Progress in Oceanography 210 (2023) 102927

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

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

Carla Freitas[a,b,*], Kjell Gundersen[a], Lotta Lindblom[c], Martin Biuw[c], Tore Haug[c]

[a] Institute of Marine Research, PO Box 1870 Nordnes, 5817 Bergen, Norway
[b] MARE, Marine and Environmental Sciences Center, Madeira Tecnopolo, 9020-105 Funchal, Portugal
[c] Institute of Marine Research, BO Box 6606 Stakkevollan, 9296 Tromsø, Norway

ARTICLE INFO

Keywords:
Arctic marine mammals
Balaenoptera acutorostrata
Nutrient recycling
Top predators
Whale pump

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 thus 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 faeces 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 defecates daily 7 ± 1.4 tonnes (t) N and 10 ± 1.7 t P during summer. 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 407 ± 70 t of carbon per day during summer as new or regenerated primary production in the SMA of Svalbard. This amounts to 0.2 to 4 % of daily net primary production in 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 seasonal changes in excreted nutrients, is needed to better assess the full potential of whale nutrient additions to dissolved nutrient pools in surface waters at regional and global scales.

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 requires light and dissolved inorganic macronutrients (nitrogen, N; and phosphorus, P; and silicate, for diatoms) for cellular growth and development (Redfield, 1934; Brzezinski, 1985). Phytoplankton also needs a suite of micronutrients, including iron (Fe), manganese (Mn), copper (Cu), cobalt (Co), and zinc (Zn) (Brand et al., 1983; Sunda, 2012; Twining and Baines, 2013). For instance, Fe and Mn are essential for carbon fixation during photosynthesis, Cu is used for methane oxidation and N utilisation, Co is required for carbon dioxide (CO_2) acquisition and calcification, while Zn is used for organic P utilization, calcification and for silicate uptake by diatoms (See Ratnarajah et al., 2014 and references herein). 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

---

* Corresponding author at: Institute of Marine Research, Postbox 1870 Nordnes, 5817 Bergen, Norway.
E-mail address: carla@hi.no (C. Freitas).

https://doi.org/10.1016/j.pocean.2022.102927
Received 8 April 2022; Received in revised form 26 August 2022; Accepted 22 November 2022

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 in whale faecal samples collected from seawater (e.g. Roman and McCarthy, 2010; Ratnarajah et al., 2014; Savoca et al., 2021), this approach cannot be used to estimate the absolute nutrient concentration in whale faeces.

Baleen whales typically aggregate during 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.

The primary objective of this study was to quantify 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 concentration data with available whale abundance, prey-consumption and prey-assimilation estimates, we further aimed to determine the daily amount of nutrients released by minke whales in the region and assess 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, Table 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 to 15 ml, were collected from the whale rectum using plastic teaspoons. Sampling of this amount of faeces did not require dissection in most cases, which was advantageous to avoid meat contamination. Samples were stored at −20 °C until analyses. Forestomach contents were visually inspected, identified to species or species group and recorded as presence data, i.e., with no quantitative measurements of prey number or biomass (Table 1).

2.2. Nutrient analyses

In order to quantify the concentration of macronutrients (N and P) and micronutrients in minke whale faeces, faeces samples were freeze dried for 72 h at − 80 °C, homogenised with a pestle and mortar into a fine powder and stored at room temperature.

Freeze dried aliquots were weighed and a subsample of 1–2 mg was used to measure the concentration of N using an automated rapid MICRO N cube elemental analyser (range 0,001–0,200 mg N). The

