Williams TM. 2006. Retrospection and review. In "Whales, whaling and ocean ecosystems," J.A. Estes, D.P. DeMaster, D.F. Doak, T.M. Williams, and R.L. Brownell, Jr., Eds, pp. 388-393. University of California Press, Berkeley, CA.

Estes JA, et al. 2011. Trophic downgrading of planet Earth. Science 333:301-306.

Evans P. 1982. Associations between seabirds and cetaceans: a review. Mammal Review 12:187-206.

Finkelstein ME, Doak DF, George D, Burnett J, Branch J, Church M, Grantham J, Smith DR. 2012. Lead poisoning and the deceptive recovery of the critically endangered California condor. Proc. Natl. Acad. Sci. U.S.A. 28:11449-11454.

Ford JBK, Reeves RR. 2008. Fight or flight: Antipredator strategies of baleen whales. Mammal Review 38:50-86.

Forney KA, Wade P. 2006. Worldwide distribution and abundance of killer whales. Pages 145-162 in Estes JA, DeMaster DP, Doak TM, Williams TM, Brownell RL, eds. Whales, whaling, and ocean ecosystems. Berkeley: University of California Press.

Frid A, Dill L. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6.

Galetti M, Moleón M, Jordano P, Pires MM, Guimaraes Jr PR, Pape T, Nichols E, Hansen D, Olesen JM, Munk M. 2018. Ecological and evolutionary legacy of megafauna extinctions. Biological Reviews 93:845-862.

Geijer CKA, Notarbartolo di Sciara G, Panigada S. 2016. Mysticete migration revisited: Are Mediterranean fin whales an anomaly? Mammal Review 46:284-296.

Gerber LR, Morissette L, Kaschner K, Pauly D. 2009. Should whales be culled to increase fishery yield?: American Association for the Advancement of Science.

Grebmeier JM, Harrison NM. 1992. Seabird feeding on benthic amphipods facilitated by gray whale activity in the northern Bering Sea. Marine Ecology Progress Series:125-133.

Gygax L. 2002. Evolution of group size in the dolphins and porpoises: interspecific consistency of intraspecific patterns. Behavioral Ecology 13:583-590.

Hamilton PK, Kraus SD. 2019. Frequent encounters with the seafloor increase right whales’ risk of entanglement in fishing groundlines. Endangered Species Research 39:235-246.

Hart TJ. 1935. On the diatoms of the skin film of whales, and their possible bearing on problems of whale movements. Cambridge University Press.

Hastings A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, Talley TS, Wilson WG. 2007. Ecosystem engineering in time and space. Ecology Letters 10:153-164.

Hays GC, Ferreira LC, Sequeira AM, Meekan MG, Duarte CM, Bailey H, Bailleul F, Bowen WD, Caley MJ, Costa DP. 2016. Key questions in marine megafauna movement ecology. Trends in Ecology & Evolution 31:463-475.

Heithaus MR. 2001. Predator–prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. Journal of Zoology 253:53-68.

Heithaus MR, Dill LM. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83:480-491.

Heithaus MR, Frid A, Wirsing AJ, Worm B. 2008. Predicting ecological consequences of marine top predator declines. Trends in Ecology & Evolution 23:202-210.

Hooper R, et al. 2018. Host-derived population genomics data provides insights into bacterial and diatom composition of the killer whale skin. Molecular Ecology https://doi.org/10.1111/mec.14860.

Jefferson TA, Stacey PJ, Baird RW. 1991. A review of killer whale interactions with other marine mammals: predation to co-existence. Mammal Review 21:151-180.

Jones ML, Swartz SL, Leatherwood S, Folkens PA. 2012. The gray whale: Eschrichtius robustus. Academic Press.

Jurasz CM, Jurasz VP. 1979. Feeding modes of the humpback whales, Megaptera novaeangliae, in Southeast Alaska. Sci Rep Whales Res Inst 31: 69-83.

Kanwisher JW, Ridgway SH. 1983. The physiological ecology of whales and porpoises. Scientific American 248:110-121.

