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Pack-ice seals contribute to biological transfers of iron in the Southern Ocean

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Abstract

The contribution of animals to biological transfers of essential nutrients in ecosystems is increasingly recognised as a significant component of ecosystem functioning. In the Southern Ocean (SO), primary productivity is primarily limited by the availability of iron in the euphotic zone, which makes animals locally releasing iron-rich faeces potential fertilizers of the SO food web. We quantified the amounts of iron released by four species of Antarctic pack-ice seals using a bioenergetic model set up with best available data on species abundance, energetics, diets and prey composition. We estimated that leopard, crabeater, Weddell and Ross seals together release 208 tonnes of iron per year (95 % confidence interval [104 - 378]). This is equivalent to the current contribution of SO humpback whales and four times that of SO sperm whales. At the population level, crabeater seals are the major contributors (73%), followed by Weddell (21%), leopard (4%) and Ross seals (1%). Locally, each species shows different daily individual iron release rates, suggesting the patchy and transient impact of these iron releases on primary producers might differ according to species. Beyond quantitative aspects, pack-ice seals' contribution to horizontal, vertical and trophic transfers of iron, depends on their habitat preferences, on their ecology and behaviours at sea and on the ice. Although their role as iron vectors has been mostly overlooked so far, our results place pack-ice seals alongside whales

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and penguins as significant components of the SO ecosystem biological iron cycling, thus contributing substantially to its productivity and functioning.

Keywords: biological iron vector; Antarctica; sea ice; primary productivity; horizontal nutrient transfers; vertical nutrient transfers

Introduction

Fluxes and transfers of essential nutrients largely determine the productivity, diversity and structure of trophic webs (Atkinson et al. 2017; Marzetz et al. 2017). This applies both to major nutrients (e.g. nitrogen N and phosphorus P), which are present in large quantities throughout the trophic web, and to trace elements (e.g. iron Fe or manganese Mn), which are present in much smaller quantities but are no less essential to ecosystem functioning. Within marine trophic webs, primary producers such as phytoplankton are tied to the euphotic zone, i.e. the surface layer where sunlight penetrates and enables photosynthesis. Nutrients naturally tend to be adsorbed on particles sinking to deeper waters outside of this euphotic zone (Boyd and Ellwood 2010), so that phytoplankton face limiting conditions for their growth in many parts of the oceans (Moore et al. 2013).

In the Southern Ocean (SO), one of the largest High Nutrient Low Chlorophyll (HNLC) regions in the world, the euphotic zone largely contains major nutrients (N and P), but primary productivity is limited by low concentrations of micronutrients, particularly iron (Hassler et al. 2012a; Tagliabue et al. 2017). Physical iron transfer processes (e.g. atmospheric dust) are limited in large areas of this ocean due to their remoteness (Martin et al. 1990). This low iron supply combined with a rapid biological uptake result in a rapid depletion of any form of bioavailable iron (i.e. chemical form that can be taken up and used by primary producers) in surface waters (Smith et al. 2021). Thus, any process providing the SO euphotic zone with iron can shape phytoplankton communities and influence the structure and productivity of trophic webs (Hassler et al. 2012a). Moreover, phytoplankton is the first component of the biological carbon pump: inorganic carbon is transferred to organic matter via photosynthesis, and part

of it is sequestered in sediments through sinking particles, passive advection, vertical migration of animals and sinking carcasses (Falkowski et al. 1998; Stukel and Ducklow 2017). This has motivated a substantial body of research to underpin iron transfers to the SO euphotic zone to further our understanding of the whole SO system, from processes regulating its productivity to the global cycling of nutrients (including carbon) and climate regulation (Hassler et al. 2012a).

The contribution of animals to biological nutrient cycling is increasingly recognised (Wing et al. 2014, 2017; Doughty et al. 2016; Allgeier et al. 2017; Ratnarajah et al. 2018). Grazing and predation by fauna, and the subsequent release of waste (faeces and urine) in the euphotic zone, retain nutrients in the surface ocean for extended periods of time, rather than them being lost to depths with sinking materials. Among the SO fauna, air-breathing megafauna such as cetaceans, seals and penguins may contribute significantly to SO productivity by releasing iron-rich waste products in surface waters (Lavery et al. 2010, 2014; Nicol et al. 2010; Ratnarajah et al. 2014; Wing et al. 2014; Otero et al. 2018; Sparaventi et al. 2021). These diving top predators differ from most marine life in that they are tied to surface waters for breathing. As they shut down non-vital body functions during their dives to limit oxygen consumption (Kooyman et al. 1981), they release their waste products during their surface intervals while breathing and resting near the surface (Roman and McCarthy 2010).

