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Abstract

Based upon a system ecological perspective, the role of the great whales for world ocean ecosystem engineering is investigated. The function of the whale pump for the recycling of limiting nutrients for primary production and for the sequestration of carbon on the sea-floor is explored. The former is significant in the Southern Ocean, but negligible in the Northern Pacific and Atlantic Oceans. The whale pump has probably no impact on the latter, the vertical export of carbon. Nutrients from sediment resuspension by feeding whales play only a role for biogeochemical cycling in the shallowest regions, along with other bottom-feeding mammals, which rarely face nutrient limitation. Whale falls are not essential to prevent species extinction in the deep-sea because their probability is so low that it may take 100 generations before deep-sea organism experience a whale fall. The all-over effect of the great whales as ecosystem engineers needs to be reconsidered for the different regions of the world ocean. Their impact as ecosystem engineers is far smaller than commonly portrayed in the literature.

1. Introduction

Important keystone species whose behavior strongly affects other organisms and biogeochemical cycling are described as ecosystem engineers (Haemig, 2012), but the term is for the most associated with terrestrial ecosystems (Coleman and Williams 2002). Recent studies suggested that the great whales operate as ecosystem engineers, potentially playing a crucial role in maintaining marine ecosystem structure and function (e.g. Roman and McCarthy, 2010; Roman et al. 2014; Smith 2014). As biogeochemical cycling of limiting elements such as the macronutrients nitrate and micronutrient iron are essential for the sustainability of primary production it has been argued that decreases in marine mammal populations may be detrimental to marine ecosystem resilience. Under the generic term "whale ecosystem engineering" the following processes have been highlighted as potential mechanisms by which the great whales can influence and shape ecosystems: a) the whale pump (whales feed in the deeper tiers of the sea to then return to the surface and release flocculent fecal plumes), b) resuspension of soft sediment (and nutrient release) on shallow continental shelves, and c) carcass export to the deep-sea floor, whale falls. Every year, up to 2,000 cetaceans beach themselves (stranded whales, e.g. Martin and Anthony, 1991; Moore et al., 2018). Also dead whales reach ashore (drift whales). Both have some significance for littoral and terrestrial ecosystems and is thus also part of whale ecosystem engineering. In this paper we evaluate the significance of the four processes for the function of marine ecosystems. For this we select a system ecological viewpoint. Here we evaluate the four processes of whales as ecosystem engineers for a few relevant regions. We apply ecological information from the literature to address and discuss the question to what extent the great whales act as important ecosystem engineers. To what extent do the four processes play a crucial role in maintaining the function of entire marine ecosystems?

2. Material and methods

Although nutrient recycling is essential for our investigation, we base our calculation on carbon as the "currency" for biomass and production (assuming Redfield ratios to convert approximately to N and P).

2.1 Marine mammal abundance and estimated prey consumption

To evaluate the significance of the whale pump and to estimate the role of whales in the carbon cycle we select the well-investigated Barents Sea ecosystem (1,400 10^3 km^2), which is rich in marine mammals (see Supplement I) . The approach closely follows that of Smith et al. (2015b) in terms of estimating marine mammal biomass and prey consumption. It is based on the most recent estimates of abundance, residence time and body mass for the species in question. For marine mammal abundance and estimated prey consumption in the Barents Sea Skern-Mauritzen et al., (2021) consider 21 marine mammal species that inhabit the Northeast Atlantic. Of these 18 are known to be present in the Barents Sea either seasonally or permanently. Of these, 7 are pinnipeds, while 14 are cetaceans. Here we consider only large whales, including Blue, Fin, Sei, Humpback, Sperm, Minke and Bowhead whales.

Due to limited knowledge on consumption rates or energy requirements for many species included in this study, we follow Skern-Mauritzen et al. (2021) and base our

estimations on the generalized form of the Kleiber equation that scales average daily consumption C to body mass M:

$$C = \alpha M^{\beta}$$

where α and β are species- or taxon-specific parameters (Kleiber, 1932; Leaper & Lavigne, 2007). Skern-Mauritzen et al. (2021) generally use parameters suggested by Smith et al. (2015b) in their thorough evaluation but exclude those that resulted in unrealistic estimates of consumption rates. For each taxonomic group (pinnipeds, odontocetes and mysticetes), several different parameterizations were available, and are presented in supplementary Table S2 in Skern-Mauritzen et al. (2021). Uncertainty estimates for consumption were obtained by running 1000 Monte Carlo simulations for each species, where a different α/β parameter pair was randomly selected from the available parameter pairs for that taxonomic group.

