SC/68D/EM/01

Sub-committees/working group name: EM

Nutrient concentrations in minke whale faeces and the potential impact on dissolved nutrient pools off Svalbard, Norway

Carla Freitas, Kjell Gundersen, Lotta Lindblom, Martin Biuw, Tore Haug

Nutrient concentrations in minke whale faeces and the potential impact on dissolved nutrient pools off Svalbard, Norway

Carla Freitas[1,2] *, Kjell Gundersen[1], Lotta Lindblom[3], Martin Biuw[3], Tore Haug[3]

[1]Institute of Marine Research, Postbox 1870 Nordnes, 5817 Bergen, Norway

[2]MARE, Marine and Environmental Sciences Center, Madeira Tecnopolo, 9020-105 Funchal, Madeira, Portugal

[3]Institute of Marine Research, Fram Centre, PO Box 6606 Stakkevollan, NO-9296 Tromsø, Norway

* Corresponding author.

E-mail address: carla@hi.no

Abstract

There is increasing interest in assessing the impact of whales on nutrient and carbon cycling in the ocean. By fertilising surface waters with nutrient-rich faeces, whales may stimulate primary production and carbon uptake, but robust assessments of such effects are lacking. Based on the analysis of faeces collected from minke whales (n=31) off Svalbard, Norway, this study quantified the concentration of macro-and micronutrients in whale faeces prior to their release in seawater. Concentrations of the macronutrients nitrogen (N) and phosphorous (P) in minke whale faces were 50.1 ± 10.3 and 70.9 ± 12.1 g kg^{-1} dry weight, respectively, while the most important micronutrients were zinc (Zn), iron (Fe), manganese (Mn) and copper (Cu). By combining measured faecal nutrient concentrations with estimated prey-consumption and prey-assimilation rates, we calculate that the current population of approximately 15 000 individuals in the small management area (SMA) of Svalbard defecate annually 1258 ± 259 tonnes (t) N and 1782 ± 305 t P. The molar ratio of N:P in minke whale faeces was 1.6:1, meaning that N was proportionally limiting, when compared to average elemental ratios of 16:1 in phytoplankton. In case of no N-limitation in surface waters at that time, the release of elemental P through defecation in surface waters has the potential to stimulate 73 000 t of carbon per year as new or regenerated primary production in the SMA of Svalbard. This amounts to 0.5 of annual new primary production and 0.4 to 4.1 % of daily net primary production to this region. This study provides the first assessment of nutrient concentration in whale faeces prior to their dissolution in sea water. Further research, namely on the amount of N released via urine and the proportion of excreted nutrients remaining in the euphotic zone, is needed to better assess the full potential of whale nutrient additions to dissolved nutrient pools in surface waters at regional and global scales.

Keywords: Arctic marine mammals, Balaenoptera acutorostrata, nutrient recycling, top predators, whale pump

1. Introduction

Top predators provide important functions and services in marine ecosystems, including regulating food webs, supporting fisheries and generating tourism (Estes et al. 2016, Hammerschlag et al. 2019, Enquist et al. 2020). In addition, there is increasing evidence that marine predators may play a role in ocean nutrient and carbon cycling (Atwood et al. 2015, Schmitz et al. 2018, Martin et al. 2021). For instance, it has been suggested that dissolved inorganic nutrients from whale faeces increase nutrient availability in surface waters and hence stimulate primary production and carbon sequestration (Lavery et al. 2010, Roman and McCarthy 2010, Ratnarajah et al. 2016, Roman et al. 2016, Ratnarajah et al. 2018).

Phytoplankton require light, dissolved inorganic macronutrients (nitrogen, N; and phosphorus, P; and silicate, for diatoms), as well as micronutrients such as iron, and other trace metals, for cellular growth and development. However, dissolved macronutrients are often limited in open ocean surface waters, while micronutrients are particularly deficient in oligotrophic waters and in the Southern Ocean (Ratnarajah et al. 2014, Ratnarajah et al. 2018). Whale faeces contain both dissolved macronutrients (Roman and McCarthy 2010, Roman et al. 2016) and micronutrients (Lavery et al. 2010, Ratnarajah et al. 2014), which may stimulate primary production (Smith et al. 2013, Roman et al. 2016). However, the amount of nutrients released by whale populations is still not fully quantified. This is mainly due to uncertainties in major biological and biogeochemical parameters, such as nutrient concentration in whale faeces, dissolution rates of excreted nutrients and proportion of excreted nutrients sinking out of the euphotic zone (see Ratnarajah et al. 2016). Filling this knowledge gap is critical in order to assess the full potential of nature-based ocean carbon sinks and their role in mitigating and adapting to climate change, especially in the context of achieving healthy and resilient oceans. While previous studies have examined the relative content of different nutrients from whale faecal samples collected from seawater, this approach cannot be used to estimate the absolute nutrient contents in whale faeces.

Baleen whales typically aggregate during spring and summer in high latitude foraging grounds and migrate in winter to breeding areas located in warmer regions (see Moore et al. 2019). In the Northeast Atlantic, the productive North Sea, Greenland Sea, Norwegian Sea and Barents Sea, constitute summer feeding grounds for various baleen whales species, including common minke whales *Balaenoptera acutorostrata*, fin whales *Balaenoptera physalus* and humpback whales *Megaptera novaeangliae* (Leonard and Øien 2020). Minke whales are by far the most numerous species in these foraging grounds, with an estimated current abundance of 149 722 (CV 0.152) individuals (Solvang et al. 2021), while there are an estimated 11,387 fin whales (95% CI: 8,072–16,063) and 10,708 humpback whales (95% CI: 4,906–23,370) (Leonard and Øien 2020). For minke whale management purposes, these northern feeding grounds are divided into so-called small management areas, SMA (IWC 2004) and abundance estimates are available within each SMA (Leonard and Øien 2020, Solvang et al. 2021). The minke whale is the only whale species that is commercially harvested by Norway. The unique opportunity to collect biological material from healthy individuals during whaling, coupled with detailed information on population size, diet and other biological parameters, make the Northeast Atlantic minke whale an ideal species for quantifying whale impacts on dissolved nutrient pools.

In this study we quantified the concentration of macro and micronutrients in minke whale faeces collected directly from animals during the Norwegian commercial minke-whale hunt in the waters around the Svalbard Archipelago. By combining nutrient data with available whale abundance and prey consumption estimates, we determined the total amount of macro and micronutrient released by minke whales in the region and assessed the significance of these nutrient loads to regional primary production.

2. Methods

2.1. Field sampling

Faecal samples were collected from minke whales (n=31) onboard a commercial whaling vessel operating off Svalbard, Norway in August 2019 (Fig. 1). Immediately after capture, whales were taken onboard for dissection and biological sampling. Total body length was measured in a straight line from the tip of the upper jaw to the apex of the tail fluke notch. Faeces samples, with approximately 10 ml, were collected from the whale rectum using plastic teaspoons. Samples were stored at -20°C until analyses. Forestomach contents were visually inspected and identified to species or species group.

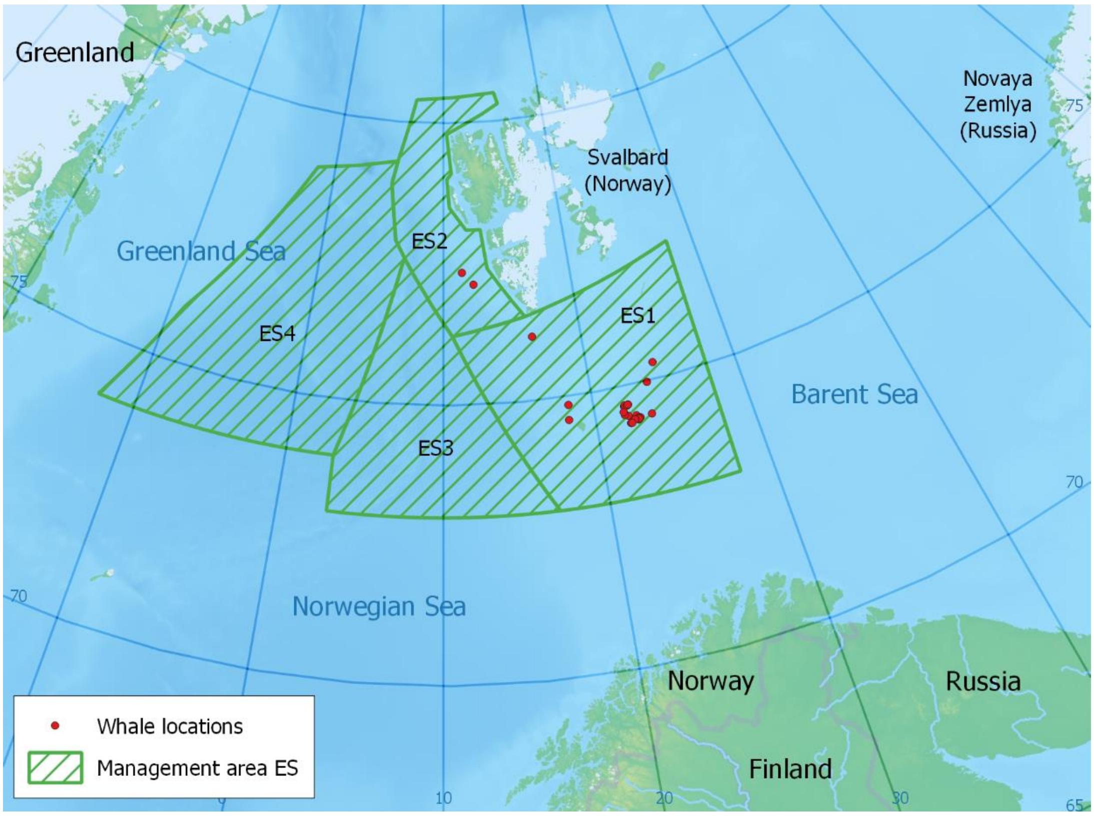

Fig. 1. Map of the study area, showing the minke whale small management area of Svalbard (ES) and its subareas (ES1 to ES4), as well as the locations where minke whales were sampled in August 2019.