At the scale of the SO, the total amount of iron recycled by top predators is thought to be minor compared to that recycled by the microfauna (microbial community, microzooplankton and krill) (Maldonado et al. 2016). The transient and localized enrichments of surface waters from waste release are also unlikely to be detected across large regions, as they operate on a smaller scale than physical iron supply processes (Smith et al. 2021). Nevertheless, the release of iron-rich faecal matter could be locally significant in stimulating phytoplankton productivity. Predator waste products are specific in that they are heavily concentrated in iron (from 63.4 to 3928 mg.Fe.kg⁻¹ dry weight) (Ratnarajah et al. 2014; Wing et al. 2014, 2017, 2021; Sparaventi et al. 2021). These total iron concentrations (i.e. both dissolved and particulate

fraction) are six to eight orders of magnitude higher than nanomolar concentrations of euphotic waters (Ratnarajah et al. 2014; Wing et al. 2014). In baleen whale faeces, the dissolved fraction alone can be three orders of magnitude higher than SO surface waters (186 – 754 nmol.Fe.L⁻¹) (Ratnarajah et al. 2017). Uncertainties remain regarding the bioavailability of iron from waste products to primary producers (Ratnarajah et al. 2017). Yet, primary producers can use iron in different chemical forms (Nodwell and Price 2001; Lis et al. 2015; Tagliabue et al. 2017), either dissolved in seawater (< 0.2 µm, labile or colloid forms) or particulate (> 0.2 µm, e.g. bound to organic ligands), and SO phytoplankton strains have shown increased growth and productivity when fertilized by seabird guano and baleen whale faeces (Smith et al. 2013; Shatova et al. 2017). Thus, at least a fraction of iron released in this waste is likely to be recycled in the trophic web, either immediately upon release, after remineralisation by the microbial community or after complexation with free bacterial ligands in surface waters (Ratnarajah et al. 2017). SO megafauna species are also highly mobile and are the largest iron vectors that can operate against physical processes. For example, they can not only contribute to maintaining the iron pool in the euphotic zone (i.e. true recycling, when iron released in waste originates in the euphotic zone), but also introduce new iron, e.g. released by sperm whales feeding at depth (Lavery et al. 2010). Finally, predators tend to form significant aggregations in space and time, which can support “hot spots” and “hot moments” of biochemical cycling (Atkinson et al. 2017; McInturf et al. 2019; Subalusky and Post 2019). These functional traits distinguish them from other biological or physical iron vectors (McInturf et al. 2019; Subalusky and Post 2019). Fully underpinning the drivers of food-web structure and productivity requires a thorough understanding of all the processes involved, including of biologically-mediated nutrient transfers, despite their complexity due to their local and transient scale.

To provide a better understanding of the role of megafauna in biologically-mediated nutrient transfers, we investigated the contribution of four resident species of pack-ice seals: the crabeater seal *Lobodon carcinophaga*, the Weddell seal *Leptonychotes weddelli*, the

leopard seal *Hydrurga leptonyx* and the Ross seal *Ommatophoca rossii* to iron transfers in the SO system. As top predators, they may impact the structure and the biomass of the SO ecosystem through predation (Krause et al. 2015; Goetz et al. 2017; Staniland et al. 2018). However, their role as vectors of limiting micronutrients has received little attention despite iron concentrations in their faeces ($950.8 \pm 148.9 \text{ mg.Fe.kg}^{-1}$ dry weight (Wing et al. 2021)) in line with that of whales and seabirds (Nicol et al. 2010; Wing et al. 2021).

As a basis for investigating their influence on the functioning of SO ecosystem through biological iron cycling, we used a bioenergetic model linking metabolism, diet and population estimates of pack-ice seals. We estimate iron release in faeces at individual and population levels, and we compare seal-mediated iron releases with those of other SO megafauna taxa (whales and penguins). Finally, we discuss the different iron transfers pack-ice seals may operate and highlight functional characteristics relevant to ecosystem functioning. While we recognise that iron is not the only essential micronutrient released in pack-ice seal faeces (e.g. cobalt Co and manganese Mn, see Wing et al. (2021)), we restricted our study to iron given its importance in the SO ecosystem functioning and in overall ocean biogeochemical cycling.

