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Global importance of supporting the krill to whale component of the pelagic food web associated with migrations following deep sea seamounts

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Abstract

The main diet of baleen whales is krill in the Arctic, Antarctic and during migrations in the Atlantic, Pacific and Indian Oceans. Hence, the aim of this paper is to quantify the global importance of the krill to baleen whale component of the pelagic food web and possible feedback loops. That was undertaken by comparing the results of Ecopath Models in the Antarctic and Arctic Oceans and to migration areas in the North Atlantic and Alaska, was well as the large Seamount area from the Antarctic and Arctic. Biological production transfer is the essential component of the prey to predator pelagic food web, which maintains the production of predators. The importance of sustaining global baleen whale migrations is to support ecosystem production by whale defecation contribution to nutrient recycling. It is important to sustain krill and fish abundance in whale migration feeding areas using ecosystem-based fishery management (EBFM) fishing rates. It was shown by the literature that migrations tended to followed deep-sea seamounts, and baleen whale defecation and nutrient cycling at seamounts led to the effects of nutrient upwelling by deep sea currents at seamounts. Hence, it is suggested seamounts be protected as important marine ecosystems. Therefore, those processes indicate sustaining krill and whale abundance is likely to support global marine ecosystem stability in open ocean migration areas.

Introduction

This study aims at defining the importance of supporting the krill to whale component of the pelagic food web. In this context, a food web is the feeding relationships for pelagic, open sea, species moving up in trophic levels (TL) from phytoplankton in TL1 to krill, a large zooplankton, in TL2, to small pelagic fish such as sardines in TL3 and to predators TL4. In the study here, baleen whales feed on krill and fish, giving a TL less than 4.0. Note that predators consume a variety of prey species in each TL and may feed sometimes other levels such as the baleen whales. Importantly, baleen whales have no teeth but filter their prey by rows of long protein based fringed plates. Hence, this study relates to the potential global scale sustainability of open ocean production by release of nutrients by baleen whale consumption of krill and other prey via defecation. The trophic transfer of krill biological production to baleen whales provides an important understanding of the pelagic food web, which can be estimated from information in Ecopath models [1]. They are an ecological model showing differences in biomass and production of species in a pelagic food web, including the amount of prey consumed by predators in the ecosystem. Trophic transfers were estimated from information in Ecopath models used in polar areas where baleen whales feed and during winter migrations to temperate areas. That global process aligns with the objectives of the UN Decade of Ocean Science for Sustainable Development [2]. Hence, this study undertakes an initial global trophic dynamics study of food flow, with related nutrient enrichment, and ecological production driven by baleen whale migrations. The study is supported by the recent understanding of worldwide baleen whale migration pathways and maps of deep-water ridges which indicate baleen whales tend to follow ridge related seamounts with potential nutrient enrichment of surface waters by deep-water ocean currents [3]. Seamounts are submarine mountains that support deep-sea ecosystems but don't reach the water surface.

In the Antarctic Ocean, krill (Euphausia superba) has been shown as an important component of the zooplankton production and is a major food source for baleen whales, particularly the Humpback Whale (Megaptera novaeangliae), [4], however krill consumption was estimated the most by Antarctic penguins by [5]. Furthermore, baleen whale consumption of krill in the Antarctic leads to nutrient recycling from fecal material and increased phytoplankton production, PP, see [6], [7] and [8]. That suggests baleen whale consumption of krill in the Antarctic Ocean may contribute to nutrient input of the circumpolar circulation promoting high Southern Ocean phytoplankton production [9], as well as supporting Krill production with feedback to whale abundance. For further information on baleen whale contribution to ecosystem production, see for example the literature by [10] and [11], as well as the food web structure of krill abundance in the Arctic [12] and the Antarctic by [13].

krill to baleen whale food web transfer

Surprisingly, there is limited literature on the global importance of supporting the krill to baleen whale food web transfer, but [14] mention benthos, the animals that live on, in, or near the bottom of a sea, is related to phytoplankton production in the Arctic Ocean food web and phytoplankton supports production of zooplankton and krill, pelagic fish and baleen whales. However, the role of baleen whale feeding on trophic transfer from phytoplankton, to zooplankton and krill, fish and ultimately baleen whales in open ocean areas is not well known. For example, [15] found baleen whales in the Barents Sea were mostly associated with the presence of krill, and to a lesser extent with capelin, amphipods and polar cod, but they had no information on transfer of krill consumption to whales. Hence, to address the global krill to whale food web, the novel approach of using published Ecopath Model data was used to describe the krill to whale trophic transfers.