Katona S, Whitehead H. 1988. Are cetacea ecologically important? Oceanography and Marine Biology Annual Review 26:553-568.

Keane M, Semeiks J, Webb AE, Li YI, Quesada V, Craig T, Madsen LB, van Dam S, Brawand D, Marques PI. 2015. Insights into the evolution of longevity from the bowhead whale genome. Cell reports 10:112-122.

Kiszka J, Heithaus M, Wirsing A. 2015. Behavioural drivers of the ecological roles and importance of marine mammals. Marine Ecology Progress Series 523:267-281.

Kiszka JJ, Perrin WF, Pusineri C, Ridoux V. 2011. What drives island-associated tropical dolphins to form mixed-species associations in the southwest Indian Ocean? Journal of Mammalogy 92:1105-1111.

Kooyman G, Castellini M, Davis R. 1981. Physiology of diving in marine mammals. Annual Review of Physiology 43:343-356.

Laidre KL, Stirling I, Estes JA, Kochnev A, Roberts J. 2018. Historical and potential future importance of large whales as food for polar bears. Frontiers in Ecology and the Environment 16:515-524.

Lambertucci S, Navarro J, Sanchez Zapata J, Hobson K, Alarcón P, Wiemeyer G, Blanco G, F H, Donázar J. 2018. Tracking data and retrospective analyses of diet reveal the consequences of loss of marine subsidies for an obligate scavenger, the Andean condor. Proc. R. Soc. B 285:20180550.

Lavery TJ, Roudnew B, Gill P, Seymour J, Seuront L, Johnson G, Mitchell JG, Smetacek V. 2010. Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. Proc. R. Soc. B. 277:3527-3531.

Lavery TJ, Roudnew B, Seurant L, Mtichell JG, Middelton.J. 2012. Can whales mix the ocean? Biogeosciences Discussions preprint.

Lavery TJ, Roudnew B, Seymour J, Mitchell JM, Smetacek V, Nicol S. 2014. Whales sustain fisheries: Blue whales stimulate primary production in the Southern Ocean. Marine Mammal Science.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Lutz SJ, Martin AH. 2014. Fish Carbon: Exploring Marine Vertebrate Carbon Services. GRID-Arendal, Norway.

Markell RW. 2011. Rockfish recruitment and trophic dynamics on the west coast of Vancouver Island: fishing, ocean climate, and sea otters. PhD dissertation, University of British Columbia.

Martin JH, Fitzwater SE, Gordon RM. 1990. Iron deficiency limits phytoplankton growth in Antarctic waters. Global Biogeochemical Cycles 4:5-12.

Martin SL, Ballance LT, Groves T. 2016. An ecosystem services perspective for the oceanic Eastern Tropical Pacific: Commercial fisheries, carbon storage, recreational fishing, and biodiversity. Frontiers in Marine Science 3:50.

Mazzoldi C, Bearzi G, Brito C, Carvalho I, Desiderà E, Endrizzi L, Freitas L, Giacomello E, Giovos I, Guidetti P. 2019. From sea monsters to charismatic megafauna: Changes in perception and use of large marine animals. Plos One 14:e0226810.

Mizroch SA, Rice DW. 2006. Have North Pacific killer whales switched prey species in response to depletion of the great whale populations? Marine Ecology Progress Series 310:235-246.

Moore MJ, Mitchell GH, Rowles TK, Early G. 2020. Dead cetacean? Beach, bloat, float, sink. Frontiers in Marine Science 7:333.

Morissette L, Kaschner K, Gerber LR. 2010. Ecosystem models clarify the trophic role of whales in Northwest Africa. Marine Ecology Progress Series 404:289-303.

Mukherjee S, Heithaus MR, Trexler JC, Ray-Mukherjee J, Vaudo J. 2014. Perceived risk of predation affects reproductive life-history traits in *Gambusia holbrooki*, but not in *Heterandria formosa*. Plos One 9.