2.2. Nutrient analyses

In order to quantify macronutrient (N and P) and micronutrient concentrations in minke whale faeces, faeces samples were freeze dried for 72h at −80 °C, homogenised with a pestle and mortar into a fine powder and stored at room temperature. Freeze dried aliquots were weighed and the N content measured using an automatic CHN analyser. Aliquots for P analysis were dissolved in nitric acid and heated using microwaves for complete decomposition of organic matter. Total P was then determined using an inductively coupled plasma mass spectrometry (ICP-MS). One separate aliquot was used to analyse micronutrients and other trace metals, using ICP-MS according to the EPA 200.8 method (EPA 1996). Analysed trace metals included: chromium (Cr), manganese (Mn), iron (Fe), cobalt (Co), Nickel (Ni), copper (Cu), zinc (Zn), cadmium (Cd), vanadium (V), arsenic (As), selenium (Se), molybdenum (Mo), silver (Ag), mercury (Hg) and lead (Pb). Note that several trace metals, such Zn, Cu, Fe, Mg, Cd, Se, Co and Mo, are considered micronutrients, as they are essential for plants and animals, while other trace elements are suspected but not unequivocally proven to be essential (Boyd 2015). The term trace metal includes thus essential trace metals (micronutrients) and non-essential trace metals. Finally, concentrations of calcium (Ca), Sodium (Na), potassium (K) and Magnesium (Mg) were quantified, using the same protocol as for total P analysis.

2.3. Total amount of nutrients recycled through faeces

The total amount of macronutrients and trace metal content excreted by minke whales via faeces was estimated from nutrient concentrations in whale faeces. Considering Z as a given nutrient, the total amount of Z defecated (Z_d) by minke whales per day (kg d^{-1}) was estimated as:

$$Z_d = Z_c T_d \qquad (1)$$

where Z_c is the concentration of Z in whale faeces (mg kg^{-1} dry weight) and T_d is the total amount of faeces defecated by minke whales (kg dry weight d^{-1}). T_d was estimated from food consumption. Minke whales in the study area feed primarily on herring (*Clupea harengus*), krill (*Thysanoessa sp.* and *Meganyctiphanes norvegica*) and capelin (*Mallotus villosus*), and to a lesser degree cod (*Gadus mohrua*), haddock (*Melanogrammus aeglefinus*) and other Gadidae fish (Haug et al. 2002, Sivertsen et al. 2006, Windsland et al. 2007, Bogstad et al. 2015). When feeding on these prey, the proportion of dry matter assimilated by minke whales is 80 ± 5 % of the dry matter consumed (Nordøy et al. 1993). We have thus considered that 20 % of the dry weight of prey biomass consumed ($Q_{\text{dry weight}}$) is ultimately defecated:

$$T_d = 0.2 \times Q_{\text{dry weight}} \qquad (2)$$

We have considered that the proportion dry matter in herring, krill and capelin during summer is 25 ± 4 %, based on the range of values reported in the literature (Mcgurk et al. 1980, Montevecchi and Piatt 1984, Bragadóttir et al. 2002, Kim et al. 2014). This implies that the estimated daily consumption in terms of dry weight $Q_{\text{dry weight}}$ is:

$$Q_{\text{dry weight}} = 0.25\ Q_{\text{wet weight}} \quad (3)$$

and therefore,

$$T_{\text{d}} = 0.2 \times 0.25\ Q_{\text{wet weight}} \quad (4)$$

Formula (1), can be thus rewritten as:

$$Z_{\text{d}} = Z_{\text{c}} \times 0.2 \times 0.25\ Q_{\text{wet weight}} \quad (5)$$

where $Q_{\text{wet weight}}$ is the prey biomass consumption for minke whales (kg d^{-1}). $Q_{\text{wet weight}}$ was obtained from Skern-Mauritzen et al. (2022). These authors estimated a total consumption of 1.666 million tonnes (t) for a population of 47 295 minke whales foraging during 6 months in the Barents Sea, considering that 10% of them remained in that area throughout the winter. This gives an average daily consumption ($Q_{\text{wet weight}}$) of 178 kg per whale (Table 1). The total amount of nutrient Z defecated by the entire population of minke whales during an assumed 6-month (180-days) residence in the Svalbard SMA was estimated as:

$$Z_{\text{dy}} = Z_{\text{d}} \times n \times 180 \quad (6)$$

Where n is the current abundance estimate, i.e. 15 693 (CV 0.19) individuals in the SMA of Svalbard (Solvang et al. 2021).

2.4. Significance of nutrient-rich defecation to primary production

Phytoplankton incorporate nutrients at a ratio that varies substantially between different species and environmental conditions, but on average occurs at a molar rate of 106 C : 16 N : 1 P : 0.0075 Fe throughout the ocean (Bristow et al. 2017). Using the estimated amount of nutrients released through faeces, and assuming that all faecal nutrients remain in the euphotic zone, we applied these C:N:P:Fe stoichiometric relationships to estimate the significance of excreted nutrients to primary production (PP) in the ES area, expressed as carbon biomass. As a back-to-envelope exercise, we compared minke-whale induced PP in the subarea ES1 with annual and daily PP estimates from the northern Barents Sea (Rey et al. 1987, Hegseth 1998). We considered that annual new PP was 49 C m^{-2} yr^{-1} (Rey et al. 1987). Daily net PP (~new PP in the Barents Sea), was considered to range from 0.043 to 0.36 C m^{-2} d^{-1}, depending on the phytoplankton bloom situation (Hegseth 1998). Minke whale abundance in the subarea ES1 was considered to be 8 471 individuals in a survey area of 164 150 km^2 in 2019 (Solvang et al. 2021). For comparison, the 2014 minke whale abundance of individuals in a survey area of 175 488 km2 (Solvang et al. 2021) was also considered.

Table 1. Parameters used to estimate the amount of nutrients excreted by minke whales in the small management area of Svalbard (ES).

Symbol	**Parameter**	**Estimate**	**Variation**	**Source**
$Q_{\text{wet weight}}$	Prey consumption per individual per day (kg)	178	sd = 40	Estimate: Skern-Mauritzen et al. (2022); sd: assumed based on 95% CI from Skern-Mauritzen et al. (2022)
$Prop_{\text{ass}}$	Proportion dry matter assimilated	0.8	sd = 0.05	Nordøy et al. 1993
$Prop_{\text{dmp}}$	Proportion dry matter in prey	0.25	sd = 0.04	Estimate and sd: based on the range of values provided by Mcgurk et al. 1980, Montevecchi and Piatt 1984, Bragadóttir et al. 2002 and Kim et al. 2014
$Q_{\text{dry weight}}$	Prey consumption (dry matter) per individual per day (Kg)	44.5		$0.25\ Q_{\text{wet weight}}$
T_{d}	Dry matter defecated per individual per day (kg)	8.9		$0.2\ Q_{\text{dry weight}}$ ($0.2 \times 0.25\ Q_{\text{wet weight}}$)
Z_{c}	Concentration of nutrient Z in faecal dry matter (mg Kg^{-1})	See results		This study
Z_{d}	Total Z defecated per individual per day (Kg)	See results		$T_{\text{d}} \times Z_{\text{c}}$
n	Minke whale abundance:			
	ES area, 2019	15 693	CV = 0.19	Solvang et al. 2021
	ES1 subarea, 2019	8 47	CV = 0.22	Solvang et al. 2021
	ES1 subarea, 2014	11 088	CV = 0.22	Solvang et al. 2021
Z_{dy}	Total Z defecated by all whales per year (Kg)	See results		$Z_{\text{dy}} \times n \times 180$

2.5. Uncertainty and sensitivity analysis

An uncertainty analysis was performed to determine the impact of each input variable in the Z_{dy} model variance. Using R software (R_Core_Team 2020) and a framework adapted from Bejarano et al. (2017), all input variables obtained from the literature ($Q_{\text{wet weight}}$, $Prop_{\text{dmp}}$, $Prop_{\text{ass}}$ and n) were set to their means, while randomly resampling 10000 times one of the variables from their respective sampling distributions, one variable at a time. $Q_{\text{wet weight}}$, $Prop_{\text{dmp}}$, $Prop_{\text{ass}}$ were assumed to follow a gaussian distribution, with mean and standard deviation (Table 2). Population size, n, was assumed to follow a lognormal distribution and was resampled based on their mean and coefficient of variation (Table 2). Nutrient concentrations (Z_{c}), measured in this study, were allowed to vary in all models, based on their mean and sd. Comparisons of model output variance from uncertainty analyses were made relative to the original model (i.e., all input variables at their mean and variance in Z_{c}). A sensitivity analysis was also performed to assess the sensitivity of model outputs to changes in each input variable. Input variables were initially set to their means and allowed to increase or decrease by 10% of this mean value, one variable at a time. Comparisons of model outputs from sensitivity analyses were made relative to the original model (i.e., all variables set to its mean).