Global importance of baleen whale consumption of krill for nutrient recycling

The literature indicates nutrient recycling process by whale consumption of krill and fish could occur globally. In terms of global processes, [16] studied the global importance of nutrient recycling for ecosystem production and [17] found nutrient cycling was associated with cetaceans, marine mammals including whales, dolphins, and porpoises, consumption of fish, rather than krill. The study by [18] sampling the Gulf of Maine was dominated by baleen whales and the whales sustained production where they occurred in high densities. Most of the nitrogen released by defecation was as ammonia in the shallower portion of their depth range. The recycled nutrients were expected to increase local phytoplankton production, leading to increased zooplankton, Euphausiids, and small pelagic fish consumed by the whales. That was upheld by [19] who found whales can influence food web biogeochemical cycles by moving nitrogen and iron to surface waters. Furthermore, [20] suggested implementation of global processes to maintain whale numbers could increase nutrient recycling and release fisheries from the effects of overfishing. The study by [21] found pre-whaling populations may have supported productivity in global large marine regions through enhanced nutrient recycling of iron and in regions limited by nitrogen or phosphorous. That was also noted by [22] who suggested the whale numbers could have increased production of marine ecosystems and the current population removing significant levels of carbon from the atmosphere. The literature also indicates increased water column nutrients by consumption of fish during migrations [17]. They noted whale defecation in the normally nutrient limited world's deep-water oceans is likely to increase the production of surface waters via upwelling processes, and likely due to returning to surface water to breathe where defecation introduces nutrients. Hence, this paper describes the global importance of quantifying the krill to whale component of the pelagic food web.

Coastal nutrient upwelling and baleen whale migrations

The global baleen whale migrations are known to occur along productive continental western coastal areas due to upwelling of nutrients on their way to breeding grounds (See migration maps in [23] and description of whale migrations in [24]. Upwelling is an oceanographic process involving movement of dense, cooler, and mostly nutrient-rich water from deep water towards the ocean surface, replacing the warmer nutrient-depleted surface waters. Due to the prevalence of upwelling of nutrients to surface water production [25] it is not surprising that whale migrations tend to occur along the west coast of continents. The migration map in [26] shows baleen whale migrations from the Bering Sea Arctic along the west coast of North America to Mexico, including out to Hawaii by humpback whales, and blue whales migrating further south to Costa Rica. In addition, blue whales, including humpback whales, are shown to migrate up the west coast of South America to southern Ecuador [27], which are likely originating from the Southern Ocean via the Antarctic Peninsula. The benefit of upwelling to whales is also supported by [28] who showed high Euphausiid densities of Thysanoessa spinifera and Euphausia pacifica are supported by high primary production on the west coast of North America in Monterey Bay, California and potentially by blue whale feeding on the krill.

In the southern hemisphere, migration was noted In Western Australia and the east coast of Australia and islands of the South Pacific (Oceania). A source of whales at islands of the South Pacific was indicated in the Ecopath Model of Bali Strait, Indonesia by [29]. They noted whales migrate from the Indian Ocean to Pacific Ocean via passages between Indonesian Islands. Although they only noted Minke Whales (Balaenoptera acutorostrata and Sperm Whales (Physeter catodon) at Bali, it is likely they came from the Antarctic via Western Australia [30], likely along the archipelagos and range of islands at Ashmore, Cartier, Timor and Suva to Indonesia. However, [24], see their Table 2, reported Blue whales from Antarctica migrate to the west coast of Australia in the eastern Indian Ocean and then north into the Banda Sea, around Timor, Indonesia. They also noted Humpback and baleen whale breeding stocks off Western and Eastern Australia, southern right whales off south-central and southwestern Australia. Furthermore, the map by [26] also shows migrations in the southern Atlantic Ocean occurred in productive coastal areas of Brazil and southwestern Africa. In the Indian Ocean, migrations were noted south of the Horn of Africa in the Somali Sea, south-eastern Africa and Madagascar, and in the Pacific Ocean. In addition, they showed breeding and calving during summer and winter areas along continental western South America to the Corcovado Gulf in Chile. Those supplement the location of global humpback whale breeding and calving areas by [23]. In addition, whale migrations from the Arctic to the Caribbean islands are shown by [31] and to the Azores Islands on west coast of South America by [32] in their Ecopath Model. Although the model does not show results for local krill species, it found the baleen whales consume 13.6% fish in their diet. The study by [33] reported whale migration from Antarctica to Tanzania, eastern Africa on the coast of the Indian Ocean for breeding,

Ecopath models for biological production transfer from krill to predators

Seven Ecopath Models were found that include the Arctic and Antarctic Ocean areas, and in migration areas in the Atlantic, Pacific and Indian Oceans. The associated feedback loops of baleen whale consumption of krill production with increased phytoplankton and benthos production due to nutrient recycling were investigated. Note that a feedback loop is a process of maintaining ecosystem stability, due to the output of a process influencing the input. Benthos production was included because detritus produced by whale defecation likely increases benthos production as [34] showed benthos surface feeders consume detritus. As the published global whale migration paths also showed baleen whales tend to migrate in productive coastal areas due to upwelling, the Ecopath Model for the Northern California Current by [56] was also included to investigate the relative contribution of baleen whales to coastal production.