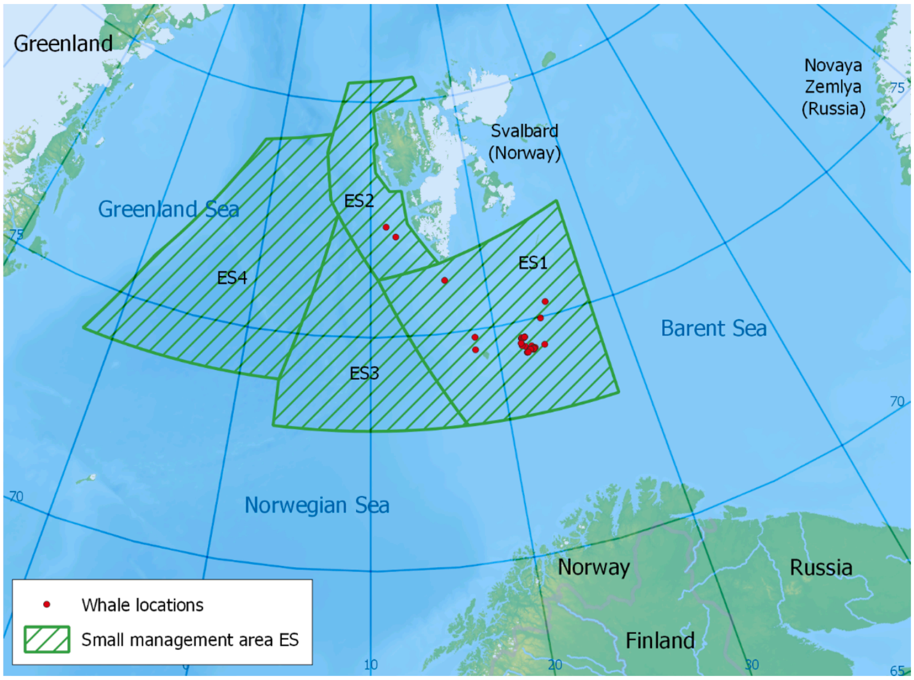

Fig. 1. Map of the study area, showing the locations where minke whales were sampled in August 2019, and the extent of the small management area (SMA) of Svalbard (ES) and its subareas (ES1 to ES4).

Table 1
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
K 67	05.08.2019	77.350	11.467	Female	9 1	Adult	Capelin
K 68	05.08.2019	77.133	12.350	Female	8.4	Adult	Capelin
K 69	06.08.2019	76.133	16.467	Male	6.8	Juvenile	Capelin
K 70	10.08.2019	75.300	24.533	Female	7.4	Adult	Capelin
K 71	10.08.2019	74.983	23.833	Male	7.8	Adult	Capelin
K 72	11.08.2019	74.417	23.667	Male	8.4	Adult	Capelin
K 73	11.08.2019	74.467	22.150	Male	8.1	Adult	Capelin
K 74	12.08.2019	74.650	22.000	Female	6.1	Juvenile	Capelin
K 75	12.08.2019	74.650	21.983	Male	8.1	Adult	Capelin
K 76	12.08.2019	74.667	22.033	Male	7.7	Adult	Capelin + Gadidae
K 77	12.08.2019	74.650	22.167	Male	7.8	Adult	Capelin
K 79	13.08.2019	74.667	22.267	Male	8.1	Adult	Capelin
K 80	13.08.2019	74.667	22.250	Male	7.9	Adult	Capelin
K 81	15.08.2019	74.383	22.450	Male	8.0	Adult	Capelin
K 82	16.08.2019	74.450	22.650	Male	7.5	Adult	Capelin
K 83	16.08.2019	74.383	22.700	Male	8.0	Adult	Capelin
K 84	16.08.2019	74.367	22.750	Male	8.0	Adult	Capelin
K 85	17.08.2019	74.400	22.783	Female	8.6	Adult	Capelin
K 86	17.08.2019	74.400	22.800	Male	7.5	Adult	Capelin
K 87	17.08.2019	74.400	22.883	Female	8.5	Adult	Capelin
K 88	18.08.2019	74.400	22.783	Female	8.2	Adult	Capelin
K 89	18.08.2019	74.383	22.783	Female	7.8	Adult	Capelin
K 90	20.08.2019	74.383	22.533	Female	7.4	Adult	Capelin
K 91	20.08.2019	74.383	22.517	Male	7.2	Adult	Capelin
K 92	21.08.2019	74.333	22.217	Male	7.6	Adult	Capelin
K 93	21.08.2019	74.333	22.217	Female	6.1	Juvenile	Capelin
K 94	21.08.2019	74.333	22.283	Female	5.9	Juvenile	Capelin
K 97	22.08.2019	74.500	21.917	Female	7.4	Adult	Capelin
K 98	22.08.2019	74.550	21.883	Male	8.1	Adult	Capelin
K 100	23.08.2019	74.583	18.267	Male	7.9	Adult	Capelin
K 101	24.08.2019	74.850	18.367	Female	8.5	Adult	Capelin

concentration of P was measured together with the concentration of calcium (Ca), Sodium (Na), potassium (K) and Magnesium (Mg), using a 0.2 g subsample of the freeze-dried material. Concentrations were determined by inductively coupled plasma-mass spectrometry (iCapQ ICP-MS, ThermoFisher Scientific, Waltham, MA, USA) equipped with an auto-sampler (FAST SC-4Q DX, Elemental Scientific, Omaha, NE, USA), after wet digestion in a microwave oven (UltraWave, Milestone, Sorisole, Italy), as described by Julshamn et al. (2019). Detailed procedures and measurement ranges are described in Rekstén et al. (2020). Finally, a separate subsample of 0.2 g was used to determine the concentration of micronutrients and other trace elements, using inductively coupled plasma-mass spectrometry, as described in Rekstén et al. (2020). Analysed trace elements 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 elements, 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 element includes thus essential trace elements (micronutrients) and non-essential trace elements.