3. Results

3.1. Sampled individuals

A total of 31 minke whales were sampled, 13 females and 18 males, ranging in size from 5.9 and 9.1 m (Table 2). Most individuals (n=27) were adults, i.e. over 7 m (Christensen 1981), while 4 were juveniles (Table 2). Forestomach contents revealed that all individuals had foraged on capelin, except one whale which had consumed both capelin and gadoid fish (Table 2).

Table 2. Summary records for 31 minke whales sampled off the Svalbard Archipelago in August 2019. Individuals over 7 m were considered adults and otherwise juveniles (Christensen 1981).

Whale ID	Date	Latitude	Longitude	Sex	Body length (m)	Maturity	Diet
KATO 67	05.08.2019	77.350	11.467	Female	9.1	Adult	Capelin
KATO 68	05.08.2019	77.133	12.350	Female	8.4	Adult	Capelin
KATO 69	06.08.2019	76.133	16.467	Male	6.8	Juvenile	Capelin
KATO 70	10.08.2019	75.300	24.533	Female	7.4	Adult	Capelin
KATO 71	10.08.2019	74.983	23.833	Male	7.8	Adult	Capelin
KATO 72	11.08.2019	74.417	23.667	Male	8.4	Adult	Capelin
KATO 73	11.08.2019	74.467	22.150	Male	8.1	Adult	Capelin
KATO 74	12.08.2019	74.650	22.000	Female	6.1	Juvenile	Capelin
KATO 75	12.08.2019	74.650	21.983	Male	8.1	Adult	Capelin
KATO 76	12.08.2019	74.667	22.033	Male	7.7	Adult	Capelin + Gadidae
KATO 77	12.08.2019	74.650	22.167	Male	7.8	Adult	Capelin
KATO 79	13.08.2019	74.667	22.267	Male	8.1	Adult	Capelin
KATO 80	13.08.2019	74.667	22.250	Male	7.9	Adult	Capelin
KATO 81	15.08.2019	74.383	22.450	Male	8	Adult	Capelin
KATO 82	16.08.2019	74.450	22.650	Male	7.5	Adult	Capelin
KATO 83	16.08.2019	74.383	22.700	Male	8	Adult	Capelin
KATO 84	16.08.2019	74.367	22.750	Male	8	Adult	Capelin
KATO 85	17.08.2019	74.400	22.783	Female	8.6	Adult	Capelin
KATO 86	17.08.2019	74.400	22.800	Male	7.5	Adult	Capelin
KATO 87	17.08.2019	74.400	22.883	Female	8.5	Adult	Capelin
KATO 88	18.08.2019	74.400	22.783	Female	8.2	Adult	Capelin
KATO 89	18.08.2019	74.383	22.783	Female	7.8	Adult	Capelin
KATO 90	20.08.2019	74.383	22.533	Female	7.4	Adult	Capelin
KATO 91	20.08.2019	74.383	22.517	Male	7.2	Adult	Capelin
KATO 92	21.08.2019	74.333	22.217	Male	7.6	Adult	Capelin
KATO 93	21.08.2019	74.333	22.217	Female	6.1	Juvenile	Capelin
KATO 94	21.08.2019	74.333	22.283	Female	5.9	Juvenile	Capelin
KATO 97	22.08.2019	74.500	21.917	Female	7.4	Adult	Capelin
KATO 98	22.08.2019	74.550	21.883	Male	8.1	Adult	Capelin
KATO 100	23.08.2019	74.583	18.267	Male	7.9	Adult	Capelin
KATO 101	24.08.2019	74.850	18.367	Female	8.5	Adult	Capelin

3.2. Faecal nutrient concentrations

Minke whale faeces comprised 20.7 ± 4.2 % dry matter (Table 3). The average concentration of N in minke whale faeces was 50.1 ± 10.3 g kg^{-1} dry weight (Fig. 2, Table 3), which corresponds to 10.4 ± 3.9 g kg^{-1} wet weight (Table 3). Average P concentration in minke whale faeces was 70.9 ± 12.1 g kg^{-1} dry weight (Fig. 2, Table 3) and 14.9 ± 3.9 g kg^{-1} in terms of wet weight (Table 3). Among trace metals Zn, Fe, Mn and Cu showed the highest concentrations, respectively, 558 ± 104.2, 498 ± 119.5, 34 ± 10.3 and 34.3 ± 24.6 mg kg^{-1} dry weight (Fig. 2, Table 4). All other trace metals were present in whale faeces, but at lower concentrations (Fig. 2, Table 4). The average concentration of Ca, Na, K, Na and Mg in minke-whale faeces was 97.9, 14.5, 6.7 and 19.8 g kg^{-1} of dry matter, respectively (Table 4).

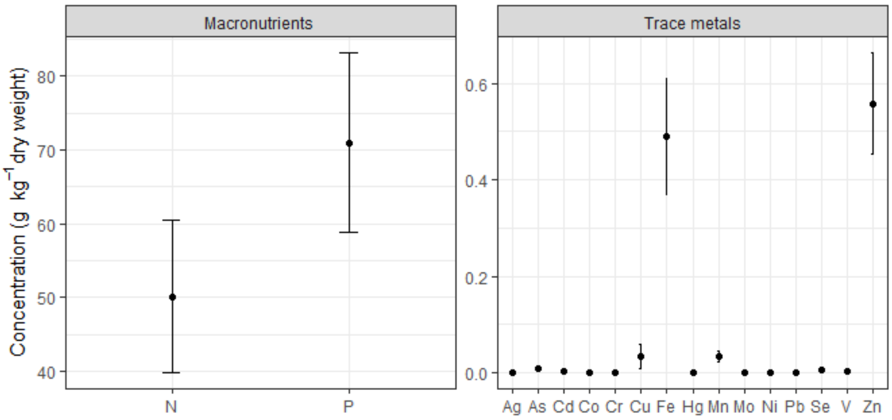

Fig. 2. Concentration of macronutrients and trace metals in minke whale faeces (mean ± sd). Number of samples included in the means was 29 for P and 31 for all other elements. Abbreviations: N=nitrogen, P=phosphorus, Ag=silver, As=arsenic, Cd=cadmium, Co=cobalt, Cr=chromium, Cu=copper, Fe=iron, Hg=mercury, Mn=manganese, Mo=molybdenum, Ni= nickel, Pb=lead, Se=selenium, V=vanadium, Zn=zinc.

Table 3. Percentage dry matter and concentration of nitrogen (N) and phosphorus (P) in minke whale faeces collected during commercial whaling off Svalbard, Norway. Values are given in g kg^{-1} of dry weight (dw) and wet weight (ww).