Material & Methods

Estimating Fe release using a bioenergetic model

We used a bioenergetic model of prey biomass consumption to estimate iron consumption and egestion of individual seals. Daily energetic needs were estimated from basal metabolic rate (*BMR*, in kJ.day^{-1}) using Kleiber's (1975) formula (previously applied to marine mammal populations, e.g. Roman and McCarthy (2010), Spitz et al. (2018)) and including the additional cost of daily activities through the species-specific metabolic index β (Spitz et al. 2012, 2018).

For an individual *i*:

$$ADMR_i = \beta_i \times BMR_i = \beta_i \times 293.1 \times BM_i^{3/4} \quad (1)$$

with $ADMR$ the seal's average daily metabolic rate (in $kJ.day^{-1}$) and BM its body mass (in kg). We then estimated the daily ration R (in $kg.day^{-1}$) needed for each individual to meet its $ADMR$, given the mean energy content of its diet (E , in $kJ.kg^{-1}$ fresh weight) and the digestive assimilation efficiency (AE):

$$R_i = \frac{ADMR_i}{AE \times E_i} \quad (2)$$

Using the average iron concentration in the diet (x_{Fe} , in $mg.kg^{-1}$ fresh weight), we estimated the daily iron consumption and thus the daily amount of iron released ($Fe_{d,i}$, in $mg.day^{-1}$) given the iron release rate r_{Fe} :

$$Fe_{d,i} = R_i \times x_{Fe_i} \times r_{Fe} \quad (3)$$

We then extended this daily individual rate to an annual population rate using population abundance estimate A . We finally obtained the total amount of iron released by each species' population in the SO (Fe_{tot} , in $t.yr^{-1}$):

$$Fe_{tot} = Fe_{d,i} \times 365 \times A \times 10^6 \quad (4)$$

Setting model parameters

Five of the seven parameters in our model (BM , β , AE , r , A) were assigned mean values based on available data in the published literature. The remaining two parameters (E and x_{Fe}) were calculated using available diet data for each species and composition data of prey items (see details below). To account for the uncertainty and/or inherent natural variability in these parameters and provide estimate intervals for the model outputs, we used Monte-Carlo simulations ($n = 10^5$) to simulate vectors of possible parameter values, based on a given base value and distribution (Table 1).

Table 1 Bioenergetic parameters' setting information, based on literature values. BM is individual body mass, β is a metabolic species-specific multiplier, AE is assimilation efficiency, E is the mean energy content of diet, x_{Fe} is the mean iron content of diet, r_{Fe} is iron release rate and A population abundance. Truncated normal parameters are indicated as follows: $\sim N(\text{mean}, \text{standard deviation}, [\text{lower limit} - \text{upper limit}])$; if only one number in brackets, it is the lower limit