2.3. *Total amount of nutrients recycled through faeces*

The total amount of macronutrients and trace elements 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:

$$Z_d = Z_c\, T_d \tag{1}$$

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 on 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:

$$T_d = 0.2\, Q_{\text{dry weight}} \tag{2}$$

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:

$$Q_{\text{dry weight}} = 0.25\, Q_{\text{wet weight}} \tag{3}$$

and therefore,

$$T_d = 0.2 \times 0.25\, Q_{\text{wet weight}} \tag{4}$$

Formula (1), can be thus rewritten as:

$$Z_d = Z_c \times 0.2 \times 0.25\, Q_{\text{wet weight}} \tag{5}$$

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 2). The total daily amount of nutrient Z defecated by the entire population of minke whales during summer in the SMA of Svalbard was estimated as:

$$Z_{dn} = Z_d\, N \tag{6}$$

Table 2
Parameters used to estimate the amount of nutrients excreted by minke whales in the small management area of Svalbard (ES). Abbreviations: sd = standard deviation, CV = coefficient of variation.

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		$Z_{\text{c}}\ \text{T}_{\text{d}}$
N	Minke whale abundance:			
	ES area, 2019	15,693	CV = 0.19	Solvang et al. 2021
	ES1 subarea, 2019	8,471	CV = 0.22	Solvang et al. 2021
	ES1 subarea, 2014	11,088	CV = 0.22	Solvang et al. 2021
Z_{dn}	Total Z defecated by all whales per day (Kg)	See results		$Z_{\text{d}}\ N$

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 Z_{dn}, 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 in the ES area, expressed as carbon biomass. As a back-to-envelope exercise, we compared minke-whale induced primary production in the subarea ES1 with daily primary production estimates from the Barents Sea (Luchetta et al., 2000; Downes et al., 2021). Daily net primary production, was considered to range from 0.04 to 0.69 g C m^{-2} d^{-1}, depending on the phytoplankton bloom situation (Luchetta et al., 2000; Downes et al., 2021). 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 11,088 individuals in a survey area of 175, 488 km^2 (Solvang et al., 2021) was also considered.

2.5. *Uncertainty and sensitivity analysis*

Uncertainty and sensitivity analyses were performed to evaluate the impact of model variable in the estimated amount of nutrients excreted by minke whales Z_{dn}. Because the impact of Z_{dn} on primary production was directly estimated by applying the C:N:P:Fe stoichiometric relationships, uncertainty and sensitivity analyses are also applicable to primary production estimates. First, a uncertainty analysis was used to determine the impact of each input variable in the Z_{dn} 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 10,000 times one of the variables from their respective sampling distributions, one variable at a time. $Q_{\text{wet weight}}$, Prop_{dmp}, Prop_{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 standard deviation. 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 1). Most individuals (n = 27) were adults, i.e., over 7 m (Christensen 1981), while 4 were juveniles (Table 1). Forestomach contents revealed that all individuals had foraged on capelin, except one whale which had consumed both capelin and gadoid fish (Table 1).

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 ± 2.9 g kg^{-1} wet weight (Table 3). Average P concentration in minke whale

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^{-1} dw)	(g kg^{-1} ww)	(g kg^{-1} dw)	(g kg^{-1} ww)
K 67	20.5	45.0	9.2	73.3	15.0
K 68	24.6	46.4	11.4	81.3	20.0
K 69	22.5	40.4	9.1	84.4	19.0
K 70	19.8	41.4	8.2	85.9	17.0
K 71	14.2	42.8	6.1	77.3	11.0
K 72	21.2	38.6	8.2	85.0	18.0
K 73	16.7	60.0	10.0	66.0	11.0
K 74	15.1	47.1	7.1	79.3	12.0
K 75	17.7	44.3	7.8	73.4	13.0
K 76	19.3	60.4	11.7	67.2	13.0
K 77	18.4	53.7	9.9	70.8	13.0
K 79	13.6	48.5	6.6	*	*
K 80	22.0	57.3	12.6	59.0	13.0
K 81	21.3	71.2	15.2	37.1	7.9
K 82	23.9	59.0	14.1	71.1	17.0
K 83	23.5	36.2	8.5	93.7	22.0
K 84	17.9	61.1	10.9	67.2	12.0
K 85	24.7	58.2	14.4	64.9	16.0
K 86	22.0	42.6	9.4	68.1	15.0
K 87	28.8	57.5	16.6	69.3	20.0
K 88	16.7	40.1	6.7	83.9	14.0
K 89	26.9	45.7	12.3	70.7	19.0
K 90	22.1	48.1	10.6	68.0	15.0
K 91	22.6	52.3	11.8	62.0	14.0
K 92	23.1	46.9	10.8	73.7	17.0
K 93	19.4	82.1	15.9	38.7	7.5
K 94	26.9	39.0	10.5	70.6	19.0
K 97	17.1	41.6	7.1	*	*
K 98	16.6	55.1	9.1	66.3	11.0
K 100	14.2	41.2	5.9	70.3	10.0
K 101	27.9	49.2	13.7	78.9	22.0
Mean	20.7	50.1	10.4	70.9	14.9
Sd	4.2	10.3	2.9	12.1	3.9

* Not enough sample to measure P.