An additional factor was that [35] suggested the amount of krill consumed by baleen whales could be reduced by consumption by other predators such as penguins. Hence, the amount of krill production consumed by other main predators was estimated using the Diet Matrix shown in the Ecopath models, which defines the proportion of each prey in the diet of every predator in the ecosystem. As trophic transfers of prey consumption to predators involve the consumption of prey biological production rather than biomass [1], the trophic transfer method developed by [36] was used to estimate biological production transfer from krill to baleen whales as well as for other predators. Hence, it is suggested the application of various Ecopath Models across key oceanic systems and the integration of ecosystembased fishery management (EBFM) principles quantifies the influence of krill-whale interactions on nutrient recycling, phytoplankton regeneration, and benthic productivity. Importantly, the EBFM for managing fisheries maintains the marine ecosystem stability by supporting the role of predators and interactions between species in trophic levels. Accordingly, the literature was used to develop new knowledge and insights for the aim of understanding the global importance of baleen whale consumption of krill and associated sustainability of ecosystem production by feedback loops. The large marine ecosystem theory discussed by [37] was the beginning for investigating potential feedback loops. However it should be understood that [38] showed an increase in phytoplankton production in the Arctic Ocean was not due to whales but may have been due to increased new or recycled nutrients by climate change effects of reduced sea ice cover.

Methods

Krill production and baleen whale consumption as well as the related phytoplankton and benthos production were estimated using the following Ecopath Models. Ecopath Model results for the Southern Ocean krill fishery area are in the supplementary file S1 in [39], and for the Antarctic Peninsula by [40], as well as during migrations from the Antarctic Peninsula to South Georgia Island, east of Cape Horn by [41]. Significant migrations also occur from the Antarctic to seamounts at the Campbell Plateau, east of New Zealand, so the Ecopath Model for Chatham Rise by [42] is also included. Ecopath models were also used for the Arctic Ocean and migrations into the north Atlantic and Pacific Ocean. The most recent Ecopath Model data for the Norwegian Sea and Barents Sea in the Arctic Ocean by [43] was used that includes biomass and P/B ratios for krill which are consistent with the finding by [15] that baleen whales aggregate in areas of high krill abundance. Note that the study by [44] was not used due to having a low krill production about 23% of that in [43]. However, the Ecopath Model at Iceland for baleen whale migrations from the Arctic Ocean, just outside the Arctic Circle, by [45] was used. That whale migrations continue into the northern Atlantic Ocean [26], their Figure 4.1. As baleen whales also tend to migrate in nutrient enriched upwelling areas along western continental shelves, the Ecopath Model for Alaska's Prince William Sound was included [46]. The Alaska Sound area is the path for baleen whales to migrate from the Arctic Ocean via the Bering Strait to the nutrient rich upwelling area of the Northern California Current (see Figure 9 in [23].

As the study of global importance for the whale to krill food web needs to be based on using consistent results for the Ecopath Models, the Ecopath Model for the California Current ecosystem by [47], see their Table 1) gives the coefficient of variation, CV, defined as standard deviation divided by the mean. In statistics, the standard deviation is the amount of variation of values about its mean. The biomass Humpback and grey whales CV was 0.15, Fin 0.18 and for the less abundant blue 0.24 and Minke 0.30. Although the biomass for phytoplankton, benthos and krill (Euphausiids) was not known, the P/B CVs were 0.1, 0.2 and 0.2, respectively. The CVs for phytoplankton and benthos were assumed to be similar for the P/B and krill biomass assumed 0.25 using values for fish. Those CV values represent the uncertainty of the Ecopath model values used here and give an acceptable level of uncertainty in the Ecopath Model results obtained.

The criteria for using Ecopath Models were: the biomass and biological production to biomass ratio, P/B ratio, are shown for phytoplankton, krill and benthos, as well as the baleen whale biomass for the species in the ocean area studied. In this context, biological production is the rate at which the biomass of marine phytoplankton and animals is produced in an ecosystem per year. To allow estimation of krill production consumption by whales and other dominant predators via the food web, the Ecopath Models used also needed to show the trophic level of the predators and the amount of krill in their diet. The Ecopath Model Diet Matrix of predators consuming prey species shows benthic animals consume some detritus non-living particulate organic matter of dead plants and anumals and fecal animal waste, so the whale biomass was compared with the benthos production, as well as the phytoplankton production in the ocean areas. Note that detritus by itself was not used to assess the effects of whale defection because [48] showed detritus could be present as dead carcasses, dissolved organic matter or particulate organic matter, while most Ecopath Models only show the total detritus. Using the krill diet from the Diet Matrix, the method by [36] was used to estimate krill production consumed by baleen whales. The method shows how to estimate the Trophic Transfer Efficiency, TTE, of prey biological production to predators using TTE's estimated from the biological production in the Ecopath Models. Here, the TTE is the amount of prey biomass biological production passed from a lower trophic level to the next higher level in an ecosystem. The method is based on fundamentals of the prey biological production TTE to the dominant predator production originally derived by [49] of about 10%, after losses to respiration and to detritus. Note that the method of [36] to quantify trophic transfer efficiencies estimates the consumptionof prey biomass biological production by the predator, not the prey biomass obtained by B x (Q/B) using the Q/B, where Q is the biomass consumption in the ratio of Ecopath Models.