Whale ID	% dry matter	N		P	
		(g/kg dw)	(g/kg ww)	(g/kg dw)	(g/kg ww)
KATO 67	20.5	45.0	219.9	73.3	15.0
KATO 68	24.6	46.4	11.4	81.3	20.0
KATO 69	22.5	40.4	9.1	84.4	19.0
KATO 70	19.8	41.4	8.2	85.9	17.0
KATO 71	14.2	42.8	6.1	77.3	11.0
KATO 72	21.2	38.6	8.2	85.0	18.0
KATO 73	16.7	60.0	10.0	66.0	11.0
KATO 74	15.1	47.1	7.1	79.3	12.0
KATO 75	17.7	44.3	7.8	73.4	13.0
KATO 76	19.3	60.4	11.7	67.2	13.0
KATO 77	18.4	53.7	9.9	70.8	13.0
KATO 79	13.6	48.5	6.6	*	*
KATO 80	22.0	57.3	12.6	59.0	13.0
KATO 81	21.3	71.2	15.2	37.1	7.9
KATO 82	23.9	59.0	14.1	71.1	17.0
KATO 83	23.5	36.2	8.5	93.7	22.0
KATO 84	17.9	61.1	10.9	67.2	12.0
KATO 85	24.7	58.2	14.4	64.9	16.0
KATO 86	22.0	42.6	9.4	68.1	15.0
KATO 87	28.8	57.5	16.6	69.3	20.0
KATO 88	16.7	40.1	6.7	83.9	14.0
KATO 89	26.9	45.7	12.3	70.7	19.0
KATO 90	22.1	48.1	10.6	68.0	15.0
KATO 91	22.6	52.3	11.8	62.0	14.0
KATO 92	23.1	46.9	10.8	73.7	17.0
KATO 93	19.4	82.1	15.9	38.7	7.5
KATO 94	26.9	39.0	10.5	70.6	19.0
KATO 97	17.1	41.6	7.1	*	*
KATO 98	16.6	55.1	9.1	66.3	11.0
KATO 100	14.2	41.2	5.9	70.3	10.0
KATO 101	27.9	49.2	13.7	78.9	22.0
Mean	20.68	50.09	10.37	70.94	14.94
Sd	4.15	10.31	2.95	12.14	3.94

* Not enough sample to measure P

Table 4. Trace metal concentration (mg kg^{-1} dry weight) in minke whale faeces collected during commercial whaling off Svalbard Archipelago, Norway. Abbreviations: Ag=silver, As=arsenic, Cd=cadmium, Co=cobalt, Cr=chromium, Cu=copper, Fe=iron, Hg=mercury, Mn=manganese, Mo=molybdenum, Ni= nickel, Pb=lead, Se=selenium, V=vanadium, Zn=zinc. Elemental concentration of calcium (Ca), Sodium (Na), potassium (K) and Magnesium (Mg) is also provided.

Whale ID	**Ag**	**As**	**Cd**	**Co**	**Cr**	**Cu**	**Fe**	**Hg**	**Mn**	**Mo**	**Ni**	**Pb**	**Se**	**V**	**Zn**	**Ca**	**Na**	**K**	**Mg**
KATO 67	0.2	8.8	5.4	0.2	0.1	45.5	587	0.6	26.4	0.4	1.1	0.1	6.4	1.6	469	102639	11730	5865	23949
KATO 68	0.2	8.1	4.1	0.3	0.1	29.3	610	1.1	34.2	0.5	1.1	0.1	6.1	1.8	569	113867	12607	6913	22367
KATO 69	0.2	11.1	4.1	0.4	0.1	30.6	844	0.3	43.5	0.3	1.3	0.1	7.1	2.1	666	128774	13321	4885	22647
KATO 70	0.3	11.6	5.0	0.3	0.1	30.3	480	0.2	46.5	0.5	1.4	0.1	6.6	2.8	657	121273	14654	3386	20212
KATO 71	0.2	9.8	4.3	0.3	0.1	22.5	513	0.3	33.0	0.4	1.3	0.1	6.5	2.1	618	112439	23893	4989	18271
KATO 72	0.3	7.6	5.2	0.3	0.1	41.6	614	0.3	43.5	0.5	1.6	0.1	6.1	2.2	803	118092	21256	4062	23146
KATO 73	0.1	7.2	2.9	0.2	0.1	18.0	492	0.1	37.2	0.3	0.7	0.1	5.3	1.9	534	89982	17397	10798	16197
KATO 74	0.3	9.9	5.4	0.3	0.1	43.6	456	0.7	44.3	0.5	1.0	0.1	6.6	2.8	727	105680	20476	5482	17173
KATO 75	0.2	10.7	4.6	0.2	0.1	26.0	429	0.2	33.9	0.6	1.0	0.1	5.6	2.0	525	95991	14116	3727	28233
KATO 76	0.2	8.3	2.5	0.3	0.1	46.0	424	0.7	25.9	0.5	0.9	0.1	5.7	1.9	491	93071	12927	7239	16546
KATO 77	0.2	8.7	2.3	0.2	0.1	21.3	496	0.2	33.8	0.4	0.7	0.1	5.4	2.3	545	103542	16349	8174	16894
KATO 79	0.2	7.0	3.8	0.2	0.1	33.2	369	0.3	33.2	0.4	0.6	0.1	5.5	1.3	501	*	*	*	*
KATO 80	0.2	8.2	2.9	0.2	0.1	32.7	377	0.3	23.1	0.5	0.8	0.1	5.9	1.7	454	81670	9982	10436	15880
KATO 81	0.1	5.2	1.2	0.1	0.0	22.5	235	0.5	12.2	0.3	0.4	0.0	4.7	0.9	296	46970	15031	8924	8924
KATO 82	0.2	7.9	2.7	0.3	0.2	25.5	669	0.3	28.0	0.4	1.2	0.1	6.3	2.3	460	100334	13378	7525	18395
KATO 83	0.2	9.8	4.1	0.3	0.1	30.2	639	0.3	40.0	0.5	0.7	0.1	6.4	2.7	681	131971	14900	3065	26394
KATO 84	0.2	8.4	2.3	0.3	0.1	22.4	470	0.4	24.1	0.4	1.1	0.1	6.7	2.0	476	83940	14550	9513	18467
KATO 85	0.2	7.3	2.7	0.2	0.1	28.4	406	0.4	32.0	0.4	0.9	0.1	6.1	2.1	527	89213	11760	7705	19870
KATO 86	0.2	12.7	2.9	0.3	0.1	35.4	544	0.2	31.8	0.5	1.2	0.1	6.4	2.8	590	104356	12704	6806	14065
KATO 87	0.2	8.7	3.3	0.2	0.2	32.9	555	0.2	34.7	0.5	1.0	0.1	6.6	2.7	624	97087	8669	7975	17337
KATO 88	0.2	10.2	2.9	0.3	0.2	26.4	545	0.4	41.3	0.5	1.7	0.1	5.9	3.2	599	119832	18574	4074	22169
KATO 89	0.2	10.8	3.2	0.3	0.2	30.1	558	0.5	33.1	0.5	1.4	0.1	6.0	2.4	595	93006	12277	7068	18229
KATO 90	0.2	8.6	3.5	0.2	0.1	31.7	499	0.2	63.5	0.3	1.0	0.1	6.8	2.2	635	90703	15873	6349	21315
KATO 91	0.2	10.6	4.4	0.3	0.2	28.4	430	0.2	34.1	0.6	1.1	0.1	5.8	1.9	576	84183	7975	6203	18166
KATO 92	0.2	7.8	3.8	0.2	0.1	30.8	563	0.3	38.1	0.5	0.9	0.1	6.1	2.2	607	103986	11265	5633	20797
KATO 93	0.2	4.7	1.9	0.1	0.1	23.2	454	0.2	15.5	0.3	0.6	0.0	6.2	1.1	340	50026	13409	11862	9283
KATO 94	0.1	9.7	2.6	0.2	0.1	21.9	483	0.6	36.0	0.5	1.0	0.1	5.6	2.6	520	118915	10033	4088	16722
KATO 97	0.2	7.6	3.0	0.2	0.1	29.2	362	0.2	28.6	0.5	0.8	0.1	5.4	2.1	560	*	*	*	*
KATO 98	0.2	7.2	2.4	0.2	0.0	27.7	362	0.3	18.1	0.4	0.7	0.0	5.7	1.7	446	84388	16275	9644	22303
KATO 100	0.5	7.7	3.7	0.7	0.2	161.6	309	0.5	50.6	0.8	2.6	0.1	8.4	1.2	597	84329	26001	6465	28110
KATO 101	0.2	7.5	4.7	0.2	0.0	35.5	395	0.4	34.1	0.6	0.8	0.1	6.8	0.9	610	89670	9326	6098	30846
Mean	0.2	8.7	3.5	0.3	0.1	34.3	489	0.4	34.0	0.5	1.0	0.1	6.1	2.1	558	97929	14507	6723	19755
Sd	0.1	1.8	1.1	0.1	0.0	24.6	119	0.2	10.3	0.1	0.4	0.0	0.7	0.6	104	19698	4323	2306	5024

* Not enough sample to measure these elements.

3.3. Total amount of nutrients defecated

Individual minke whales with an average daily prey consumption of 178 kg are expected to defecate 8.9 kg dry matter each day (Table 1). This corresponds to 43 kg faecal wet matter, or 24 % of prey wet weight consumed. The estimated amount of N defecated by individual minke whales was 445 ± 92 g d^{-1}, while the entire population was estimated to defecate 1258 ± 259 t yr^{-1} during their 6-month foraging season in the Svalbard SMA (Table 5). The amount of P defecated by individual minke whales was estimated to be 631 ± 108 g d^{-1}, corresponding to an excretion of 1782 ± 305 t

yr^{-1} (Table 5). Further, the population of minke whales in the Svalbard SMA was estimated to release 14 ± 3 t Zn, 12 ± 3 t Fe, 0.85 ± 0.3 t Mn and 0.86 ± 0.6 t Cu annually, in addition to lower amounts of other trace metals (Table 5). Moreover, minke whales are expected to annually defecate over 2400 t Ca, 364 t Na, 169 t K and 496 t Mg off Svalbard (Table 5).