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 elements, Zn, Fe, Mn and Cu showed the highest concentrations, respectively, 558 ± 104, 498 ± 119, 34 ± 10.3 and 34.3 ± 24.6 mg kg^{-1} dry weight (Fig. 2, Table 4). All other trace elements 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).

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 2). 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 7 ± 1.4 t N d^{-1} in the Svalbard SMA during summer (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 9.9 ± 1.7 t d^{-1} by all individuals in the region (Table 5). Further, the population of minke whales in the Svalbard SMA was estimated to release daily 78 ± 15 kg Zn, 68 ± 17 kg Fe, 5 ± 1.4 kg Mn and 5 ± 3.4 kg Cu, in addition to lower amounts of other trace elements (Table 5). Moreover, minke whales are expected to daily defecate over 13 t Ca, 2 t Na, 0.9 t K and 2.7 t Mg off Svalbard during summer (Table 5).

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.. If no other nutrients are limiting, the estimated release of P has the potential to generate a net primary production of 407 ± 70 t C per day in the SMA of Svalbard (ES) and approximately 220 t C d^{-1} in the subarea ES1 (Table 6). This corresponds to approximately 0.2 to 4 % of daily primary production in the region, depending on phytoplankton bloom condition (Table 6).

3.5. *Uncertainty and sensitivity analysis*

Uncertainty analysis of the effect of input variables on the estimated daily 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 2), had the second highest impact on model variance (Fig. 3).

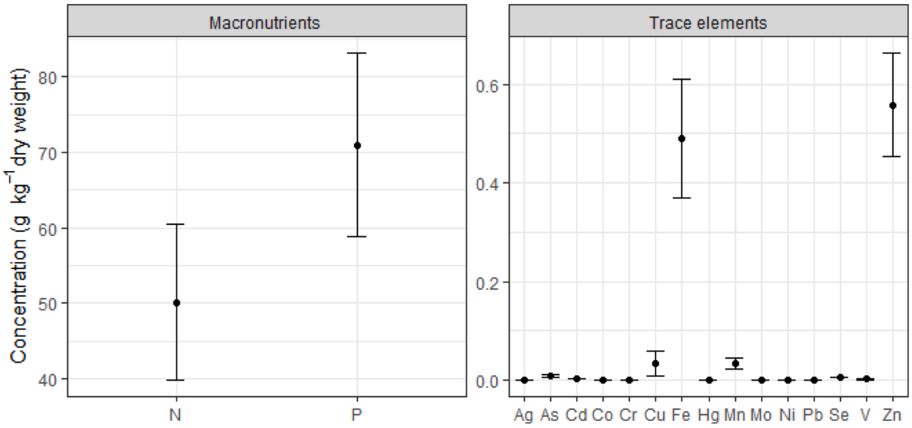

Fig. 2. Concentration of macronutrients and trace elements in minke whale faeces (mean ± standard deviation). Number of samples included in the means was 29 for P and 31 for all other elements. Abbreviations: N = nitrogen, P = phosphorus, Ag = silver, As = arsenic, Cd = cadmium, Co = cobalt, Cr = chromium,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

Table 4
Trace element 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
K 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	102,639	11,730	5,865	23,949
K 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	113,867	12,607	6,913	22,367
K 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	128,774	13,321	4,885	22,647
K 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	121,273	14,654	3,386	20,212
K 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	112,439	23,893	4,989	18,271
K 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	118,092	21,256	4,062	23,146
K 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	89,982	17,397	10,798	16,197
K 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	105,680	20,476	5,482	17,173
K 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	95,991	14,116	3,727	28,233
K 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	93,071	12,927	7,239	16,546
K 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	103,542	16,349	8,174	16,894
K 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	*	*	*	*
K 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	81,670	9,982	10,436	15,880
K 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	46,970	15,031	8,924	8,924
K 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	100,334	13,378	7,525	18,395
K 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	131,971	14,900	3,065	26,394
K 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	83,940	14,550	9,513	18,467
K 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	89,213	11,760	7,705	19,870
K 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	104,356	12,704	6,806	14,065
K 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	97,087	8,669	7,975	17,337
K 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	119,832	18,574	4,074	22,169
K 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	93,006	12,277	7,068	18,229
K 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	90,703	15,873	6,349	21,315
K 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	84,183	7,975	6,203	18,166
K 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	103,986	11,265	5,633	20,797
K 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	50,026	13,409	11,862	9,283
K 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	118,915	10,033	4,088	16,722
K 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	*	*	*	*
K 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	84,388	16,275	9,644	22,303
K 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	84,329	26,001	6,465	28,110
K 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	89,670	9,326	6,098	30,846
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	97,929	14,507	6,723	19,755
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	19,698	4,323	2,306	5,024

* Not enough sample to measure these elements.