Baleen whale consumption of krill

The Ecopath Model by [39] for the Antarctic Ocean Krill (*Euphausia superba*) fishery area of 3.7 million Km^2 was used to estimate the krill to baleen whale TTE and krill consumption. The average transfer efficiency from prey production to predator production for a given trophic level ranging from TL 1 phytoplankton to TL5 upper predators was estimated by Equation 6 from [36] by:

$$TTE = 0.54 \times TL_{pred}^{-1.26} \qquad (1).$$

In this situation, TL_{pred} is the trophic level of the predator, in this case baleen whales are the main predator in the Ecopath Model with krill as the dominant prey. Additionally, the biological production transfer is the essential component of the prey to predator pelagic food web, which [36] showed maintains the production of predators for ecosystem stability.

To estimate the biological production consumption of prey by a predator it is necessary to know the biological production, P, of the prey, shown by [1] from Ecopath Model results by multiplying biomass, B, by the production to biomass ratio, P/B, giving P = B x (P/B). From ecosystem food web principles, [36], see their reported Equation 4, estimated the consumption of prey biological production by a predator, Q_{pred}, was related to the prey biological production, P_{prey}, and the TTE by:

$$Q_{pred} = P_{prey} \times \sqrt{(TTE)} \qquad (2).$$

The prey biological production consumption, Q_{pred}, in equation 2 is modified by applying the proportion of krill in the predator diet from the Diet Matrix in the seven Ecopath Models to the prey biological production, P_{prey}. Hence, the prey biological production is adjusted in equation 3 by:

$$Q_{pred} = P_{prey} \times \sqrt{(TTE)} \times Diet_{Pred} \qquad (3).$$

Note that Q_{pred} is not the total consumption of prey production by a predator because most of the food consumed, other than the approximate 10% food web transfer, is lost due to respiration and to detritus, as explained in the Ecopath Model by [1]. The production transfer does not include losses, as Q_{pred} is the krill prey production consumed by baleen whales, in this case, during summer. Also, during migrations the literature indicates baleen whales consume a mix of krill and fish species, which was recorded at the Chatham Rise Diet Matrix, so the total consumption by whales was estimated using krill and fish diets. As the krill species vary in migration areas, the Ecopath Model takes the various biomass and P/B ratios into account for estimation of biological production.

As the number of suitable Ecopath Models was limited to seven, a comparison is shown below for possible further research on the global importance of baleen whales contributing to nutrient recycling.

Results

The krill *Euphausia superba* consumption by baleen whales in the Antarctic Ocean was compared with that for the combined Arctic Ocean krill species *Meganyctiphanes norvegica*, Thysanoessa *inermis* and *T. longicaudata*, while at Chatham Rise, New Zealand in the Southwest Pacific Ocean, the krill species *Euphausia superba* was stated as the main food item, including the krill *Thysanoessa macrura*.

Consumption of krill by baleen whales and associated phytoplankton and benthos production

The seven Ecopath Model results are shown in Table 1 and Figure 1, below. Krill biological production and consumption by baleen whales was estimated using equation 3 and the biological characteristics for each ocean area are shown in Table 1 and the footnotes.

The Ecopath Models gave consistent results for biological characteristics in all the areas except baleen whale biomass and benthos production at the Antarctic Peninsula, which were low relative to the high phytoplankton and krill production in [40]. Their low benthos production was by sampling in offshore areas with low biomass, which could be an order of magnitude lower than in nearshore areas, as shown

Table 1. Ecopath Model results for the Antarctic Ocean and Arctic Ocean and during migrations to South Georgia Island, Chatham Rise, New Zealand, Iceland, and Prince William Sound, Alaska, with possible relationship with phytoplankton and benthos production. Units: biomass tww/Km^2, P/B (/year), production and krill consumption by baleen whales tww/Km^2/year. Estimated whale biomass and benthos production are in square brackets.