Nelson CH, Johnson KR. 1987. Whales and walruses as tillers of the sea floor. Scientific American 256:112-117.

Nicol S, Bowie A, Jarman S, Lannuzel D, Meiners KM, van der Merwe P. 2010. Southern Ocean iron fertilization by baleen whales and Antarctic krill. Fish and Fisheries 11:203-209.

Norris KS, Dohl TP. 1980. Behavior of the Hawaiian spinner dolphin, Stenella longirostris. Fishery Bulletin 77:821-849.

Norris KS, Wursig B, Wells RS, Wursig M. 1994. The Hawaiian spinner dolphin. Univ of California Press.

Oliver JS, Slattery PN. 1985. Destruction and opportunity on the sea floor: effects of gray whale feeding. Ecology 66:1965-1975.

Oliver JS, Slattery PN, Silberstein MA, O'Connor EF. 1984. Gray whale feeding on dense ampeliscid amphipod communities near Bamfield, British Columbia. Canadian Journal of Zoology 62:41-49.

Ortiz RM. 2001. Osmoregulation in marine mammals. Journal of Experimental Biology 204:1831-1844.

Passow U, Carlson CA. 2012. The biological pump in a high CO2 world. Marine Ecology Progress Series 470:249-271.

Perrin WF, Warner R, Fiscus C, Holts D. 1973. Stomach contents of porpoise, Stenella spp., and yellowfin tuna, Thunnus albacares, in mixed-species aggregations. Fishery Bulletin 71:1077-1092.

Pershing AJ, Christensen LB, Record NR, Sherwood GD, Stetson PB. 2010. The impact of whaling on the ocean carbon cycle: Why bigger was better. Plos One 5:e12444.

Pirotta E, Merchant ND, Thompson PM, Barton TR, Lusseau D. 2015. Quantifying the effect of boat disturbance on bottlenose dolphin foraging activity. Biological Conservation 181:82-89.

Pitman RL, Ballance LT, Mesnick SI, Chivers SJ. 2001. Killer whale predation on sperm whales: observations and implications. Marine Mammal Science 17:494-507.

Pitman RL, Deecke VB, Gabriele CM, Srinivasan M, Black N, Denkinger J, Durban JW, Mathews EA, Matkin DR, Neilson JL. 2017. Humpback whales interfering when mammal-eating killer whales attack other species: Mobbing behavior and interspecific altruism? Marine Mammal Science 33:7-58.

Pitman RL, Durban JW, Joyce T, Fearnbach H, Panigada S, Lauriano G. 2019. Skin in the game: Epidermal molt as a driver of long-distance migration in whales. Marine Mammal Science.

Ratnarajah L, Bowie AR, Lannuzel D, Meiners KM, Nicol S. 2014. The biogeochemical role of baleen whales and krill in Southern Ocean nutrient cycling. Plos One 9(12):e114067.

Ratnarajah L, Melbourne-Thomas J, Marzloff MP, Lannuzel D, Meiners KM, Chever F, Nicol S, Bowie AR. 2016. A preliminary model of iron fertilisation by baleen whales and Antarctic krill in the Southern Ocean: sensitivity of primary productivity estimates to parameter uncertainty. Ecological Modelling 320:203-212.

Ratnarajah L, Nicol S, Bowie AR. 2018. Pelagic iron recycling in the southern ocean: exploring the contribution of marine animals. Frontiers in Marine Science 5:109.

Reeves RR, Berger J, Clapham PJ. 2006. Killer whales as predators of large baleen whales and sperm whales. Pages 174-187 in Estes JA, DeMaster DP, Doak DF, Williams TM, Brownell Jr. RL, eds. Whales, Whaling and Ocean Ecosystems. Berkeley: University of California Press.

Reisewitz SE, Estes JA, Simenstad CA. 2006. Indirect food web interactions: sea otters and kelp forest fishes in the Aleutian archipelago. Oecologia 146:623-631.

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP. 2014. Status and ecological effects of the world's largest carnivores. Science 343.