2.2.Carbon content of total prey consumption and in feces

To estimate the role of large whales in the Barents Sea carbon cycle based on the estimated prey consumption presented in Table 1, we use estimates from Lavery et al. (2014). We assume a dry weight equal to 20% of total consumption, whereof 50% is assumed to represent carbon, i.e. a prey carbon content of 10%. Further, we assume an assimilation rate of 90% of dry weight. This means that 10% of the ingested dry weight will be excreted in the feces, representing 2% of the total biomass consumed. Assuming 50% of this dry weight is carbon leads to fecal carbon content representing 1% of the total ingested prey biomass. Therefore, dividing the prey consumption estimates in Table 1 by 1000 gives us an estimate of the amount of carbon released by large whales annually in the Barents Sea (Table 2).

2.3 Global whale biomass and 'whale falls'

To estimate both historical and current carbon contribution of whale falls into the deep ocean, we use abundance estimates from Christensen (2006). To estimate biomass, we simulate 1000 population sizes, based on mean and CVs presented in Table 1. In each of these simulated populations, we randomly assign a body mass for each individual, using body masses in Table 1 and a common CV of 0.2. Note that in terms of body size, we assume all individuals are adults. We then calculate the total biomass for each of the simulated populations. We then estimate the number of whales dying annually, assuming that 20% of the population are calves and that annual mortality rates are 0.1 and 0.03 for calves and adults respectively. Note that, while we assume different mortality rates for calves and adults, we do not model entire population demographics in this simple example. Summary statistics across these simulated populations are presented in Tables 3 (pre-whaling) and 4 (current).

3. Results

3.1 The whale pump

To evaluate the potential role of the whale pump of the great whales we estimated how much of the available biomass by primary produces would be grazed and recycled. As an example for the Northern Hemisphere we select the Barents Sea (e.g., Sakshaug, 2004; Sakshaug et al., 2009) where great whales are prominent (Table 1). The average annual primary production for the entire Barents Sea is estimated to be about 142 10^6 t C, of which 42 % is new production, i.e. the biomass that could be consumed or sink to the bottom (Wassmann et al. 2006). The annual prey consumption by the great whales in the Barents Sea is 345,620 t C (Table 2), comprising about 0.6 % of the new (or harvestable) production. As compared to the prey consumption of mesozooplankton (i.e., about 29 10^6 t C), comprising 20 % of the harvestable production (Wassmann et al., 2006) the consumption (and recycling of nutrients) of the great whales is small. Among the great whales Minke whales have the greatest share in prey consumption (48%).

To evaluate the potential role of whale pump of the great whales for sequestration of carbon on the sea floor we assumed that all their feces would sink to the bottom. The potential vertical export of feces by the great whales is 34,560 t C (Table 2) and comprises only 0.09 % of the estimated vertical C flux in the Barents Sea (Wassmann et al., 2006). Because most of the fecal matter of the great whales is discharged in the surface as fecal plumes, they contribute negligible amounts of carbon to the benthos.

Based upon the Skern-Mauritzen et al. (2021) similar analyses have been made for all marine mammals, implying that seals consume amounts of prey that are similar to that of whales (Supplement 2).