Ocean Area	Reported Baleen Whale TL	Average TTE	Krill Production	Krill production Consump-tion by Baleen Whales[f]	Baleen Whale Biomass	Phyto-plankton Production	Benthos Production	Detritus[e] B
Antarctic Ocean[a]	3.54	0.110	62.5	16.58 (26.5%)	2.16	9000	450	80.0
Antarctic Peninsula[b]	4.01	0.0938	161.9	11.9 (7.4%)	1.26	5174	288	-
South Georgia Island[c]	3.71	0.1035	79.2	20.38 (25.7%)	0.03	1560	38.9	-
Chatham Rise, NZ[d]	3.6	0.1075	49.1	10.8 (22.0%)	0.005	2761	48.4	-
Norwegian and Barents Sea, Arctic Ocean[e]	3.90	0.097	117.5	15.37 (13.1%)	0.134	1766	99	25
Iceland Waters[f]	3.333	0.1185	98.8	17.68 (17.9%)	0.19	1429	57.3	20.5
Prince William Sound, Alaska[g]	3.7	0.1039	69.7	11.17 (16.0%)	0.158	2028	90.0	114.48

a) Data from [39], Ecopath Model in supplementary Table S4 including with the diet matrix and model parameters for each species or group: Krill B 25.0, P/B 2.5, , whale krill diet 0.8, phytoplankton B 120, P/B 75, benthos TL 2.22, B 60.0, P/B 7.5, detritus diet not known but Benthos had detritus as their main diet in the Arctic Ocean.

b) Ecopath Model Table 6 from [40] Baleen whale krill diet 0.24 including krill larvae, adult krill B 105.35 P/B 1.0 krill larvae B 14.14 P/B 4.0, total krill P 56.56 +105.35 =161.91, phytoplankton B 300 P/B 17.58. Most detritus consumed and by bacteria. Detritus biomass was not known. Most krill consumption was by penguins, fish and birds. Baleen whale estimated B 1.26 estimated by average of low biomass Humpback 2.68, Fin 0.93 and Minke 0.17 t/Km^2 in [50] with Sei whales assumed too low to measure. Benthos estimated from [52] B 51.6 tww/Km^2 from 0.391 KgCx11% AFDW to WW x 12%soft sediment sample area of Peninsula, P 288 by multiply B with average P/B 5.58.

c) Ecopath Model, Table 3 by [41] baleen whale krill diet 0.8, krill *Euphausia superba* B 33 P/B 2.4, PP B 26 P/B 60, benthos B 72 P/B 0.54.

d) Ecopath Model, see Table 6 by [42] and 7a): Biomass adjusted from gC to wet weight.by information in Appendices. Area 240000 Km^2, baleen whale TL adjusted from 4.6 to 3.6, Krill B 5.76 P/B 8.53, baleen whale krill diet 0.67 and 0.16 for Meso-pelagic fish B 2.15 P/B 1.2 P 2.58 whale consumption by equation 3 of 0.135 or 5.2%, phytoplankton B 28.6 P/B 96.53, Macro -benthos B 43.8 P/B 0.84 P 36.8 detritus diet 0.42, Meio-benthos B 1.125, P/B 10.32.

e) Data from [43]: Baleen whale krill diet 0.42, Krill B 47.0, P/B 2.5, phytoplankton B 15.0, P/B 117.73, benthos B 66.0, P/B 1.5, benthos detritus diet 0.769, detritus from [48], Table 1) Detritus-POM 25 t/Km^2 in Norwegian and Barents Seas.

f) Ecopath Model [45] Table A.2 baleen whale krill diet 0.52 (from Table B in Sigurjónsson and Víkingsson, 1997 mostly northern krill *Meganyctiphanes norvegica*), krill B 39.52 P/B 2.5, phytoplankton B 12.151 P/B 117.6, benthos B 38.23 P/B 1.5

g) Alaska's Prince William Sound Ecopath Model Table 78 in [46] with diet composition Appendix 5. baleen whale B includes Minke whales in Table 65, krill diet 0.497, Deep epibenthos B 30.0 P/B 3.0, Appendix 3 *Euphausiacea* B 27.33 P/B 2.55, phytoplankton offshore B 10.672 P/B 190, detritus offshore.

by [46] in Prince William Sound, Alaska. For that reason, baleen whale biomass was estimated from detailed studies for whale biomass by [50] and for benthos production by [52] in the Antarctic Peninsula. The average baleen whale biomass was estimated as 1.26 t/Km^2 using the lowest values in [50], see their Table 2 and Figure 5). They showed the Antarctic Peninsula is an area of active whale migration, and [51] noted baleen whales only feed on krill for about three to 4 months in the Ross Sea and then migrate to warmer waters, so it appears the Ecopath Model whale biomass, an order of magnitude lower at 0.17 t/Km^2 by [40] was based on a period low whale numbers.