Par.	Leopard seal <i>H. leptonyx</i>	Crabeater seal <i>L. carcinophagus</i>	Weddell seal <i>L. weddellii</i>	Ross seal <i>O. rossii</i>	Ref.
BM (kg)	$\sim N(350, 0.2)$	$\sim N(200, 0.2)$	$\sim N(300, 0.2)$	$\sim N(160, 0.2)$	a
β	$\sim N(3, 0.5, [2 - 3.5])$	$\sim N(2, 0.5, [1.5 - 3])$	$\sim N(2, 0.5, [1.5 - 3])$	$\sim N(2, 0.5, [1.5 - 3])$	b
AE	$\sim N(0.9, 0.05, [0.80 - 0.95])$	$\sim N(0.9, 0.05, [0.80 - 0.95])$	$\sim N(0.9, 0.05, [0.80 - 0.95])$	$\sim N(0.9, 0.05, [0.80 - 0.95])$	c
E (kJ.k g ⁻¹)	$\sim N(12.1, 0.2 \times 12.1, [0.2 \times 12.1])$	$\sim N(5.1, 0.2 \times 5.1, [0.2 \times 5.1])$	$\sim N(5.4, 0.2 \times 5.4, [0.2 \times 5.4])$	$\sim N(4.8, 0.2 \times 4.8, [0.2 \times 4.8])$	See Eq. (5-6) & Table 2)
x_{Fe}	$\sim N(165, 0.2 \times 165, [0.2 \times 165])$	$\sim N(10.1, 0.2 \times 10.1, [0.2 \times 10.1])$	$\sim N(22.6, 0.2 \times 22.6, [0.2 \times 22.6])$	$\sim N(15.6, 0.2 \times 15.6, [0.2 \times 15.6])$	See Eq. (5-6) & Table 2)
r_{Fe}	$\sim U(0.7, 0.9)$	$\sim U(0.7, 0.9)$	$\sim U(0.7, 0.9)$	$\sim U(0.7, 0.9)$	d
A (No.)	$\sim N(35\ 500, 22\ 925, [10\ 900 - 102\ 600])$	$\sim N(5\ 869\ 400, 1\ 229\ 325, [3\ 699\ 400 - 8\ 616\ 700])$	$\sim N(633\ 000, 278\ 500, [221\ 000 - 1\ 335\ 000])$	$\sim N(78\ 500, 47\ 950, [39\ 400 - 231\ 200])$	e

^a Bryden and Erickson (1976); Laws (1977); Skinner and Klages (1994); Trites and Pauly (1998); Van Den Hoff et al. (2003); Williams and Yeates (2004); McDonald et al. (2008); Shirihai (2008); Bengtson (2009); Castellini et al. (2009); Forcada et al. (2009); Rogers (2009); Thomas and Rogers (2009)

^b Castellini et al. (1992); Renouf and Gales (1994); Williams et al. (2001); Hoelzel (2009)

^c Ashwell-Erickson and Elsner (1981); Keiver et al. (1984); Ronald et al. (1984); Martensson et al. (1994)

^d Candela et al. (1984); Lavery et al. (2010); Ratnarajah et al. (2016a)

^e Southwell et al. (2012)

Body mass BM

The average seals' body mass BM (in kg) for each species were taken from ranges found in the literature (Table 1). BM was set up as a random variable following a normal distribution with the above-mentioned mean value and a standard deviation of 20 %. Only adults were considered for our calculations.

Species-specific metabolic multiplier β

The metabolic index β is a species-specific indicator of the "cost of living": it accounts for the cost of activities and metabolic efficiency (Spitz et al. 2012). Studies focusing on the metabolism of pack-ice seals (e.g. Castellini et al. (1992), Renouf and Gales (1994)) suggest they may have a relatively low metabolism. Based on what is known of the metabolism of polar seals and estimated Activity Metabolic Rates of Weddell seals (Williams et al. 2001; Hoelzel 2009), we considered β as a random variable with a mean value of 2 ± 0.5 for Weddell, Ross and crabeater seals and 3 ± 0.5 for leopard seals, and set minimum and maximum values using a truncated normal distribution to exclude non-physiologically viable values (Table 1). As this factor accounts for the cost of activities averaged over the individual year cycle (i.e. including breeding and moulting period), we did not include any fasting period in the model.

Assimilation efficiency AE

Experimental studies on captive pinnipeds measured AE ranging between 79 and 96.8 % (Ashwell-Erickson and Elsner 1981; Keiver et al. 1984; Ronald et al. 1984; Mårtensson et al. 1994). We applied a truncated normal distribution around the mean value of 0.9 with a standard deviation of 0.05 and lower and upper bounds at 0.80 and 0.95 (Table 1).

Iron release rate r_{Fe}

Adult mammals (excluding pregnant and lactating females) release most consumed micronutrients - including iron - through faeces, with release rates $\geq 90\%$ (Candela et al. 1984). Bioenergetic models that estimated iron egestion for cetaceans used an iron release rate of 0.85 (Lavery et al. 2010) or of 0.7 - 0.9 with a base value at 0.8 (Ratnarajah et al. 2016a). We considered r_{Fe} as a random variable following a uniform distribution with a minimum of 0.70 and a maximum of 0.9 (Table 1).