Table 5. Estimated daily and annual amount of macronutrient (N, P) and trace metals defecated by minke whales in the small management area (SMA) of Svalbard. Daily values are given by individual, while annual amounts are given for the current population of 15 693 individuals during their 6 months stay in this region.

	Per individual (g d^{-1})		All population (t yr^{-1})	
Element	Mean	Sd	Mean	Sd
N	445.467	91.675	1258.330	258.958
P	630.853	107.939	1781.996	304.899
V	0.018	0.005	0.052	0.014
Cr	0.001	0.000	0.003	0.001
Mn	0.302	0.092	0.854	0.259
Fe	4.350	1.063	12.289	3.002
Co	0.002	0.001	0.007	0.002
Ni	0.009	0.004	0.026	0.010
Cu	0.305	0.219	0.862	0.619
Zn	4.963	0.927	14.018	2.618
As	0.077	0.016	0.218	0.044
Se	0.055	0.006	0.154	0.017
Mo	0.004	0.001	0.012	0.002
Ag	0.002	0.001	0.005	0.002
Cd	0.031	0.010	0.087	0.027
Hg	0.003	0.002	0.009	0.005
Pb	0.001	0.000	0.002	0.000
Ca	870.851	175.172	2459.928	494.816
Na	129.008	38.446	364.413	108.600
K	59.782	20.509	168.867	57.932
Mg	175.679	44.681	496.248	126.213

3.4. Importance of faecal nutrients to primary production

While the molar ratio of N:P:Fe in phytoplankton is on average 16:1:0.0075, the ratio of N:P:Fe in minke whale faeces was 1.6:1:0.0038, meaning that N and Fe were proportionately limited in the faecal nutrients fraction. Assuming that minke whales release 13 times more N in urine than via faeces, as harp seals (Keiver et al. 1984), then N:P ratios become 20:1, thus not limited any more. If no other nutrients were limiting, the estimated annual release of P has the potential to generate a net primary production of 73 249 t C during their six-month stay in the SMA of Svalbard (ES) and approximately 40 000 t in the subarea ES1 (Table 6). This corresponds to approximately 0.5 % of the annual new primary production in the ES1 area (Table 6). Depending on phytoplankton bloom condition, P enrichment from minke whales has the potential to contribute to 0.4 to 4.1% of daily primary production in the region (Table 6).

Table 6. Daily and annual primary production (PP) in the subarea ES1, located south of Svalbard in the Barents Sea, and potential primary production from phosphorus (P) excreted by minke whales (PP_{Whale}). Two minke whale abundance scenarios are considered, based on the 2014 and 2019 abundance surveys (Solvang et al. 2021). Daily estimates consider four phytoplankton bloom conditions, based on the data provided by Hegseth (1998).

Phytoplankton condition	Whale survey year	Survey area (km^2)	Whale abundance	Daily PP per m^2 ($g\ C\ m^2\ d^{-1}$)*	Daily PP total area ($t\ C\ d^{-1}$)	P defecated ($t\ d^{-1}$)	PP_{Whale} (t C d-1)	% of PP
No bloom min	2 019	164 150	8 471	0.043	7 058	5.3	220	3.1
No bloom max	2 019	164 150	8 471	0.12	19 698	5.3	220	1.1
Bloom min	2 019	164 150	8 471	0.187	30 696	5.3	220	0.7
Bloom max	2 019	164 150	8 471	0.36	59 094	5.3	220	0.4
No bloom min	2 014	175 488	11 088	0.043	7 546	7.0	288	4.1
No bloom max	2 014	175 488	11 088	0.12	21 059	7.0	288	1.5
Bloom min	2 014	175 488	11 088	0.187	32 816	7.0	288	0.9
Bloom max	2 014	175 488	11 088	0.36	63 176	7.0	288	0.5

	Whale survey year	Area (km^2)	Whale abundance	Annual PP per m^2 ($g\ C\ m^2\ d^{-1}$)**	Annual PP total area ($t\ C\ d^{-1}$)	P defecated ($t\ yr^{-1}$)	PP_{Whale} ($t\ C\ y^{-1}$)	% of PP
	2 019	164 150	8 471	49	8 043 350	961.9	39 539	0.5
	2 014	175 488	11 088	49	8 598 912	1259.1	51 755	0.6

* Daily PP for the northern Barents Sea from Hegseth 1998

* Annual PP for the northern Barents Sea from Rey et al. 1987

3.5. Uncertainty and sensitivity analysis

Uncertainty analysis of the effect of input variables on the estimated annual amount of nutrients excreted by minke whales is presented in Fig. 3. Estimates with input variables with assigned sampling distributions indicated that the proportion dry matter assimilated by minke whales ($Prop_{ass}$) had the highest effect on model variance (Fig. 3). Likewise, sensitivity analyses showed that when annual estimates were made based on ±10% changes of individual input variables, the greatest changes were also associated with $Prop_{ass}$. A 10% change in this variable (i.e. from 0.8 to 0.88 and 0.72) had an inflating effect on results (40%). Changes in all other variables influenced results proportional to their magnitude of change, i.e. 10% (Fig. 3). Prey consumption estimates, with its relatively large standard deviation (Table 1), had the second highest impact on model variance (Fig. 3).

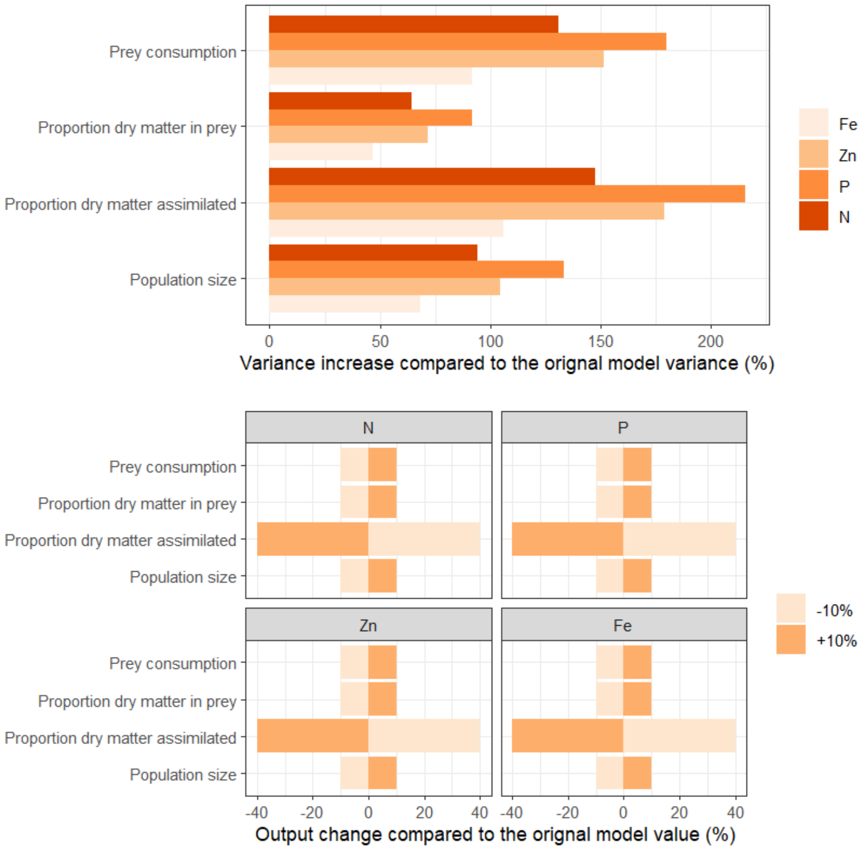

Fig. 3. Results of the uncertainty (top) and sensitivity (bottom) analyses, illustrating the influence of model variables on model outputs.

4. Discussion

There is growing interest in assessing the contribution of whales to nutrient recycling in surface waters (e.g. Lavery et al. 2010, Nicol et al. 2010, Roman and McCarthy 2010, Ratnarajah et al. 2014, Ratnarajah et al. 2018, Savoca et al. 2021). However, uncertainties on several model parameters have impeded progress in obtaining robust quantifications of this contribution (Ratnarajah et al. 2016). This study has overcome the challenges associated with getting reliable estimations of elemental nutrients from whale faeces, by measuring nutrient concentration in faecal matter prior to their release and dissolution in seawater. This enabled to estimate the amount of macro and micronutrients released by minke whales in the Svalbard study area. The potential impact of these nutrient additions to regional primary production is discussed below.

4.1. Methodology

Whales sampled in our study were healthy animals taken in the Norwegian whaling. Commercial whaling in Norway is regulated according to procedures developed by the International Whaling Commission (IWC) to ensure that the activity is sustainable in terms of population size (Skaug et al.

2004, Haug et al. 2011 , Glover et al. 2012). Contrary to faeces collected from the sea following defecation, samples collected directly from whales allowed us to obtain the actual nutrient concentration of minke whale faeces.