The study by [52], see their Table 4 and Figures 3 and 6 for Antarctic Peninsula benthos production was mostly in bays and inlets along the peninsula and the species consuming organic matter were on soft sediments in <20m depth. They estimated the soft sediment benthos standing stock as 391 tC/km^2, but Figure 3 shows the measured biomass at the two sampling sites in ash free dry weight (AFDW) g/m^2, indicating the units are 391 KgC/km^2. To make the units consistent with tww/Km^2 used for biomass in Ecopath Models, The study by [54] showed the conversion factor from AFDW to wet weight typically requires multiplying by 11%, slightly higher than the 10% used by [42] for gC converted to wet weight. That adjustment gave a biomass about 4.3 tww/Km^2. In addition, [52] showed the two sampling sites represented about 12% of the soft sediment sites in their Figure 6, so the Antarctic Peninsula biomass was estimated by multiplying 4.3 tww/Km^2 by 12, giving a total biomass of 51.6 tww/Km^2. To estimate the benthos production, the average P/B for benthos of 5.58 in the Cornejo-Ecopath Model by [40] was used, giving 288 tww/km^2/year.

The findings in Table 1 show some important differences between ocean areas. The Antarctic Ocean had the highest baleen whale biomass and estimated krill consumption, phytoplankton and benthos production, but the second lowest krill production, likely due to high consumption by whales and other predators such as penguins. The high benthos production in the Antarctic was likely due to the high whale consumption of krill with defecation to detritus. The lowest of proportion of krill consumption of 7.4% was in the Antarctic Peninsula, similar to the 4–6% of the krill biomass by [53], but the krill biomass in the Peninsula area by [54] was unknown. The highest krill production was at the Antarctic Peninsula, due to the low baleen whale diet of only 24% compared with 80% in the Diet Matrix for Antarctic Ocean. The reason for low Peninsula krill consumption appears due to competition with high krill consumption by Antarctic lantern fish, small and medium pelagic fish and the whales consuming an estimated 27% of Antarctic lantern fish, small pelagic fish and 12% cephalopods rather than krill. The finding is consistent with the Peninsula being an active migration area, so it appears whales don't spend much time feeding on krill and aim for larger prey. The Antarctic Peninsula high phytoplankton and benthos production, with moderately high baleen whale biomass supported the importance of whale biomass defecation on ecosystem production. In contrast, the low baleen whale biomass at South Georgia Island was possibly due to as an important migration path, suggesting the whales pass through rather than stay to feed, possibly because krill fishing is allowed in the area. In relation to whale migrations, large populations of Humpback whales are shown migrating from the Antarctic to the Chatham Rise seamount area east of New Zealand by [26]. The Ecopath Model at Chatham Rise by [42] shows the low krill production was supplemented by consuming fish and possibly benthos at the seamounts. The Diet Matrix shows baleen whales consume 16% of mesopelagic fish (Lantern fish and other small midwater fish) in their diet, which indicates the importance of sustaining fish abundance in whale migration feeding areas.

Comparison of the Arctic Ocean with the Antarctic shows the Arctic Ocean has a higher krill production than in the Antarctic, probably due to lower consumption by the low baleen whale biomass and lower whale krill diet of 42%. The 15% higher krill production at Iceland is supported by the higher baleen whale migration from the Arctic Ocean to seamounts forming Iceland shelf waters [26]. Surprisingly, the continued migration into the Pacific Ocean at Alaska showed only a 15% higher phytoplankton production and benthos and similar benthos production to that in the Arctic, but a 40% lower krill production than at Iceland. The Alaskan Diet Matrix showed krill was heavily preyed by carnivorous zooplankton, large jellyfish, cephalopods, squid, octopus, cuttlefish, or nautilus, forage fish, also called bait fish, small pelagic fish that feed on zooplankton, mesopelagic fish, in the middle layer of the ocean, Pacific Sardines and Mackerel, which probably explains the lower krill production. The potential contribution to production of the similar baleen whale biomass at Alaska to that at the Arctic and Iceland was investigated by including Alaska in the statistical comparison of phytoplankton and benthos production with whale biomass, below.

Relationship of baleen whales with ecosystem production feedback loops

The above results for feedback loops for phytoplankton and benthos production show the highest levels in the Antarctic Ocean with the highest baleen whale biomass. The relationships shown in Figure 1 provide a preliminary indication of the global importance of baleen whale biomass on increased ecosystem production via defecation and nutrient recycling.

PP (tww/Km^2/y) = 3441.4 x Whale Biomass (tww/Km^2) + 1282.1 (4).

R^2 = 0.9863, n = 7, p<0.001.

Benthos Production (tww/Km^2/y) = 187.42 x Whale Biomass (tww/Km^2) + 47.682 (5).

R^2 = 0.988, n = 7, p<0.001.