Does the whale pump stimulate primary production of the whale feeding grounds in the Southern Ocean and around Antarctica? The Southern Ocean is rich in macronutrients (such as silicate and nitrate) but primary production, in contrast to the northern and Arctic Oceans, limited by the micronutrient iron (e.g. Moore et al. 2013). Also, the Southern Ocean is characterized by the Antarctic Circumpolar Circulation, which circles the Antarctic continent. It acts as a natural border between Antarctic water masses and water masses to the north, thereby effectively reducing northward nutrient export. This is in stark contrast to the internal circular circulation in the Arctic Ocean, which is driven by poleward advection through the Bering Strait and the Fram and St. Anna Straits (Hunt et al. 2013, Wassmann et al. 2015, Wassmann et al. 2019). In the Southern Ocean whales and other organisms continuously fertilize their feeding grounds that engirdle the Antarctic continent. Preliminary estimates of the defecation contribution by Blue, Fin and Humpback whales to the limiting Fe for primary production were published by Ratnarajah et al. (2015). The maximum regeneration of Fe through grazing by Blue, Fin and Humpback whales that could support primary production was up to 23.4, 13.9 and 1.7 g C m^{-2} y^{-1}, respectively. Assuming an average primary production the Southern Ocean in the range of 50-70 g C m^{-2} y^{-1} (Pabi et al., 2008), Blue, Fin and Humpback whales may contribute a maximum of 40, 24 and 3 % of the primary production limiting iron. In concert, Blue, Fin and Humpback whales could thus possibly support about 56 to 78 % of today's primary production estimates for the Southern Ocean (Ratnarajah et al. 2015).

3.2 Sediment resuspension

In shallow waters sediment resuspension by whales comprises a mechanism that may contribute to increased primary production. This is particularly the case in the Bering Strait, adjacent sectors of the Chukchi Sea and eastern coastal sections of Alaska (Grebmeier, 1993). Sediment resuspension is not quantified and only speculations can be presented. The approximately 26,000 North Pacific Gray whales seem to favor feeding planktonically in most of their feeding grounds, but benthically in shallower waters along their migration routes (Oliver et al. 1981; Newell and Coles 2006, Moore et al. 2007). Their grazing on bottom living amphipods in shallow regions of the Pacific sector of the Arctic Ocean (e.g., Coyle et al. 2007) may thus contribute nutrients for photosynthesis, with an estimated average primary production rates of 124 g C m^{-2} yr^{-1} (Brown et al., 2011). Their exact contribution of nutrients has not been assessed. However, the vertically mixed, inflowing Pacific water is rich in macronutrients and nutrient depletion of any significance is first observed in late summer (Cota et al. 1993, Mordy et al. 2017). As a consequence, availability of nutrients by continues advection during the productive season, vertical mixing and release from the benthos is far higher than what sediment resuspension by Gray whales or other bottom feeding mammals provides. The contribution of bottom feeding marine mammals is thus probably not significant to sustain the extensive primary production in the Bering Strait and the shallow Chukchi Sea and eastern coastal sections of Alaska. Other polar regions that support major whale populations are so deep that nutrients from sediment resuspension cannot support primary production.

3.3 Whale falls and stranded/drift whales

How significant are the great whales' carcasses in terms of nutrient and energy delivery to deep sea ecosystems (>200 m depth, cover about 300 million km^2)? We estimated the whale biomass of the World Ocean and their carbon contribution of whale falls by assuming 3.5 million individuals of the time prior to industrial whaling (Christensen, 2006). A summary statistics across these simulated populations for preindustrial and present times are presented in Tables 3 and 4, respectively.

The estimated total global wet weight biomass of great whales prior to industrial whaling is estimated to 153.5 (95% CI: 122.7 - 184.4) million t. The wet weight biomass for whales dying annually is estimated to 6.76 (95% CI: 5.4 - 8.11) million t (Table 3). The equivalent numbers for estimated 2001 populations are 39.5 (95% CI: 25.7 - 53.3) million t of live biomass and 1.74 (95% CI: 1.13 - 2.35) million t of estimated dead biomass, i.e. a reduction of 74% (Table 4). Assuming the same ratios of wet to dry weight and carbon content of dry matter as above, these estimates translate to 675,516 (95% CI: 539,865 - 811,167) t of carbon per year contained in dead whales during pre-whaling times, and 173,775 (95% CI: 112,961 - 234,589) t of carbon per year contained in dead whales using the 2001 estimates from Christensen (2006). This suggests that, on average, a supply by whale falls to the deep-sea benthos of 2.25 and 0.58 mg C g m^{-2} y^{-1}, respectively. Assuming a vertical export of particulate organic carbon to the deep sea of 1 g m^{-2} y^{-1} (Lampitt and Antia, 1997; Lampitt et al. 2010; Wiedmann et al. 2020) whale carcasses represent, on average, 0.2 and 0.05 % of the annual carbon supply to the deep sea.