Population abundance A

The largest survey on abundance estimates of the four species of pack-ice seals in the SO was the Antarctic Pack-Ice Seal (APIS) program survey, initiated by the Scientific Committee on

Antarctic Research (SCAR) in 1999/2000 (Southwell et al. 2012). It used a unified distance sampling protocol based on the counting of hauled-out animals and satellite tagging studying haul-out behaviours, and had the broadest spatial coverage in the SO. We applied a truncated normal distribution using mean values and intervals from the APIS survey (Southwell et al. 2012) to simulate variability in the abundance parameter (Table 1).

Average energy E and iron content x_{Fe} of the diet

We described the diet of each species using five functional prey groups: krill, fish, cephalopod, pinniped and penguins. For crabeater and Ross seals, we used diets described in McCormack et al. (2020) resulting from the compilation of dietary sample results from 21 studies over the SO, available in the SCAR Southern Ocean Diet and Energetic Database (Scientific Committee on Antarctic Research (SCAR) 2018) (Table 2). For Weddell and leopard seals, we made small adjustments to the diets in McCormack et al. (2020) to adapt to the functional prey groups we used, and to better match descriptions of diets reported in the literature that differed from those in McCormack et al. (2020). Krill was included as part of the diet of Weddell seals, in small proportions (see Casaux et al. (1997), Lake et al. (2003)), and the percentage of consumption of cephalopods of leopard seals was lowered whereas that of krill and penguins was increased (see Hall-Aspland and Rogers (2004), Casaux et al. (2009), Forcada et al. (2009)) (Table 2).

To determine an average energy content and iron concentration per prey group (E_{pg} and $x_{Fe,pg}$, with pg being the prey group index), we compiled analytical data of 205 prey samples from 9 studies and 300 prey samples from 17 studies, respectively (see Table 2 for references). We then used these values and the percentage of prey groups in diets (in weight, W_{pg}) to determine the mean energy content (E) and the mean iron concentration (x_{Fe}) in each species' diet (Table 1, 2):

$$E = \sum_{pg} W_{pg} \times E_{pg} \quad (5)$$

$$x_{Fe} = \sum_{pg} W_{pg} \times x_{Fe,pg} \quad (6)$$

Diets vary individually, seasonally and spatially, sometimes significantly depending on species. The energy content and iron concentration of their prey also vary depending on life stage, season, location or body part (e.g. Yamamoto et al. (1987), Jerez et al. (2013b), Kim et al. (2014), Ruck et al. (2014)). We set up a normally distributed standard deviation of 20% around the calculated mean values (E and x_{Fe}) to account for the intrinsic variability in the composition of both prey items and diets of individuals.

Table 2 Data and literature sources (References) used to estimate the energy content (E_{pg}) and iron (Fe) concentration ($x_{Fe,pg}$) of the functional prey groups (pg) used to describe the diet of each pack-ice seal species, and diets as established with percentage of consumption (in weight) of each prey group

Prey group pg	Mean energy content E_{pg} ($\text{kJ}\cdot\text{g}^{-1}$)	lean iron content $x_{Fe,pg}$ ($\text{mg}\cdot\text{kg}^{-1}$ wet weight)	% in diet (in weight)				References
			Leopard seal <i>H. leptonyx</i>	Crabeater seal <i>L. carcinophagus</i>	Weddell seal <i>L. weddellii</i>	Ross seal <i>O. rossii</i>	
Krill	5.1	11.3	30	98.5	2	35	[energy] ^a [Fe] ^b
Fish	5.5	24.3	42	0.5	90	30	[energy] ^c [Fe] ^d
Cephalopods	3.8	14.3	1	1	8	35	[energy] ^e [Fe] ^f
Pinniped (muscle)	10	194.9	21	0	0	0	[energy] ^g [Fe] ^h
Penguins (muscle)	10	180.4	6	0	0	0	[energy] ⁱ [Fe] ^j

^a Armstrong and Siegfried (1991); Martensson et al. (1996); Kjørboe (2013); Ruck et al. (2014)

^b Palmer Locamini and Presley (1995); Caroli et al. (1998); Barbante et al. (2000); Nicol et al. (2010); Kim et al. (2014)

^c Tierney et al. (2002); Chouvelon et al. (2022b, a)

^d Honda et al. 1987; Goutte et al. 2015; Chouvelon et al. (2022b, a)

^e Croxall and Prince (1982); Chouvelon et al. (2022a)

^f Lourenço et al. (2009); Chouvelon et al. (2022a)