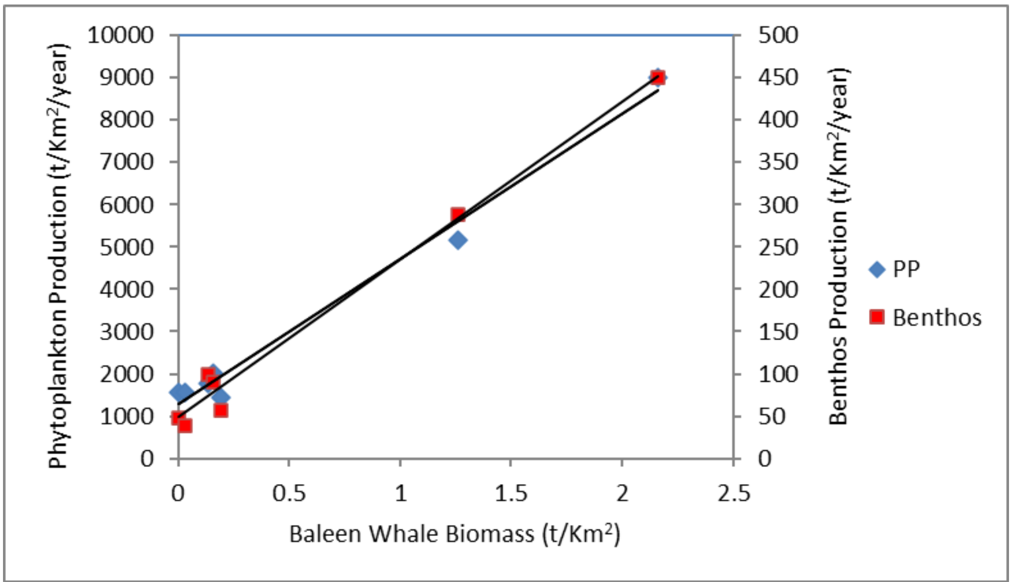

Figure 1. Relationship between baleen whale biomass with phytoplankton and benthos production in the Arctic and Antarctic Oceans and during migrations for potential relation to feedback loop of whale consumption and defecation promoting ecosystem production. The benthos production is included because it is a major consumption of accumulated detritus with likely nutrient recycling into the water column, which then promotes phytoplankton production.

The baleen whale biomass contribution to phytoplankton and benthos production at Alaska was estimated using the above equations and gave phytoplankton production as 1862 ± 186 tww/Km^2/year, about 90% of the Ecopath Model, and benthos production 77 ± 8.5 tww/Km^2/year, 86%. Errors are from the overall CV error for the seven regressions in Figure 1 for phytoplankton production, which gave average 0.10, maximum 0.35 and minimum 0.01, and the seven benthos production averaged 0.11, maximum 0.45 and minimum 0.07. The comparisons show baleen whales made a significant contribution to the Alaskan coastal production, probably by their influence on nutrient regeneration, and aided production of krill with a similar production as at the Antarctic with consumption by the other predators.

However, further along the high upwelling American western continental shelf where baleen whales also tend to migrate, the Ecopath model by [55] Field *et al*. (2006) for the Northern California Current found the phytoplankton production 6,600 t/Km^2/year, about 3-fold higher than at Alaska. That gave a higher krill production of 216 tww/Km^2/year but the baleen whale biomass was about half at 0.083 tww/Km^2, and similar benthos production 110 tww/Km^2/year. The contribution by the lower whale biomass by equations 4 and 5 show they could gave have provided 1568 (24%) and 63 tww/Km^2/year (57%), to the Northern California Current production, respectively. The higher krill production is also consistent with the higher phytoplankton production, giving a similarly expected 227 tww/Km^2/year krill production (Alaskan krill 69.7 x 6600/Alaskan PP 2028), indicating baleen whales contribute to upwelling driven production in coastal areas.

Discussion

The results raise fundamental questions about oceanographic processes required to bring the regenerated nutrient from whale defecation to surface waters. The interrelationships are briefly reviewed in relation to the global importance of the krill to whale food web and feedback loops of nutrient recycling, baleen whale migration and oceanic conditions in the open ocean.

Global *nutrient recycling during whale migration*

The actual increase on phytoplankton production in surface waters by baleen whale defecation is not well defined, particularly when feeding on fish during migrations. However, baleen whale defecation was shown by [56] to provide dissolved iron input to Antarctic surface waters, and that may apply during migration to warmer areas. The study by [57] suggested baleen whales undertake northern winter migrations after consuming large amounts of krill in the Southern Ocean during summer. That also occurs because the calves need warmer water temperatures to survive [58]. During their long migrations to the temperate and tropical areas they consume small pelagic fish such as herring [59], anchovies [60] and benthopelagic species such as sand ells [31], which live and feed near the sea floor, in midwaters or near the surface, feeding on benthic as well as free swimming fish, apparently to provide additional energy and minimize weight loss. In terms of global migrations, and [61] suggested the Southern Ocean has an important role in the global ocean biogeochemistry for the chemical, physical, geological, and biological processes of the natural environment, as well as primary production by supplying nutrients to the global gravitational circulation and currents, caused by a sinking mass of dense sea water that moves toward the ocean floor due to gravity, winds, and the rotation of the earth.