Roman J, Altman I, Dunphy-Daly MM, Campbell C, Jasny M, Read AJ. 2013. The Marine Mammal Protection Act at 40: status, recovery, and future of US marine mammals. Year in Ecology and Conservation Biology 1286:29-49.

Roman J, Dunphy-Daly MM, Johnston DW, Read AJ. 2015. Lifting baselines to address the consequences of conservation success. Trends Ecol. Evol 30:299-302.

Roman J, Estes J. 2017. Ecology of Marine Mammals. Pages 299-303 in Würsig B, Thewissen JGM, Kovacs KM, eds. Encyclopedia of Marine Mammals. London: Academic Press.

Roman J, Estes J, Morrisette L, Smith C, Costa D, McCarthy J, Nation JB, Nicol S, Pershing A, Smetacek V. 2014. Whales as marine ecosystem engineers. Frontiers in Ecology and the Environment 12:377-385.

Roman J, McCarthy JJ. 2010. The whale pump: marine mammals enhance primary productivity in a coastal basin. Plos One 5:e13255.

Roman J, Nevins J, Altabet M, Koopman H, McCarthy J. 2016. Endangered Right Whales Enhance Primary Productivity in the Bay of Fundy. Plos One 11.

Schmitz OJ, Hawlena D, Trussell GC. 2010. Predator control of ecosystem nutrient dynamics. Ecology Letters 13:1199-1209.

Schmitz OJ, Wilmers CC, Leroux SJ, Doughty CE, Atwood TB, Galetti M, Davies AB, Goetz SJ. 2018. Animals and the zoogeochemistry of the carbon cycle. Science 362:eaar3213.

Schweiger AH, Svenning JC. 2018. Down-sizing of dung beetle assemblages over the last 53 000 years is consistent with a dominant effect of megafauna losses. Oikos 127:1243-1250.

Senigaglia V, Christiansen F, Bejder L, Gendron D, Lundquist D, Noren D, Schaffar A, Smith J, Williams R, Martinez E. 2016. Meta-analyses of whale-watching impact studies: comparisons of cetacean responses to disturbance. Marine Ecology Progress Series 542:251-263.

Smith C, Roman J, Nation JB. 2019. A metapopulation model for whale-fall specialists: the largest whales are essential to prevent species extinctions. Journal of Marine Research 77:283–302.

Smith CR. 2006. Bigger is better: the role of whales as detritus in marine ecosystems. Pages 286–302 in Estes JA, DeMaster DP, Doak TM, Williams TM, Brownell RL, eds. Whales, whaling and ocean ecosystems. Berkeley: University of California Press.

Smith CR, Glover AG, Treude T, Higgs ND, Amon DJ. 2015. Whale-fall ecosystems: Recent insights into ecology, paleoecology, and evolution. Annual Review of Marine Science 7:571–596.

Smith LV, McMinn A, Martin A, Nicol S, Bowie AR, Lannuzel D, van der Merwe P. 2013. Preliminary investigation into the stimulation of phytoplankton photophysiology and growth by whale faeces. Journal of Experimental Marine Biology and Ecology 446:1-9.

Somaweera R, Nifong J, Rosenblatt A, Brien ML, Combrink X, Elsey RM, Grigg G, Magnusson WE, Mazzotti FJ, Pearcy A. 2020. The ecological importance of crocodylians: towards evidence-based justification for their conservation. Biological Reviews.

Sparling CE, Fedak MA, Thompson D. 2007. Eat now, pay later? Evidence of deferred food-processing costs in diving seals. Biology Letters 3:95-99.

Springer AM, Estes J, Van Vliet G, Williams T, Doak D, Danner E, Pfister B. 2008. Mammal-eating killer whales, industrial whaling, and the sequential megafaunal collapse in the North Pacific Ocean: A reply to critics of Springer et al. 2003. Marine Mammal Science 24:414-442.

Springer AM, Estes JA, Van Vliet GB, Williams TM, Doak DF, Danner EM, Forney KA, Pfister B. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? Proc. Natl. Acad. Sci. U.S.A. 100:12223.