Estimating the total amount of nutrients egested by whales depends on a number of parameters, such as population size estimates, prey consumption and prey assimilation rates. Population size estimates are absent in many regions due to logistical and financial limitations. In the Northeast Atlantic high-latitude summer feeding grounds (i.e., North, Norwegian, Greenland and Barents Seas), minke-whale abundance surveys are undertaken each year, covering subsets of the region, so that the entire area is covered every six years. This study used the most updated population size estimates, i.e. for the period 2014-2019, which shows an overall increase in minke whale abundance, though abundance in the Svalbard area has stabilised over the last surveys periods (Solvang et al. 2021).

Another key parameter when estimating nutrient excretion from whales is prey consumption rates. To date, prey consumption of large whale species, including the estimates used in this study, have been determined by bioenergetic models. A recent study that used high resolution foraging measurements from tag deployments suggests that previous studies may have underestimated baleen whale prey consumption by threefold and more in some ecosystems (Savoca et al. 2021). While these recent estimates are noteworthy, they are inconsistent with previous estimates of stomach capacity and digestive rates of cetaceans (Haug et al. 1997, Vikingsson 1997). Furthermore, since estimates in Savoca et al. (2021) are also based on short-term (>24h) tag attachments (often in known feeding hotspots) it is uncertain how representative these data are of average consumption rates throughout an entire feeding season.

A third key parameter, unknown for most whale species, is the assimilation rate of dry matter, i.e., the proportion of dry matter assimilated during digestion. Uncertainty and sensitivity analyses in this study indicate that this was the parameter that had the highest impact on the outcomes of the model. Assimilation rates of dry matter by minke whales are in the order of 80 ± 5 % when feeding on fish and krill (Nordøy et al. 1993). In comparison, the assimilation efficiency of dry matter by pinnipeds is slightly higher (81-94%) when feeding on fish (Keiver et al. 1984, Ronald et al. 1984, Fadely et al. 1990, Lawson et al. 1997a, Lawson et al. 1997b, Goodman-Lowe et al. 1999, Rosen and Trites 2000). On the other hand, seals seem to be less efficient than minke whales to digest krill (Mårtensson et al. 1994). This is probably because pinnipeds have a single stomach system, while minke whales and other baleen whales depend to a great extent on microbial fermentation in a multi-stomach system. Therefore, assimilation efficiencies of dry matter in other baleen whales are likely to be more similar to minke whales than to pinnipeds. Based on the findings from Nordøy et al.

(1993) we considered that 20 ± 5 % of ingested dry matters was ultimately defecated by minke whales. Previous studies assuming that baleen whales excrete all ingested dry matter (Savoca et al. 2021), have most likely overestimated nutrient egestion substantially.

Given the challenges associated with obtaining reliable nutrient concentrations in faeces collected from the sea, some studies have instead estimated nutrient egestion based on the concentration of nutrients in prey and on assumed nutrient assimilation rates (e.g. Roman and McCarthy 2010, Ratnarajah et al. 2016, Savoca et al. 2021). Nutrient assimilation rates are unknown for whales, while few data exist for pinnipeds. Care should be taken when assuming the same nutrient assimilation rates for whales as for terrestrial mammals. For example, marine mammals are expected to have a high Fe intake, as they have exceptionally high values of haemoglobin and myoglobin in comparison to terrestrial mammals (Ponganis 2011). Assuming the same assimilation rates of Fe in whales as in humans and pigs (Ratnarajah et al. 2016, Savoca et al. 2021) may drastically change the output of the estimates. We concur with the recommendations from Ratnarajah et al. (2016) that further research is needed to refine model parameters in nutrient egestion studies.

4.2. Macronutrients

Macronutrients are elements that phytoplankton require in high quantities for photosynthetic growth. As anticipated, the concentration of macronutrients N and P in minke whale faeces was larger than trace metal micronutrients. Elemental P concentrations in our minke whale samples were higher than the concentration measured in humpback whales, and lower than in fin and blue whale faeces samples collected from the Southern Ocean (Ratnarajah et al. 2014). It is unclear whether differences may arise from sampling methods (faeces collected directly from intestines or indirectly from seawater) or to differences among species and ecosystems. Faeces collected from seawater may be at different dissolution stages, as elements may dissolve at different rates, and this may explain the large variations in N and P sometimes found between samples (Roman et al. 2016).

On average, phytoplankton use 16 times more N than P for a balanced cellular synthesis and growth. Contrary to expectations, the concentration of N in whale faeces was lower than P. Instead of a molar ratio of N:P of 16:1, the ratio in minke whale faeces was 1.6:1, implying that N was proportionally limiting in faecal nutrients. However, relatively more N is excreted by mammals through urine, mainly in the form of urea (Wright 1995, Birukawa et al. 2005). Harp seals, for example, excrete approximately 6 % of ingested N via faeces and 78% though urine (Keiver et al. 1984). Assuming the same for minke whales, i.e., that N excreted via urine is 13 times larger than in faeces, the N:P ratio would be 20:1, suggesting that N is not a limiting nutrient. Future analyses of minke-whale urine are needed to confirm the amount of N egested through urine. Silicate was the only macronutrient not quantified in this study. This macronutrient is important for diatom growth and can control the availability and distribution of these macroalgae (Yool and Tyrrell 2003). Silicate recycling via whale excretions is so far unknown.

4.3. Trace metal micronutrients

Elemental Zn and Fe were the trace metals found at the highest concentrations in minke whale faeces and this is similar to what has been observed in faeces of other large whales in the Southern Ocean (Ratnarajah et al. 2014). However, Fe concentration in our samples (498 ± 119.5 mg kg^{-1}) was approximately three times larger than the concentration measured in baleen whales in the Southern Ocean (Nicol et al. 2010, Ratnarajah et al. 2014). This might be because the Southern Ocean is an iron-limited ecosystem or because of differences in diet - baleen whales in the Southern Ocean feed on krill while the studied minke whales had foraged on capelin. Again, differences may also be caused by sampling issues, as faecal samples in the Southern Ocean were collected from seawater (by conducting net-tows in surface waters following a defecation event). Partial dissolution of Fe and other nutrients may therefore have occurred instantly, and initial concentrations may not have been captured in these studies. An Fe solubility experiment, reported by Ratnarajah et al. (2017), did not cover Fe dissolution prior to sampling of faeces from the sea, but showed that Fe leaching was generally larger immediately after seawater had been added to the faeces slurry. Iron is an important nutrient for phytoplankton growth and development. This nutrient is particularly limiting in the so-called high nitrate low chlorophyll (HNLC) regions, such as the Southern Ocean. Therefore, most studies of nutrient recycling by whale in the Southern Ocean have focused on this element (e.g. Nicol et al. 2010, Ratnarajah et al. 2016, Ratnarajah et al. 2018, Savoca et al. 2021). Similar to whales, other marine taxa may also recycle Fe through excretion and it has been suggested that commercial fish harvesting has removed significant amounts of iron from the ocean (Moreno and Haffa 2014). At the same time, iron availability can limit fish growth (Galbraith et al. 2019), suggesting that Fe recycling via predator faeces is likely to have a positive cascading effect on higher trophic levels. The analysed minke whale faeces had an elemental P:Fe ratio of 1:0.0038, which is approximately half the average elemental ratio found in phytoplankton (1:0.0075), implying that elemental iron could still be limiting relative to the macronutrients released in surface waters of the Barents Sea during summer.

Along with Fe, other essential trace metals constitute important building blocks in phytoplankton cellular synthesis (Twining and Baines 2013). For instance, Cu is vital for methane oxidation and N utilisation, while Zn is essential for organic P utilization, calcification and for Si uptake by large diatoms (See Ratnarajah et al. 2014 and references herein). Other important elements for cell synthesis (e.g., manganese Mn and cobalt Co) are also essential but they are not necessarily limiting phytoplankton growth in seawater. Along with Fe, elemental Mn is utilized during carbon fixation, while Co is essential for carbon dioxide (CO2) acquisition and calcification (Ratnarajah et al. 2014).

4.4. Significance to primary production

The estimated amount of P defecated by 15000 minke whales in the Svalbard SMA exceeded 1700 t per year. The total Northeast Atlantic population of approximately 150000 whales (Solvang et al. 2021) may excrete 10 times as much P annually in the entire feeding grounds, i.e. over 17000 t yr^{-1}. Dissolved macronutrients within the euphotic zone in the Northeast Atlantic are typically at maximum concentrations prior to the annual spring bloom (e.g. Wassmann et al. 1999). During the spring bloom event, these nutrients are depleted and remain low during summer stratification (Olsen et al. 2003). Seasonal depletion of nutrients is not only local but can be observed in surface source waters extending far south of the SMA of Svalbard (Ibrahim et al. 2014). Surface macronutrient concentrations are therefore at a minimum during the whale feeding season (April-October) and hence, at a time when nutrients from whale faecal matter will be most significant to new production. The input of N and P from whale faeces during this season is therefore well-timed and, due to a tight coupling between mostly regenerated nutrient pools and the primary producers during the spring-summer season, we may not see an increase from this activity in bulk nutrient measurements during this time. Likewise, bulk Chlorophyll-biomass may stay low, even during elevated primary production in summer, due to a continuing and efficient removal by zooplankton grazers during this time of the year.