The number of reported stranded whales (usually toothed whales) and those drift whales (usually bearded whales) is low as compared to the global death rate of whales (Table

4). Although locally of significance for both littoral and terrestrial organisms and considering the length of the global costal line (356,000 km) strand falls are of little global significance for ecosystem engineering. This, strand falls will not be considered any further.

4. Discussion

A range of publications launched and supported the idea that the great whales have a significant impact on ecosystem function (e.g. Smetacek et al., 2008; Roman et al. 2010, Roman et al. 2010, 2014; Smith et al. 2019). No doubt, the great whales, along with all the other organism groups, have an impact upon other organisms and biogeochemical cycling, as elaborated in Roman et al. (2014). But what is the relative contribution of whales for ecosystem engineering? Ecosystem engineers are defined as important keystone species in an ecosystem whose behavior strongly affects other organisms and biogeochemical cycling (Haemig, 2012). Do the great whales qualify as significant ecosystem engineers? How strongly does the ecosystem impact by the great whale's effect other organisms and biogeochemical cycling? What is their relative contribution to ecosystem engineering in the various regions and ecosystems of the world ocean?

4.1 Is the whale pump of generic significance for primary production?

Over the expanse of the Southern Ocean the great whales do indeed act as ecosystem engineers. Primary production is not limited by macronutrients, but by the micronutrient Fe. Birds and whales redistribute bioavailable iron in the Southern Ocean (Wing et al. 2014), but also eolian deposition plays a role (Graham et al., 2015). In concert, today's abundance of Blue, Fin and Humpback whales could possibly support about 56 to 78 % of current primary production estimates for the Southern Ocean (Pabi et al., 2008; Ratnarajah et al., 2015). Bobble curtains produced by feeding whales may represent an additional source of Fe supply that may stimulate primary production (Smetacek et al., 2008). Considering a great whale abundance 100 years ago (Christensen, 2006) whales probably supplied more iron in earlier times, influencing primary and krill production (Willis, 2014).   Thus primary and krill production may have originally been greater than today, as suggested by Smetacek (2008), Nicol et al. (2010) and Lavery et al. (2010, 2014).   A mutual dependency between Fe availability, primary and krill production and whale populations seems to exist in Southern Ocean. Indeed, the great whales are keystone species in Southern Ocean ecosystem whose behavior strongly affects other organisms and biogeochemical cycling. Thus they act truly as ecosystem engineers.

That is in contrast to the Northern Hemisphere where the whale pump does not qualify as significant ecosystem engineers.   For the whale-rich north-easter North Atlantic (Moore et al., 2019) estimates suggest that the maximum contribution to vertical export of carbon through fecal matter is negligible. In the Barents Sea whale feces comprise at maximum only 0.09 % of the estimated vertical C flux (Table 2; Wassmann et al., 2006). The annual prey consumption by the great whales in the Barents Sea comprises only about 0.6 % of the harvestable production (Table 2; Wassmann et al. 2006). As a consequence the recycling of the limiting macronutrient ammonium/nitrate is small. Even if we assume that the feeding of the great whales in the Barents Sea is limited to only 30 % of the total area, the whale pump contributes potentially less than 2 % of the nutrients. Seals, fish, birds and in particular

zooplankton and the microbial loop strongly impact ecosystem behavior biogeochemical cycling of macro nutrients and comprise thus the prime ecosystem engineers.

To study experimentally how marine mammals become facilitators of rapid and efficient nutrient recycling in coastal and offshore waters Roman et al. (2016) suggests that whales contribute to nutrient availability in the Bay of Fundy, a macrotidal estuary with the world's largest tidal amplitude (16 m). Because of the tides nutrients never become limiting (Keizer and Gordon, 1985). Even in the vicinity of salmonid net pens, a strong source of nutrient release, no increase of ambient nutrients could be detected in the Bay of Fundy (Wildish et al., 1993). The rapid and efficient nutrient recycling by whales in macrotidal estuaries and bays is so small, as compared to the tidal supply and vertical mixing, that their enhancement of primary production is negligible.

Even when we assume the population of whales during pre-whaling times the whale pump cannot represent a major contributor of macronutrient recycling in the Northern Hemisphere.   However, they play an essential role in regions where micronutrients play the limiting role.