Srinivasan M, Grant WE, Swannack TM, Rajan J. 2010. Behavioral games involving a clever prey avoiding a clever predator: An individual-based model of dusky dolphins and killer whales. Ecological Modelling 221:2687-2698.

Srinivasan M, Markowitz TM. 2010. Predator threats and dusky dolphin survival strategies. Pages 133-150. The Dusky Dolphin, Elsevier.

Steffen W, Richardson K, Rockström J, Cornell SE, Fetzer I, Bennett EM, Biggs R, Carpenter SR, De Vries W, De Wit CA. 2015. Planetary boundaries: Guiding human development on a changing planet. Science 347.

Subalusky AL, Post DM. 2019. Context dependency of animal resource subsidies. Biological Reviews 94:517-538.

Swartz SL, Taylor BL, Rugh DJ. 2006. Gray whale Eschrichtius robustus population and stock identity. Mammal Review 36:66-84.

Tagliabue A, Bowie AR, Boyd PW, Buck KN, Johnson KS, Saito MA. 2017. The integral role of iron in ocean biogeochemistry. Nature 543:51-59.

Tavares DC, Moura JF, Acevedo-Trejos E, Merico A. 2019. Traits shared by marine megafauna and their relationships with ecosystem functions and services. Frontiers in Marine Science 6:262.

Taylor BL, Chivers SJ, Larese J, Perrin WF. 2007. Generation length and percent mature estimates for IUCN assessments of cetaceans. NOAA, NMFS, Southwest Fisheries Science Center Administrative Report LJ-07–01 21.

Trebilco R, Melbourne-Thomas J, Constable AJ. 2020. The policy relevance of Southern Ocean food web structure: Implications of food web change for fisheries, conservation and carbon sequestration. Marine Policy:103832.

Trites AW. 2018. Predator–prey relationships. Pages 780-783. Encyclopedia of marine mammals, Elsevier.

Trites AW, Deecke VB, Gregr EJ, Ford JK, Olesiuk PF. 2007. Killer whales, whaling, and sequential megafaunal collapse in the North Pacific: a comparative analysis of the dynamics of marine mammals in Alaska and British Columbia following commercial whaling. Marine Mammal Science 23:751-765.

Tulloch VJ, Plagányi ÉE, Brown C, Richardson AJ, Matear R. 2019. Future recovery of baleen whales is imperiled by climate change. Global Change Biology 25:1263-1281.

Veit RR, Harrison NM. 2017. Positive interactions among foraging seabirds, marine mammals and fishes and implications for their conservation. Frontiers in Ecology and Evolution 5:121.

Wade PR, Burkanov VN, Dahlheim ME, Friday NA, Fritz LW, Loughlin TR, Mizroch SA, Muto MM, Rice DW, Barrett-Lennard LG. 2007. Killer whales and marine mammal trends in the North Pacific—a re-examination of evidence for sequential megafauna collapse and the prey-switching hypothesis. Marine Mammal Science 23:766-802.

Werner EE, Peacor SD. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083-1100.

Whitehead H, Moore MJ. 1982. Distribution and movements of West Indian humpback whales in winter. Canadian Journal of Zoology 60:2203-2211.

Williams R, Lusseau D, Hammond PS. 2006. Estimating relative energetic costs of human disturbance to killer whales (Orcinus orca). Biological Conservation 133:301-311.

Wilmers CC, Estes JA, Edwards M, Laidre CL, Konar B. 2012. Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis for sea otters and kelp forests. Frontiers in Ecology and the Environment 10:409-415.

Wing SR, Jack L, Shatova O, Leichter JJ, Barr D, Frew RD, Gault-Ringold M. 2014. Seabirds and marine mammals redistribute bioavailable iron in the Southern Ocean. Marine Ecology Progress Series 510:1-13.

Wirsing AJ, Heithaus MR, Frid A, Dill LM. 2008. Seascapes of fear: evaluating sublethal predator effects experienced and generated by marine mammals. Marine Mammal Science 24:1-15.