Primary production is a mix of new production (based on new nutrient inputs to the euphotic zone) and regenerated production, whereby phytoplankton growth is supported by regenerated nutrients by zooplankton grazing and degradation of organic matter by heterotrophic bacteria (Downes et al. 2021). Minke whale forage on species that occur both within and below the euphotic zone. Capelin, for instance, remain in bottom layers during the day and migrate to surface layers at night, particularly during spring and autumn (Gjøsæter 1998). Depending on foraging depths relative to the nutricline, minke whales may contribute to both new and recycled production. Prey captured below the nutricline contains nutrients that are already lost to surface waters and, as such, faecal matter released in surface waters is considered a reintroduction and contribution to new production. This is contrary to prey captured in surface waters and released as faecal matter within the nutricline, as this must be considered a source of nutrients to regenerated production. Source identification, and hence vertical location, of prey is therefore crucial in determining the proportion of faecal matter contributing to new and regenerated production in surface waters. Comparatively to whales, fish are expected be less effective in recycling nutrients in open water, as they excrete particulate N and P in faecal pallets that sink rapidly to depth (Saba et al. 2021). Anyway, the relative importance of whales and their prey to recycled nutrients needs further research.

Assuming that no other nutrients were limiting, the estimated annual release of P from minke whales has the potential to generate a net primary production of over 73 000 t C during their six-month stay in the SMA of Svalbard (ES), corresponding to 407 t carbon per day in the ES area and 220 t of carbon per day in the ES1 subarea, in the north-western Barents Sea. Therefore, P enrichment from minke whales has the potential to contribute to 0.4 to 4.1% of daily primary production in the region. Taking into account that marine mammals in the Barents Sea consume four times as much prey as minke whales alone (Skern-Mauritzen et al. 2022), the overall contribution of marine mammals to Barents Sea primary production is potentially higher. Note that these estimates assume that recycled N, P and Fe remain in the euphotic zone and are used by phytoplankton and that further research is needed to verify these assumptions.

5. Conclusions

This first assessment of nutrient contents in whale faeces prior to their dissolution in seawater, has overcome the challenges associated with getting reliable estimations of elemental nutrients from whale faeces. By combining measured faecal nutrient concentrations with the best available prey-consumption and prey-assimilation estimates, we calculated the expected contribution of minke whale faeces to nutrient pools in surface waters. Additional contribution from minke-whale urine needs to be quantified. Several other research questions remain, namely the impact of prey type on excreted nutrients, and the fate of faecal and urine nutrients in seawater following excretion. Further research is therefore needed to better assess the full potential of whale nutrient additions to dissolved nutrient pools in surface waters at regional and global scales.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the Institute of Marine Research, Norway. Whale samples were collected in the context of the project "The Nansen Legacy", funded by the Research Council of Norway (grant number 276730). We thank the crew of the whaling vessel "Kato" for cooperation in the field. We also thank all colleagues involved in the analyses of the whale faeces samples, in particular M. E. Kristoffersen and E. Erdal at the Inorganic Chemistry Laboratory and L. F. Lunde and her crew at the Plankton Chemistry Laboratory at the Institute of Marine Research.

References

Atwood, T. B., R. M. Connolly, E. G. Ritchie, C. E. Lovelock, M. R. Heithaus, G. C. Hays, J. W. Fourqurean, and P. I. Macreadie. 2015. Predators help protect carbon stocks in blue carbon ecosystems. Nature Clim. Change **5**:1038-1045.

Bejarano, A. C., R. S. Wells, and D. P. Costa. 2017. Development of a bioenergetic model for estimating energy requirements and prey biomass consumption of the bottlenose dolphin *Tursiops truncatus*. Ecological Modelling **356**:162-172.

Birukawa, N., H. Ando, M. Goto, N. Kanda, L. A. Pastene, H. Nakatsuji, H. Hata, and A. Urano. 2005. Plasma and urine levels of electrolytes, urea and steroid hormones involved in osmoregulation of cetaceans. Zoological Science **22**:1245-1257.

Bogstad, B., H. Gjøsæter, T. Haug, and U. Lindstrøm. 2015. A review of the battle for food in the Barents Sea: cod vs. marine mammals. Frontiers in Ecology and Evolution **3**.

Boyd, C. E. 2015. Micronutrients and other trace elements. Pages 277-311 *in* C. E. Boyd, editor. Water Quality: An Introduction. Springer International Publishing, Cham.

Bragadóttir, M., H. Pálmadóttir, and K. Kristbergsson. 2002. Seasonal changes in chemical composition and quality parameters in capelin (*Mallotus villosus*). Journal of Aquatic Food Product Technology **11**:87-103.

Bristow, L. A., W. Mohr, S. Ahmerkamp, and M. M. M. Kuypers. 2017. Nutrients that limit growth in the ocean. Current Biology **27**:R474-r478.

Christensen, I. 1981. Age determination of minke whales, *Balaenoptera acutorostrata*, from laminated structures in the tympanic bullae.

Downes, P. P., S. J. Goult, E. M. S. Woodward, C. E. Widdicombe, K. Tait, and J. L. Dixon. 2021. Phosphorus dynamics in the Barents Sea. Limnology and Oceanography **66**:S326-S342.

Enquist, B. J., A. J. Abraham, M. B. J. Harfoot, Y. Malhi, and C. E. Doughty. 2020. The megabiota are disproportionately important for biosphere functioning. Nature Communications **11**:699.

EPA, U. 1996. Method 200.8 - Determination of trace elements in waters and wastes by inductevely coupled plasma - mass spectrometry,

methods for the determination of metals in environmental samples. Pages 88–145 *in* William Andrew Publishing, editor., Westwood, NJ.

Estes, J. A., M. Heithaus, D. J. McCauley, D. B. Rasher, and B. Worm. 2016. Megafaunal Impacts on Structure and Function of Ocean Ecosystems. Annual Review of Environment and Resources **41**:83-116.

Fadely, B. S., A. J. W. Graham, and D. P. Costa. 1990. Assimilation efficiency of northern fur seals determined using dietary manganese. The Journal of Wildlife Management **54**:246-251.

Galbraith, E. D., P. Le Mézo, G. Solanes Hernandez, D. Bianchi, and D. Kroodsma. 2019. Growth limitation of marine fish by low iron availability in the open ocean. Frontiers in Marine Science **6**.

Gjøsæter, H. 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in the barents sea. Sarsia **83**:453-496.

Glover, K. A., T. Haug, N. Øien, L. Walløe, L. Lindblom, B. B. Seliussen, and H. J. Skaug. 2012. The Norwegian minke whale DNA register: a data base monitoring commercial harvest and trade of whale products. Fish and Fisheries **13**:313-332.

Goodman-Lowe, G. D., J. R. Carpenter, and S. Atkinson. 1999. Assimilation efficiency of prey in the Hawaiian monk seal (*Monachus schauinslandi*). Canadian Journal of Zoology **77**:653-660.

Hammerschlag, N., O. J. Schmitz, A. S. Flecker, K. D. Lafferty, A. Sih, T. B. Atwood, A. J. Gallagher, D. J. Irschick, R. Skubel, and S. J. Cooke. 2019. Ecosystem function and services of aquatic predators in the anthropocene. Trends in Ecology & Evolution **34**:369-383.

Haug, T., A. Bjørge, N. Øien, and S. V. Ziryanov. 2011 7. Marine mammals; 7.1 Marine mammals of the Barents Sea. Pages 395-430 *in* T. Jakobsen and V. K. Ozhigin, editors. The Barents Sea; Ecosystem, resources, management; Half a century of Russian-Norwegian cooperation. Tapir Academic Press.

Haug, T., U. Lindstrøm, and K. Nilssen. 2002. Variations in minke whale (*Balaenoptera acutorostrata*) diet and body condition in response to ecosystem changes in the Barents Sea. Sarsia **87**:409 - 422.

Haug, T., K. T. Nilssen, U. Lindstrøm, and H. J. Skaug. 1997. On the variation in size and composition of minke whale (*Balaenoptera acutorostrata*) forestomach contents. Journal of Northwest Atlantic Fishery Science **22**:105-114.

Hegseth, E. N. 1998. Primary production of the northern Barents Sea. Polar Research **17**:113-123.

Ibrahim, A., A. Olsen, S. Lauvset, and R. F. 2014. Seasonal variations of the surface nutrients and hydrography in the Norwegian Sea. International Journal of Environmental Science and Development **5**:496-505.

IWC, I. W. C. 2004. Report of the Scientific Committee. Annex D, Appendix 14. Report of the working group on North Atlantic minke whales RMP Implementation Review. . Journal of Cetacean Resource Management **66**:171-183.