Table 5
Estimated daily amount of macronutrient (N, P) and trace elements defecated by minke whales in the small management area (SMA) of Svalbard. Values are given by individual and for the current population of 15,693 individuals that forage during summer in this region.

	Per individual (g d^{-1})		All population (kg d^{-1})	
Element	Mean	Sd	Mean	Sd
N	445.467	91.675	6,990.721	1,438.657
P	630.853	107.939	9,899.978	1,693.882
V	0.018	0.005	0.286	0.080
Cr	0.001	0.000	0.014	0.006
Mn	0.302	0.092	4.746	1.441
Fe	4.350	1.063	68.272	16.676
Co	0.002	0.001	0.037	0.013
Ni	0.009	0.004	0.145	0.058
Cu	0.305	0.219	4.791	3.438
Zn	4.963	0.927	77.877	14.542
As	0.077	0.016	1.213	0.247
Se	0.055	0.006	0.858	0.095
Mo	0.004	0.001	0.065	0.014
Ag	0.002	0.001	0.028	0.010
Cd	0.031	0.010	0.485	0.150
Pb	0.001	0.000	0.010	0.003
Ca	870.851	175.172	13,666.268	2,748.978
Na	129.008	38.446	2,024.518	603.335
K	59.782	20.509	938.152	321.842
Mg	175.679	44.681	2,756.936	701.183

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. Despite the considerable number of samples (n = 31), all were collected from whales feeding on capelin during summer. Additional research is needed to investigate how excreted nutrients vary seasonally and with diet. The potential impact of excreted nutrients on summer 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.,

Table 6

Daily 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 two phytoplankton bloom conditions, based on the data provided by Luchetta et al. (2000), and Downes et al. (2021).

PP condition	Daily PP (g C m^{-2} d^{-1})	Reference	Whale survey year	Whale abundance	Survey area (km^2)	PP survey area (t C d^{-1})	P defecated (t d^{-1})	PP_{Whale} (t C d^{-1})	% of PP
Min (no bloom)	0.08	Luchetta et al. 2000	2019	8,471	164,150	13,132	5.3	220	1.7
Min (no bloom)	0.04	Downes et al. 2021	2019	8,471	164,150	6,730	5.3	220	3.3
Max (bloom)	0.69	Luchetta et al. 2000	2019	8,471	164,150	113,264	5.3	220	0.2
Max (bloom)	0.66	Downes et al. 2021	2019	8,471	164,150	108,339	5.3	220	0.2
Min (no bloom)	0.08	Luchetta et al. 2000	2014	11,088	175,488	14,039	7.0	288	2.0
Min (no bloom)	0.04	Downes et al. 2021	2014	11,088	175,488	7,195	7.0	288	4.0
Max (bloom)	0.69	Luchetta et al. 2000	2014	11,088	175,488	121,087	7.0	288	0.2
Max (bloom)	0.66	Downes et al. 2021	2014	11,088	175,488	115,822	7.0	288	0.2