^g Forcada et al. (2009)

^h Yamamoto et al. (1987); Noda et al. (1995); Julshamn and Grahl-Nielsen (2000)

ⁱ Forcada et al. (2009)

^j Honda et al. (1986); Szefer et al. (1993); Yamamoto et al. (1996); Jerez et al. (2013b, a)

Differences between levels of iron release

Dimensions of parameters and outputs ($n = 1^{e5}$) resulting from the Monte Carlo simulations precluded the use of standard statistical tests of significance when comparing outputs for two species (at both daily individual and annual population levels). Instead, we assessed unilateral binary relations calculating the proportion of values from one group superior to the other group. We considered a difference to be significant if this proportion, called p , was $\geq 95\%$ or $\leq 5\%$. To express results in a way comparable to classic statistical tests (i.e. significant difference when $p\text{-value} \leq 0.05$), we either reported p directly if it was $\leq 5\%$, or reported $(1 - p)$ when it was $\geq 95\%$, adjusting for the direction of the binary relation of interest. For example, if the result of a test looking at difference in iron released between species A and B was 0.99, we considered iron release by species A to be significantly greater than iron release by species B with $p = 0.01$.

In addition, levels of iron release by pack-ice seals were compared with that reported in the literature for other S0 megafauna taxa and species (large whales and penguins).

Sensitivity analysis

We conducted a sensitivity analysis to quantify how the sources of uncertainty in the model parameters affected the uncertainty of the final output, and identify which parameters were more important in influencing this uncertainty (Saltelli et al. 2008). We adopted a global approach, in which the effect of a factor on the output can be estimated when all other inputs are varying. It enables the identification of interactions, and does not require an additive or linear model (Cariboni et al. 2007). We opted for the Sobol method, a variance-based approach where the variance of the output can be decomposed into the contributions imputable to each input factor. We used R package “sensitivity” (version 1.27.0) with function “sobolSalt”, and computed first-order (with respect to each input factor individually) and total (inclusive of interactions between input factors) sensitivity indices for all parameters of the model.

Code to reproduce the full analysis in R is available on Github (<https://github.com/Lola-san/FeSthOpinn.git>).

Results

Statistics associated to all parameters of the model as a result of Monte-Carlo simulations (Table 1) and calculations from the bioenergetic model (equations 1-6, Table 2) are available in Online Resource 1.

Table 3 Means and 95% confidence intervals [in brackets] for metabolic requirements, prey consumption, iron ingestion and release parameters estimated from our bioenergetic model for the four Southern Ocean species of pack-ice seals

Species	Leopard seal	Crabeater seal	Weddell seal	Ross seal
Average daily metabolic rate (kJ.d⁻¹)	68 151 [43 135 - 95 014]	33 143 [20 962 - 49 213]	44 587 [27 344 - 66 535]	28 072 [17 853 - 41 449]
Daily food ration (kg.d⁻¹)	12 [6 - 20]	8 [4 - 14]	10 [5 - 18]	7 [4 - 12]
% of biomass consumed per day	3 [2 - 6]	4 [2 - 7]	3 [2 - 6]	4 [2 - 7]
Iron concentration in the diet x_{Fe} (mg.kg⁻¹ wet weight)	67 [41 - 93]	11 [7 - 16]	23 [14 - 32]	16 [10 - 23]
Daily individual iron consumption rate (mg.day⁻¹)	773 [349 - 1460]	87 [39 - 170]	226 [99 - 442]	112 [50 - 217]
Daily individual iron release rate (mg.day⁻¹)	618 [275 - 1180]	70 [31 - 137]	181 [78 - 357]	90 [39 - 176]
Population annual iron release (t.yr⁻¹)	9 [2 - 23]	151 [60 - 315]	44 [13 - 106]	3 [1 - 8]