4.2 Is sediment resuspension significant for biogeochemical cycling?

The resuspension of soft sediments and the concomitant release of nutrients connected to the migration of Gray Whales through the shallow and high productive Bering Strait is well documented (e.g. Roman et al. 2014). Also from deeper sediments, such as the Barents Sea reports of whale feeding on bottom-living fish such as sandeel exist (M. Biuw, pers. com.). For the local primary production the nutrient release through sediment resuspension from deeper sea floors cannot play an important role. In the vertically mixed, inflowing and nutrient-rich Pacific water through the Bering Street nutrient depletion is observed in late summer (Cota et al. 1993, Mordy et al. 2017). As a consequence, the availability of nutrients by continues advection during the productive season, vertical mixing and release through benthos is far higher than what sediment resuspension by bottom feeding mammals provides.   The contribution of bottom feeding marine mammals, although not quantified, is probably not significant.   Thus the Bering Strait share similarities with the Bay of Fundy (and other coastal regions) where much of the nutrients are supplied by advection, not local recycling. Sediment resuspension by feeding whales has thus probably no major impact on ecosystem function.

4.3 Are whale falls essential to prevent species extinction in the deep-sea?

It has been postulated that whale falls impact deep-sea biodiversity by providing evolutionary steppingstones to move and adapt to new environmentally challenging habitats (Smith et al. 2015a). However, today's average annual supply of dying whales to the deep-sea has been calculated to comprise only 0.06 % of the vertical C export. 150 years ago the percentage was higher, but still only 0.2 %. The great whales are not evenly distributed (e.g. Hamilton et al., 2021). They migrate between feeding and mating regions, the accumulate at hot spots where food is abundant, such as fronts, eddies, the Polar Front, the North Pacific Convergence Zone or the Antarctic Circumpolar Current. Carcasses may move with currents and accumulate in gyres before they sink. It is thus challenging to relate the relative distribution of whale falls to the entire deep-sea area. In order to approximate the significance of whale falls, for nutrition and energy delivery to deep sea ecosystems we assume that whale falls take place in only 10%

of the worlds deep-sea region. Still, their contribution is far less than 1% of the annual particulate carbon supply.

Whale falls are singular events that all the sudden supply the deep-sea benthos with hundreds to thousands kg C m^{-2} of highly nutritious food. They create complex, highly localized ecosystems that supply highly transient sustenance to deep-sea organisms (Little, 2010; Smith et al. 2015a). A whale of 20 m length, 2 m width and a wet weight of 50 t comprises a supply that is 125,000 times greater than the average vertical C supply. The deep-sea fauna is able to consume whale falls rapidly and is thus extremely well-prepared to tackle these rare events. However, how often will a whale fall happen? Even if we assume that whale falls take place in only 10 % of the deep-sea regions the probability to experience a whale fall is > 10,000 years. Assuming a life length of 100 years for deep-sea species it takes more than > 100 generations to experience a whale fall. The probability of a whale fall is too low for even the longest deep-sea organism to become part of the evolutionary strategy. The feeding strategy that deep-sea species apply to take advantage of whale falls is savaging and they must be opportunists.

It has been postulated that whale falls generate biodiversity by providing evolutionary steppingstones (Smith et al. 2015a). However, as a consequence of the multitude of generations between each whale fall, the ecosystem engineering effect of the great whales falls upon the deep-sea benthos in general must be minute. Whale falls are thus not essential to prevent species extinction in the deep-sea.

4.4 Conclusion

Whales are significant ecosystem engineers that support biogeochemical cycling of bio elements in regions where micronutrients limit primary production. In regions where primary production is determined by macronutrient availability their impact upon biogeochemical cycling of bio elements is small. The great whales have probably no impact on carbon sequestration. Although of utmost significance when whale falls occur, the carcasses of the great whales are not essential to prevent species extinction in the deep-sea.

By omitting to evaluate the relative role of whales as ecosystem engineers in a system ecological context and by extrapolating Southern Ocean studies to the entire world ocean we believe that the role of whales as global ecosystem engineers can be exaggerated. Whales are only a small portion of the ocean's overall biomass and our research cannot support the conclusion of Pershing et al. (2010) that whaling has altered the ocean's ability to store and sequester carbon in quantities relevant for the global carbon cycle. This may be in contrast to fisheries which probably do play a role for the global carbon cycle. Marine birds, fish and particularly zooplankton and the microbial organisms are the "real" engineers in the world ocean.