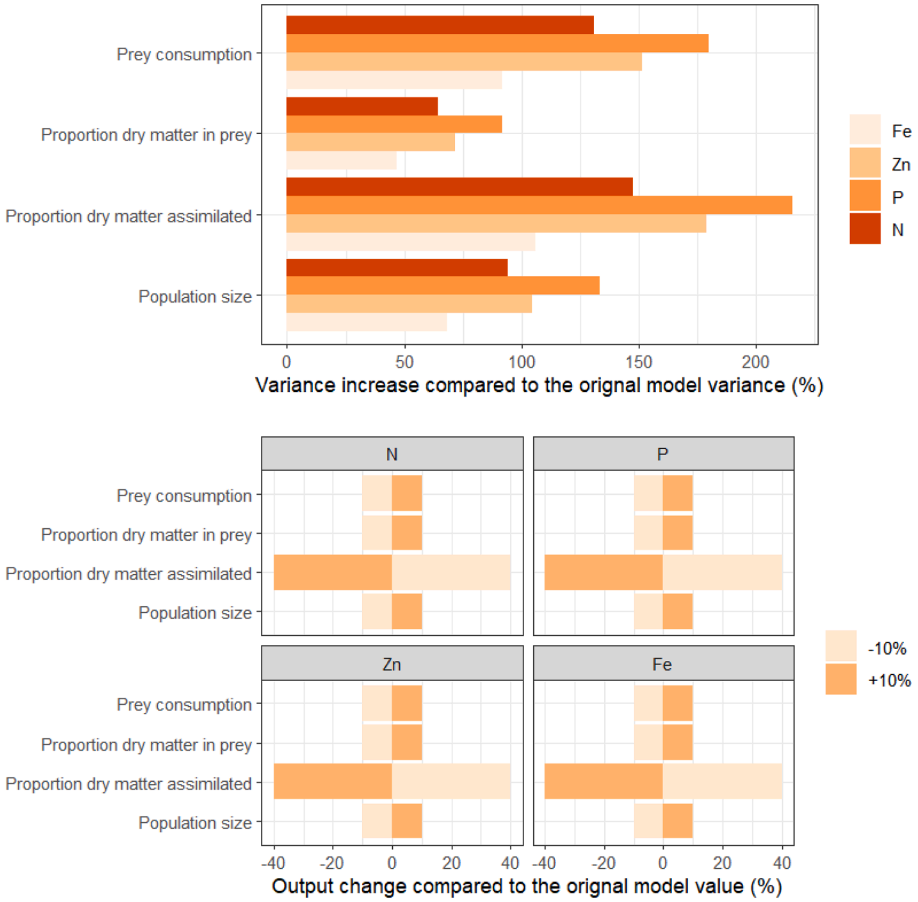

Fig. 3. Results of the uncertainty (top) and sensitivity (bottom) analyses, illustrating the influence of model variables on the estimated daily amount of nutrients excreted by minke whales off Svalbard.

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 based on short-term tag attachments (often in known feeding hotspots) it is uncertain how representative these data are of the 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 substantially affect 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 element 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 differences among species, from distinct nutrient levels in different prey or from sampling methods (faeces collected directly from whales or indirectly from seawater). 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). Urea concentration in minke whale urine is two to four times higher than in cattle (Birukawa et al., 2005), but the relative proportion of urea excreted via urine vs faeces by minke whales and other baleen whales is unknown. Captive harp seals 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 elements

Elemental Zn and Fe were the trace elements 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 mainly 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 elements, such as Cu, Co, Zn and Mn constitute important building blocks in phytoplankton cellular synthesis (Twining and Baines, 2013; Ratnarajah et al., 2014). In opposite, non-essential elements, such as Ag, Cd, Hg, Pb are potentially toxic elements for living organisms including phytoplankton (Boyd, 2015), and were found in very low concentration in the analysed samples.

4.4. Significance to primary production

The significance of whale-faeces nutrients to primary production was explored in this study. In case of no N limitation (i.e., enough N is excreted via urine), the release of P through minke-whale defecation has the potential to stimulate over 400 t of carbon per day as new or regenerated primary production in the SMA of Svalbard, and 220 t 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 0.2 to 4 % 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 and P remain in the euphotic zone and is used by phytoplankton and that further research is needed to verify these assumptions.

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, Tuerena et al. 2021). 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 minke whale feeding season (April-October) and hence, the input of N and P from whale faeces during this season is probably well-timed. Due to a tight coupling between mostly regenerated nutrient pools and the primary producers during the summer season (Kristiansen et al. 1994) we may not see an increase from this activity in bulk nutrient measurements during this time. Therefore, 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 (Eilertsen et al. 1989, Verity et al. 2002).

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 to 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.

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 during summer. Additional contribution from minke-whale urine needs to be quantified. Several other research questions remain, namely how nutrient concentration in faeces vary seasonally and with prey type, 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 annual 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.

Data availability

Data will be made available on request.

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

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

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

Bogstad, B., Gjøsæter, H., Haug, T., Lindstrøm, U., 2015. A review of the battle for food in the Barents Sea: cod vs. marine mammals. Front. Ecol. Evol. 3.

Boyd, C.E., 2015. Micronutrients and other trace elements. In: Boyd, C.E. (Ed.), Water Quality: An Introduction. Springer International Publishing, Cham, pp. 277–311.

Bragadóttir, M., Pálmadóttir, H., Kristbergsson, K., 2002. Seasonal changes in chemical composition and quality parameters in capelin (*Mallotus villosus*). J. Aquat. Food Prod. Technol. 11, 87–103.

Brand, L.E., Sunda, W.G., Guillard, R.R.L., 1983. Limitation of marine phytoplankton reproductive rates by zinc, manganese, and iron1. Limnol. Oceanogr. 28, 1182–1198.