In the Arctic Ocean, [62] showed baleen whales on the western Greenland continental shelf consume the high concentrations of krill *Meganyctiphanes norvegica* and *Thysanoessa* sp. Those aggregations likely aid the start of migrations to the tropics during winter and [63] showed in the Arctic Ocean during summer, baleen whales mostly feed on Krill species or fish. In addition, [64] estimated globally, prior to the whale population being reduced by fishing, that whales contributed significant nutrient enrichment of surface waters by their high prey consumption providing increased fish production. That condition most likely applies at present because [65] estimated, post-whaling, the whale population has globally recovered by about 70%. In relation to obtaining fish food during migrations, [66] showed that by moving north from the Antarctic waters, baleen whales could also obtain food by consuming small pelagic fish by diving at productive seamount areas, which is briefly reviewed in the next section.

Migrations following deep sea seamounts

A detailed report on seamounts was presented in [67] and recent research on baleen whale migrations has found they tend to follow seamounts associated with nutrient release from hydrothermal vents [68], which act as hot springs on the ocean floor, releasing heated, mineral-rich water into the ocean water. In the South Pacific Ocean, whale migration occurs from the Southern Ocean to the large area of seamounts shown by [69] around New Zealand, mostly on the eastern side of the islands, where most whales are reported. The whales were probably following seamounts associate with the Southern Pacific Antarctic Ridge hydraulic vents, north of the Southern Ocean [70], see their Figure 1, and then along the east Coast of New Zealand via the Macquarie Ridge to the Campbell Plateau . The ridge then turns west via the Norfolk Island Ridge to New Caledonia, in the South West Pacific Ocean, where seamounts also occur [71].

The association of seamounts with whale migrations is reported by [72] who showed increased production of the waters associated with seamounts was due to upwelling of nutrients by interaction with local deep sea water currents of the Antarctic Circumpolar Current, **an ocean current that flows clockwise (as seen from the South Pole**) from west to east around Antarctica. In addition, [73] showed oceanic conditions at deep-water hydrothermal vents could provide increased phytoplankton production by upwelling of dissolved iron from the vent plume to surface waters of the Southern Ocean. That was confirmed by [74], who found ammonia and iron in vent plumes may reach some surface waters in temperate areas.

In the Arctic Ocean, humpback whales (*Megaptera novaeangliae*) are shown migrating from the Norwegian Svalbard archipelago in the Barents Sea to the Caribbean Islands, via Iceland, by [75], see their Figure 1. The migration was along the mid-Atlantic Ocean ridge deep-ocean hydrological vent map shown in [70] and deviated from the ridge to the eastern extent of islands in the Caribbean Sea. The return whale migration from the West Indies tended to follow the mid-Atlantic Ridge and went close to the Azore islands off the west coat of Africa, then rejoined the original migration path at Iceland. The comparison is consistent with seamounts associated with the mid-ocean ridges as important for pelagic fish and their predators [76], [77], [78] and [79].

Conclusions

The findings of this investigation present the importance of sustaining global baleen whale migrations to support ecosystem production by nutrient recycling, aided by oceanographic upwelling processes to surface waters in open ocean areas. In a related way, [80] suggested toothed whales bring nutrients from deep waters after feeding on fish and cephalopods, and the contribution could be similar to the gross nutrient dynamics in upwelling areas. They noted toothed whale defecation is mostly liquid and tends to disperse rather than sink, increasing surface water production. Therefore, it is suggested process be put in place to maintain global migration of all the great whales for sustainability of open ocean production.

Furthermore, the literature showed relationships between baleen whale defecation and nutrient cycling at seamounts and during baleen whale migrations, which also led to the effects of nutrient upwelling by deep sea currents at seamounts [81], apparently encouraging baleen whale migrations in those areas. Accordingly, [78] suggested seamounts be protected as important marine ecosystems. As seamounts are indicated as important for fish, particularly small pelagic fish and their whale predators, it is suggested small pelagic fish be sustained by ecosystem-based fishery management (EBFM) fishing rates, estimated by [36] as 23% ± 3% of the fishery biomass, and applied in the main global whale migration areas. Hence, further research is suggested to show how the baleen whale consumption and defecation processes sustains krill, fish, as well as phytoplankton and benthos biological production in open ocean areas. It is hoped that these insights for the ecological and oceanographic basis for krill and baleen whale feedback loops to sustain ecosystem production will be of assistance to fishery managers, biologists and ecosystem modellers for ongoing management of whale feeding and migration areas with potentially increased ecological stability of the world's open ocean areas.

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Declaration of interests

I have nothing to declare.

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