The literature considering great whale engineering has resulted in problematic interpretations in the quasi-popular and popular literature. For example, the International Monetary Fund, based upon some of the above-mentioned literature, suggests that protecting whales can limit greenhouse gas emission and global warming (Chami et al., 2019) and concludes that whales are nature's solution to climate change. According to these arguments, as whale populations recover, the magnitude of the whale pump will also grow, helping to mitigate the impact of fossil fuel use. Such generalizations are based upon unrealistic interpretations on the role of whales as ecosystem engineers. They do not support system

ecological based balanced scientific evaluations of the potential role that organisms play in shaping the structure and maintaining the resilience of marine ecosystems.

The term ecosystem engineer is surprisingly rarely applied marine ecological literature (Wright et al. 2002; Berke et al. 2010; Haemi 2012). It induces lines of thought that consider ecosystems as simplistic, mechanistic systems that through dedicated engineering procedures may be managed and regulated. To comprehend the physical-biological coupling of marine ecosystem, to understand the function and structure of foods webs, let alone to conduct responsible resource and ecosystem management, requires detailed, comprehensive and systemic ecosystem understanding (e.g. Carmack and Wassmann, 2006; Wassmann et al., 2020). Care should be taken to omit simplistic interpretations such as ecosystem engineering. They do not adequately support what we need to most to obtain knowledge-based resource- and ecosystem management: a balanced comprehension of physical-biological coupling and marine ecosystem food webs.

5. Acknowledgement

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Table 1. Abundance (mean, Coefficient of variation), average body mass (kg) residence time (days) of large whales in the Barents Sea. Also shown are their estimated prey consumption (median and 95% confidence limits).

Species	Abundance	Body mass (kg)	Residence time (d)	Consumption (x 1000 T)
Blue	100 (0.5)	100,000	180	23.9 (8, 50.8)
Fin	4,506 (0.54)	55,500	180	691.9 (217.4, 1,510.1)
Sei	0 (0)	17,000	0	0 (0, 0)
Humpback	8,563 (0.81)	30,400	180	953.3 (223.6, 2,391.8)
Sperm	806 (0.71)	40,000	150	58.4 (10.3, 157.7)
Minke	47,295 (0.3)	6,600	180	1,665.5 (742.4, 3,082.6)
Bowhead	173 (0.49)	80,000	365	63.2 (23.7, 131.5)

Table 2. Total prey consumption (wet weight), dietary dry weight, dietary carbon content, fecal dry weight and fecal carbon content. All are expressed in 1000 tons

Species	Prey consumption	Prey dry weight	Prey carbon	Fecal dry weight	Fecal carbon
Blue	23.9	4.78	2.39	0.48	0.24
	(8, 50.8)	(1.6, 10.16)	(0.8, 5.08)	(0.16, 1.02)	(0.08, 0.51)
Fin	691.9	138.38	69.19	13.84	6.92
	(217.4, 1,510.1)	(43.48, 302.02)	(21.74, 151.01)	(4.35, 30.2)	(2.17, 15.1)
Sei	0	0	0	0	0
	(0, 0)	(0, 0)	(0, 0)	(0, 0)	(0, 0)
Humpback	953.3	190.66	95.33	19.07	9.53
	(223.6, 2,391.8)	(44.72, 478.36)	(22.36, 239.18)	(4.47, 47.84)	(2.24, 23.92)
Sperm	58.4	11.68	5.84	1.17	0.58
	(10.3, 157.7)	(2.06, 31.54)	(1.03, 15.77)	(0.21, 3.15)	(0.1, 1.58)
Minke	1,665.5	333.1	166.55	33.31	16.66
	(742.4, 3,082.6)	(148.48, 616.52)	(74.24, 308.26)	(14.85, 61.65)	(7.42, 30.83)
Bowhead	63.2	12.64	6.32	1.26	0.63
	(23.7, 131.5)	(4.74, 26.3)	(2.37, 13.15)	(0.47, 2.63)	(0.24, 1.32)
Total		345.62	34.56		

Table 3. Estimated pre-whaling total biomass and biomass contained in animals dying during one year, expressed in 1000 tonnes. NA = North Atlantic, NP = North Pacific, SH = Southern Hemisphere.