Bristow, L.A., Mohr, W., Ahmerkamp, S., Kuypers, M.M.M., 2017. Nutrients that limit growth in the ocean. Curr. Biol. 27, R474–R478.

Brzezinski, M.A., 1985. The Si: C: N ratio of marine diatoms: interspecific variability and the effect of some environmental variables 1. J. Phycol. 21, 347–357.

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

Downes, P.P., Goult, S.J., Woodward, E.M.S., Widdicombe, C.E., Tait, K., Dixon, J.L., 2021. Phosphorus dynamics in the Barents Sea. Limnol. Oceanogr. 66, S326–S342.

Eilertsen, H.C., Tande, K.S., Taasen, J.P., 1989. Vertical distributions of primary production and grazing by Calanus glacialis jaschnov and C. hyperboreus krøyer in Arctic waters (Barents Sea). Polar Biol. 9, 253–260.

Enquist, B.J., Abraham, A.J., Harfoot, M.B.J., Malhi, Y., Doughty, C.E., 2020. The megabiota are disproportionately important for biosphere functioning. Nat. Commun. 11, 699.

Estes, J.A., Heithaus, M., McCauley, D.J., Rasher, D.B., Worm, B., 2016. Megafaunal Impacts on Structure and Function of Ocean Ecosystems. Annu. Rev. Env. Resour. 41, 83–116.

Fadely, B.S., Graham, A.J.W., Costa, D.P., 1990. Assimilation efficiency of northern fur seals determined using dietary manganese. J. Wildl. Manag. 54, 246–251.

Galbraith, E.D., Le Mézo, P., Solanes Hernandez, G., Bianchi, D., Kroodsma, D., 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., Haug, T., Øien, N., Walløe, L., Lindblom, L., Seliussen, B.B., Skaug, H.J., 2012. The Norwegian minke whale DNA register: a data base monitoring commercial harvest and trade of whale products. Fish Fish. 13, 313–332.

Goodman-Lowe, G.D., Carpenter, J.R., Atkinson, S., 1999. Assimilation efficiency of prey in the Hawaiian monk seal (*Monachus schauinslandi*). Can. J. Zool. 77, 653–660.

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

Haug, T., Nilssen, K.T., Lindstrøm, U., Skaug, H.J., 1997. On the variation in size and composition of minke whale (*Balaenoptera acutorostrata*) forestomach contents. J. Northwest Atl. Fish. Sci. 22, 105–114.

Haug, T., Lindstrøm, U., Nilssen, K., 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., Bjørge, A., Øien, N., Ziryanov, S.V., 2011. Marine mammals of the Barents Sea. In: Jakobsen, T., Ozhigin, V.K. (Eds.), The Barents Sea; Ecosystem, Resources, Management; Half a Century of Russian-Norwegian Cooperation. Tapir Academic Press, pp. 395–430.

Ibrahim, A., Olsen, A., Lauvset, S., 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, 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.

Julshamn, K., Maage, A., Norli, H.S., Grobecker, K.H., Jorhem, L., Fecher, P., Collaborators, 2019. Determination of Arsenic, Cadmium, Mercury, and Lead by Inductively Coupled Plasma/Mass Spectrometry in Foods after Pressure Digestion: NMKL Interlaboratory Study. Journal of AOAC INTERNATIONAL 90, 844–856.

Keiver, K.M., Ronald, K., Beamish, F.W.H., 1984. Metabolizable energy requirements for maintenance and faecal and urinary losses of juvenile harp seals (*Phoca groenlandica*). Can. J. Zool. 62, 769–776.

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

Kristiansen, S., Farbrot, T., Wheeler, P.A., 1994. Nitrogen cycling in the Barents Sea - Seasonal dynamics of new and regenerated production in the marginal ice zone. Limnol. Oceanogr. 39, 1630–1642.

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., Hare, J.A., Noseworthy, E., Friel, J.K., 1997a. Assimilation efficiency of captive ringed seals (*Phoca hispida*) fed different diets. Polar Biol. 18, 107–111.

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

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

Luchetta, A., Lipizer, M., Socal, G., 2000. Temporal evolution of primary production in the central Barents Sea. J. Mar. Syst. 27, 177–193.

Mårtensson, P.E., Nordøy, E.S., Blix, A.S., 1994. Digestibility of krill (Euphausia superba and Thysanoessa sp.) in minke whales (Balaenoptera acutorostrata) and crabeater seals (Lobodon carcinophagus). Br. J. Nutr. 72, 713–716.

Martin, A.H., Pearson, H.C., Saba, G.K., Olsen, E.M., 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., Piatt, J., 1984. Composition and energy contents of mature inshore spawning capelin (mallotus villosus): Implications for seabird predators. Comp. Biochem. Physiol. A Physiol. 78, 15–20.