Keiver, K. M., K. Ronald, and F. W. H. Beamish. 1984. Metabolizable energy requirements for maintenance and faecal and urinary losses of juvenile harp seals (*Phoca groenlandica*). Canadian Journal of Zoology **62**:769-776.

Kim, M.-A., H.-R. Jung, Y.-B. Lee, B.-S. Chun, and S.-B. Kim. 2014. Monthly variations in the nutritional composition of Antarctic krill *Euphausia superba*. Fisheries and Aquatic Sciences **17**:409-419.

Lavery, T. J., B. Roudnew, P. Gill, J. Seymour, L. Seuront, G. Johnson, J. G. Mitchell, and V. Smetacek. 2010. Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. Proceedings of the Royal Society B: Biological Sciences **277**:3527-3531.

Lawson, J. W., J. A. Hare, E. Noseworthy, and J. K. Friel. 1997a. Assimilation efficiency of captive ringed seals (*Phoca hispida*) fed different diets. Polar Biology **18**:107-111.

Lawson, J. W., E. H. Miller, and E. Noseworthy. 1997b. Variation in assimilation efficiency and digestive efficiency of captive harp seals (*Phoca groenlandica*) on different diets. Canadian Journal of Zoology **75**:1285-1291.

Leonard, D., and N. Øien. 2020. Estimated Abundances of Cetacean Species in the Northeast Atlantic from Norwegian Shipboard Surveys Conducted in 2014–2018. NAMMCO Scientific Publications **11**.

Martin, A. H., H. C. Pearson, G. K. Saba, and E. M. Olsen. 2021. Integral functions of marine vertebrates in the ocean carbon cycle and climate change mitigation. One Earth **4**:680-693.

Mcgurk, M. D., J. M. Green, W. D. McKone, and K. Spencer. 1980. Condition indices, energy density and water and lipid content of Atlantic herring (*Clupea harengus harengus*) of southeastern Newfoundland.

Montevecchi, W. A., and J. Piatt. 1984. Composition and energy contents of mature inshore spawning capelin (mallotus villosus): Implications for seabird predators. Comparative Biochemistry and Physiology Part A: Physiology **78**:15-20.

Moore, S. E., T. Haug, G. A. Víkingsson, and G. B. Stenson. 2019. Baleen whale ecology in arctic and subarctic seas in an era of rapid habitat alteration. Progress in Oceanography **176**:102118.

Moreno, A. R., and A. L. M. Haffa. 2014. The impact of fish and the commercial marine harvest on the ocean iron cycle. PloS One **9**:e107690.

Mårtensson, P. E., E. S. Nordøy, and A. S. Blix. 1994. Digestibility of krill (Euphausia superba and Thysanoessa sp.) in minke whales (Balaenoptera acutorostrata) and crabeater seals (Lobodon carcinophagus). British Journal of Nutrition **72**:713-716.

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

Nordøy, E. S., W. Sørmo, and A. S. Blix. 1993. In vitro digestibility of different prey species of minke whales (*Balaenoptera acutorostrata*). British Journal of Nutrition **70**:485-489.

Olsen, A., T. Johannessen, and F. Rey. 2003. On the nature of the factors that control spring bloom development at the entrance to the Barents Sea and their interannual variability. Sarsia **88**:379-393.

Ponganis, P. J. 2011. Diving mammals. Compr Physiol **1**:447-465.

R_Core_Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, ISBN 3-900051-07-0, URL http://www.R-project.org/, Vienna, Austria.

Ratnarajah, L., A. R. Bowie, D. Lannuzel, K. M. Meiners, and S. Nicol. 2014. The Biogeochemical Role of Baleen Whales and Krill in Southern Ocean Nutrient Cycling. PloS One **9**:e114067.

Ratnarajah, L., D. Lannuzel, A. T. Townsend, K. M. Meiners, S. Nicol, A. S. Friedlaender, and A. R. Bowie. 2017. Physical speciation and solubility of iron from baleen whale faecal material. Marine Chemistry **194**:79-88.

Ratnarajah, L., J. Melbourne-Thomas, M. P. Marzloff, D. Lannuzel, K. M. Meiners, F. Chever, S. Nicol, and A. R. Bowie. 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., S. Nicol, and A. R. Bowie. 2018. Pelagic iron recycling in the Southern Ocean: exploring the contribution of marine animals. Frontiers in Marine Science **5**:1-9

Rey, F., H. R. Skjoldal, and D. Slagstad. 1987. Primary

production in relation to climatic changes in the Barents Sea.*in* H. Loeng, editor. The effect of oceanographic conditions on distribution and population dynamics of conimercial fish stocks in the Barents Sea. Institute of Marine Research.

Roman, J., and J. J. McCarthy. 2010. The Whale Pump: Marine Mammals Enhance Primary Productivity in a Coastal Basin. PloS One **5**:e13255.

Roman, J., J. Nevins, M. Altabet, H. Koopman, and J. McCarthy. 2016. Endangered right whales enhance primary productivity in the Bay of Fundy. PloS One **11**:e0156553.

Ronald, K., K. M. Keiver, F. W. H. Beamish, and R. Frank. 1984. Energy requirements for maintenance and faecal and urinary losses of the grey seal (*Halichoerus grypus*). Canadian Journal of Zoology **62**:1101-1105.

Rosen, D. A. S., and A. W. Trites. 2000. Digestive efficiency and dry-matter digestibility in Steller sea lions fed herring, pollock, squid, and salmon. Canadian Journal of Zoology **78**:234-239.

Saba, G. K., A. B. Burd, J. P. Dunne, S. Hernández-León, A. H. Martin, K. A. Rose, J. Salisbury, D. K. Steinberg, C. N. Trueman, R. W. Wilson, and S. E. Wilson. 2021. Toward a better understanding of fish-based contribution to ocean carbon flux. Limnology and Oceanography **66**:1639-1664.

Savoca, M. S., M. F. Czapanskiy, S. R. Kahane-Rapport, W. T. Gough, J. A. Fahlbusch, K. C. Bierlich, P. S. Segre, J. Di Clemente, G. S. Penry, D. N. Wiley, J. Calambokidis, D. P. Nowacek, D. W. Johnston, N. D. Pyenson, A. S. Friedlaender, E. L. Hazen, and J. A. Goldbogen. 2021. Baleen whale prey consumption based on high-resolution foraging measurements. Nature **599**:85-90.

Schmitz, O. J., C. C. Wilmers, S. J. Leroux, C. E. Doughty, T. B. Atwood, M. Galetti, A. B. Davies, and S. J. Goetz. 2018. Animals and the zoogeochemistry of the carbon cycle. Science **362**:eaar3213.

Sivertsen, S. P., T. Pedersen, U. Lindstrøm, and T. Haug. 2006. Prey partitioning between cod (*Gadus morhua*) and minke whale (*Balaenoptera acutorostrata*) in the Barents Sea. Marine Biology Research **2**:89-99.

Skaug, H. J., N. Øien, T. Schweder, and G. Bøthun. 2004. Abundance of minke whales (*Balaenoptera acutorostrata*) in the Northeast Atlantic: variability in time and space. Canadian Journal of Fisheries and Aquatic Sciences **61**:870-886.

Skern-Mauritzen, M., U. Lindstrøm, M. Biuw, B. Elvarsson, T. Gunnlaugsson, T. Haug, K. M. Kovacs, C. Lydersen, M. M. McBride, B. Mikkelsen, N. Øien, and G. Víkingsson. 2022. Marine mammal consumption and fisheries removals in the Nordic and Barents Seas. ICES Journal of Marine Science (in press).

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

Solvang, H. K., H. J. Skaug, and N. I. Øien. 2021. Abundance of common minke whales in the Northeast Atlantic based on survey data collected over the period 2014-2019. International Whaling Commission Scientific Committee.

Twining, B. S., and S. B. Baines. 2013. The trace metal composition of marine phytoplankton. Annual Review of Marine Science **5**:191-215.

Vikingsson, G. A. 1997. Feeding of fin whales (*Balaenoptera physalus*) off Iceland - diurnal and seasonal variation and possible rates. Journal of Northwest Atlantic Fishery Science **22**:77-89.

Wassmann, P., T. Ratkova, I. Andreassen, M. Vernet, G. Pedersen, and F. Rey. 1999. Spring bloom development in the marginal ice zone and the central Barents Sea. Marine Ecology **20**:321-346.

Windsland, K., U. Lindstrøm, K. T. Nilssen, and T. Haug. 2007. Relative abundance and size composition of prey in the common minke whale diet in selected areas of the northeast Atlantic during 2000–04. Journal of Cetacean Research and Management **9**.

Wright, P. A. 1995. Nitrogen excretion: three end products, many physiological roles. Journal of Experimental Biology **198**:273-281.

Yool, A., and T. Tyrrell. 2003. Role of diatoms in regulating the ocean's silicon cycle. Global Biogeochemical Cycles **17**.