Species	Ba:	N	Biomass	N Dead	Dead biomass
Bowhead	Arc	89,013 (0.13)	7,121 (5,363, 8,880)	3,917 (0.13)	313 (236, 391)
Sperm	Glo	955,142 (0.11)	38,206 (29,785, 46,626)	42,026 (0.11	1,681 (1,311, 2,051)
Sei	N.	10,571 (0.15)	180 (128, 232)	465 (0.15)	8 (6, 10)
Fin	N.	72,549 (0.13)	4,026 (3,032, 5,021)	3,192 (0.13)	177 (133, 221)
Blue	N.	7,395 (0.1)	739 (591, 888)	325 (0.1)	33 (26, 39)
Humpback	N.	16,131 (0.15)	490 (342, 638)	710 (0.15)	22 (15, 28)
Minke	N.	211,409 (0.13	1,395 (1,047, 1,744)	9,302 (0.13)	61 (46, 77)
Right whale (N Atl)	N.	14,089 (0.15)	1,198 (852, 1,543)	620 (0.15)	53 (37, 68)
Right whale (N Pac)	N	14,158 (0.14)	1,203 (868, 1,538)	623 (0.14)	53 (38, 68)
Sei	N	68,564 (0.1)	1,166 (931, 1,400)	3,017 (0.1)	51 (41, 62)
Fin	N	64,567 (0.11)	3,583 (2,781, 4,386)	2,841 (0.11)	158 (122, 193)
Grey	N	21,194 (0.06)	848 (749, 947)	933 (0.06)	37 (33, 42)
Blue	N	5,841 (0.11)	584 (457, 711)	257 (0.11)	26 (20, 31)
Bryde	N	52,325 (0.1)	2,093 (1,684, 2,502)	2,302 (0.1)	92 (74, 110)
Humpback	N	16,579 (0.18)	504 (322, 686)	729 (0.18)	22 (14, 30)
Minke	N	47,346 (0.11)	312 (243, 382)	2,083 (0.11)	14 (11, 17)
Sei	Sl	166,815 (0.03	2,836 (2,668, 3,003)	7,340 (0.03)	125 (117, 132)
Southern right	Sl	85,787 (0.08)	7,292 (6,182, 8,402)	3,775 (0.08)	321 (272, 370)
Fin	Sl	624,268 (0.13	34,647 (25,563, 43,731)	27,468 (0.13	1,524 (1,125, 1,924)
Blue	Sl	327,444 (0.04	32,744 (29,971, 35,518)	14,408 (0.04	1,441 (1,319, 1,563)
Bryde	Sl	94,125 (0.13)	3,765 (2,790, 4,740)	4,142 (0.13)	166 (123, 209)

Table 4. Estimated current (2001) total biomass and biomass contained in animals dying during one year, expressed in 1000 tonnes. NA = North Atlantic, NP = North Pacific, SH = Southern Hemisphere.