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

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

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

Nordøy, E.S., Sørmo, W., Blix, A.S., 1993. In vitro digestibility of different prey species of minke whales (*Balaenoptera acutorostrata*). Br. J. Nutr. 70, 485–489.

Olsen, A., Johannessen, T., Rey, F., 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.

Ratnarajah, L., Bowie, A.R., Lannuzel, D., Meiners, K.M., Nicol, S., 2014. The biogeochemical role of baleen whales and krill in Southern Ocean nutrient cycling. PLoS One 9, e114067.

Ratnarajah, L., Melbourne-Thomas, J., Marzloff, M.P., Lannuzel, D., Meiners, K.M., Chever, F., Nicol, S., Bowie, A.R., 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. Ecol. Model. 320, 203–212.

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

Ratnarajah, L., Nicol, S., Bowie, A.R., 2018. Pelagic iron recycling in the Southern Ocean: exploring the contribution of marine animals. Front. Mar. Sci. 5, 1–9.

Redfield, A.C., 1934. On the proportions of organic derivatives in sea water and their relation to the composition of plankton. University Press of liverpool Liverpool.

Reksten, A.M., Bøkevoll, A., Frantzen, S., Lundebye, A.-K., Kögel, T., Kolås, K., Aakre, I., Kjellevold, M., 2020. Sampling protocol for the determination of nutrients and contaminants in fish and other seafood – The EAF-Nansen Programme. MethodsX 7, 101063.

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

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

Ronald, K., Keiver, K.M., Beamish, F.W.H., Frank, R., 1984. Energy requirements for maintenance and faecal and urinary losses of the grey seal (*Halichoerus grypus*). Can. J. Zool. 62, 1101–1105.

Rosen, D.A.S., Trites, A.W., 2000. Digestive efficiency and dry-matter digestibility in Steller sea lions fed herring, pollock, squid, and salmon. Can. J. Zool. 78, 234–239.

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

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

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

Sivertsen, S.P., Pedersen, T., Lindstrøm, U., Haug, T., 2006. Prey partitioning between cod (*Gadus morhua*) and minke whale (*Balaenoptera acutorostrata*) in the Barents Sea. Mar. Biol. Res. 2, 89–99.

Skaug, H.J., Øien, N., Schweder, T., Bøthun, G., 2004. Abundance of minke whales (*Balaenoptera acutorostrata*) in the Northeast Atlantic: variability in time and space. Can. J. Fish. Aquat. Sci. 61, 870–886.

Skern-Mauritzen, M., Lindstrøm, U., Biuw, M., Elvarsson, B., Gunnlaugsson, T., Haug, T., Kovacs, K.M., Lydersen, C., McBride, M.M., Mikkelsen, B., Øien, N., Víkingsson, G., 2022. Marine mammal consumption and fisheries removals in the Nordic and Barents Seas. ICES J. Mar. Sci. 79, 1583–1603.

Smith, L.V., McMinn, A., Martin, A., Nicol, S., Bowie, A.R., Lannuzel, D., van der Merwe, P., 2013. Preliminary investigation into the stimulation of phytoplankton photophysiology and growth by whale faeces. J. Exp. Mar. Biol. Ecol. 446, 1–9.

Solvang, H.K., Skaug, H.J., Øien, N.I., 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.

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.

Sunda, W. 2012. Feedback Interactions between Trace Metal Nutrients and Phytoplankton in the Ocean. Frontiers in Microbiology **3**.

Tuerena, R.E., Hopkins, J., Ganeshram, R.S., Norman, L., de la Vega, C., Jeffreys, R., Mahaffey, C., 2021. Nitrate assimilation and regeneration in the Barents Sea: insights from nitrate isotopes. Biogeosciences 18, 637–653.

Twining, B.S., Baines, S.B., 2013. The trace metal composition of marine phytoplankton. Ann. Rev. Mar. Sci. 5, 191–215.

Verity, P.G., Wassmann, P., Frischer, M.E., Howard-Jones, M.H., Allen, A.E., 2002. Grazing of phytoplankton by microzooplankton in the Barents Sea during early summer. J. Mar. Syst. 38, 109–123.

Vikingsson, G.A., 1997. Feeding of fin whales (*Balaenoptera physalus*) off Iceland - diurnal and seasonal variation and possible rates. J. Northwest Atl. Fish. Sci. 22, 77–89.

Wassmann, P., Ratkova, T., Andreassen, I., Vernet, M., Pedersen, G., Rey, F., 1999. Spring bloom development in the marginal ice zone and the central Barents Sea. Mar. Ecol. 20, 321–346.

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

Wright, P.A., 1995. Nitrogen excretion: three end products, many physiological roles. J. Exp. Biol. 198, 273–281.

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