Species	Bas	N	Biomass	N Dead	Dead biomass
Bowhead	Arc	9,443 (0.1)	755 (603, 907)	415 (0.1)	33 (27, 40)
Sperm	Glol	376,060 (0.11)	15,042 (11,912, 18,173)	16,547 (0.11)	662 (524, 800)
Sei	N/	6,933 (0.12)	118 (90, 146)	305 (0.12)	5 (4, 6)
Fin	N/	55,531 (0.12)	3,082 (2,350, 3,814)	2,443 (0.12)	136 (103, 168)
Blue	N/	370 (0.15)	37 (26, 48)	16 (0.15)	2 (1, 2)
Humpback	N/	12,351 (0.1)	375 (302, 449)	543 (0.1)	17 (13, 20)
Minke	N/	157,424 (0.13)	1,039 (781, 1,297)	6,927 (0.13)	46 (34, 57)
Right whale (N Atl)	N/	368 (0.15)	31 (22, 41)	16 (0.15)	1 (1, 2)
Right whale (N Pac)	Nl	369 (0.16)	31 (22, 41)	16 (0.16)	1 (1, 2)
Sei	Nl	14,412 (0.23)	245 (136, 354)	634 (0.23)	11 (6, 16)
Fin	Nl	31,221 (0.31)	1,733 (663, 2,803)	1,374 (0.31)	76 (29, 123)
Grey	Nl	15,764 (0.04)	631 (582, 679)	694 (0.04)	28 (26, 30)
Blue	Nl	3,172 (0.15)	317 (224, 411)	140 (0.15)	14 (10, 18)
Bryde	Nl	41,175 (0.13)	1,647 (1,234, 2,059)	1,812 (0.13)	72 (54, 91)
Humpback	Nl	7,211 (0.14)	219 (161, 277)	317 (0.14)	10 (7, 12)
Minke	Nl	31,719 (0.12)	209 (158, 260)	1,396 (0.12)	9 (7, 11)
Sei	SH	27,581 (0.25)	469 (243, 695)	1,214 (0.25)	21 (11, 31)
Southern right	SH	66,685 (0.47)	5,668 (415, 10,922)	2,934 (0.47)	249 (18, 481)
Fin	SH	23,314 (0.19)	1,294 (817, 1,771)	1,026 (0.19)	57 (36, 78)
Blue	SH	1,179 (0.13)	118 (88, 148)	52 (0.13)	5 (4, 7)
Bryde	SH	91,050 (0.13)	3,642 (2,689, 4,595)	4,006 (0.13)	160 (118, 202)
Humpback	SH	22,484 (0.14)	683 (495, 872)	989 (0.14)	30 (22, 38)
Minke	SH	319,350 (0.11)	2,108 (1,666, 2,550)	14,051 (0.11)	93 (73, 112)

Supplement I.
Abundance, biomass (wet eight) and consumption of marine mammals (wet weight) in the Barents Sea.

Species	Abundance	Biomass (x 1000 tons)	Consumption (x 1000 tons)
Harbour seals	6 432 (0.50)	0.6 (0.2, 1.4)	8.4 (2.7, 17.6)
Grey seals	6 011 (0.27)	1.2 (0.6, 2.2)	13.7 (6, 24.2)
Ringed seals	100 000 (0.50)	7.5 (2.4, 17.9)	112.2 (36.1, 244.8)
Bearded seals	10 000 (0.50)	2.5 (0.8, 5.8)	27.5 (9.5, 58.2)
Harp seals	1 497 189 (0.07)	182 (104, 264.5)	2391.6 (1244.8, 3741.9)
Hooded seals	0	0 (0, 0)	0 (0, 0)
Walrus	15 000 (0.5)	18.3 (5.9, 46.7)	130.5 (39.9, 292.8)
White whales	10 000 (0.50)	13.5 (4.4, 32.6)	137.8 (35.8, 304.1)
Narwhals	3 500(0.50)	4.5 (1.5, 10.5)	47.3 (12.1, 100.8)
Killer whales	503 (0.71)	2.2 (0.4, 6.5)	17.1 (3.1, 47.8)
Sperm whales	806 (0.71)	31.4 (6.3, 88.4)	58.4 (10.3, 157.7)
Lagenorhynchus dolphins	144 453 (0.53)	31.5 (9, 82)	512.5 (117.5, 1203.4)
Pilot whales	500 (0.5)	0.9 (0.3, 2.2)	4.5 (1.1, 10.2)
Harbour porpoise	85 731 (0.57)	4.9 (1.4, 12.6)	100.1 (21.9, 237.9)
Bottlenose whales	100 (0.5)	0.6 (0.2, 1.4)	2 (0.5, 4.7)
Minke whales	47 295 (0.30)	304 (135, 580.1)	1665.5 (742.4, 3082.6)

Fin whales	4 506 (0.54)	250.8 (69.7, 617.9)	691.9 (217.4, 1510.1)
Humpback whales	8 563 (0.81)	268.1 (48.4, 881.6)	953.3 (223.6, 2391.8)
Blue whales	100 (0.50)	9.9 (3.2, 23.1)	23.9 (8, 50.8)
Sei whales	0	0 (0, 0)	0 (0, 0)
Bowhead whales	173 (0.49)	14.0 (4.4, 33.4)	63.2 (23.7, 131.5)