The average daily metabolic rates of pack-ice seals ranged from 28 072 kJ.d⁻¹ (95% confidence interval - hereafter [CI 95%], i.e. [17 853 - 41 449]) for Ross seals (the smallest species) to 68 151 [43 135 - 95 014] kJ.d⁻¹ for leopard seals (the largest and most metabolically

active species) (Table 3). They require from 7 [4 - 12] kg of prey daily for Ross seals to 12 [6 - 20] kg for leopard seals, which represents 3 to 4% [2 - 7] of seals' individual body mass for all 4 species. The diet of a leopard seal is the most concentrated in iron (67 [41 - 93] mg.Fe.kg⁻¹ wet weight), followed by that of a Weddell seal (23 [14 - 32] mg.Fe.kg⁻¹ wet weight), a Ross seal (16 [10 - 23] mg.Fe.kg⁻¹ wet weight) and a crabeater seal (11 [7 - 16] mg.Fe.kg⁻¹ wet weight) (Table 3). This order remains for individual daily iron consumption and release rates, so that an individual leopard seal is estimated to consume and release ~ 9 times more iron per day than a crabeater seal ($p < 0.01$) (Fig. 1).

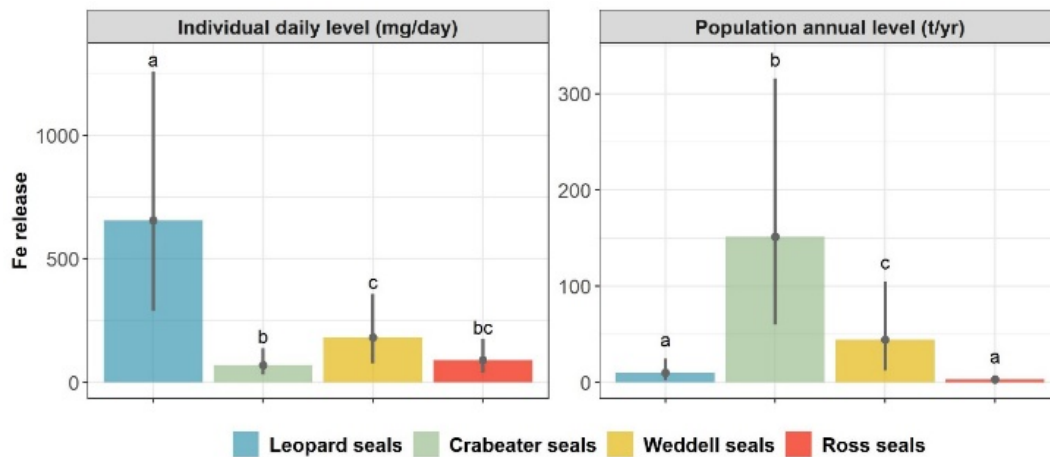


Fig. 1 Iron released in the faeces of Southern Ocean leopard, crabeater, Weddell and Ross seals. Individual, daily level (left panel, vertical axis in mg per day) and populational annual level (right panel, vertical axis in tonne per year), as estimated by means of a bioenergetic model. Central point represents mean estimates and lower and upper bar limit the 2.5 and 97.5 percentiles, respectively. Letters indicate the significance of the difference between species as assessed based on unilateral binary relations between estimates (see Methods): if two species are associated with different letters, the difference between the two estimates is significant ($p < 0.05$); if they share a common letter, it is not significant ($p > 0.05$)

Annual estimates at the population level show that crabeater seals are the main contributors to iron release (151 [60 - 315] t.Fe.yr⁻¹, significantly above the other three species with $p < 0.01$). They are followed by Weddell seals (44 [13 - 106] t.Fe.yr⁻¹, significantly above leopard and Ross seals with $p < 0.03$). The contribution of leopard seals (9 [2 - 23] t.Fe.yr⁻¹) is then not significantly higher than that of Ross seals (3 [1;8] t.Fe.yr⁻¹, $p = 0.09$) (Fig. 1, Table 3). Together, these four species release 208 [104 - 378] t.Fe.yr⁻¹ through their faeces (Fig. 2). This is equivalent to the current contribution of populations of SO humpback whales (221 [144 - 394] t.Fe.yr⁻¹) or the iron released in guano of Chinstrap, Adelie and Gentoo penguins populations in a year (169 t.Fe.yr⁻¹) (Fig. 2 and references therein, Online Resource 2). It is also

~ 4 times the contribution of sperm whales (50 t.Fe.yr^{-1}), and about 3 and 2 times less than the contribution of Antarctic minke whales ($630 [420 - 937] \text{ t.Fe.yr}^{-1}$) and Antarctic fin whales ($367 [193 - 590] \text{ t.Fe.yr}^{-1}$), respectively.

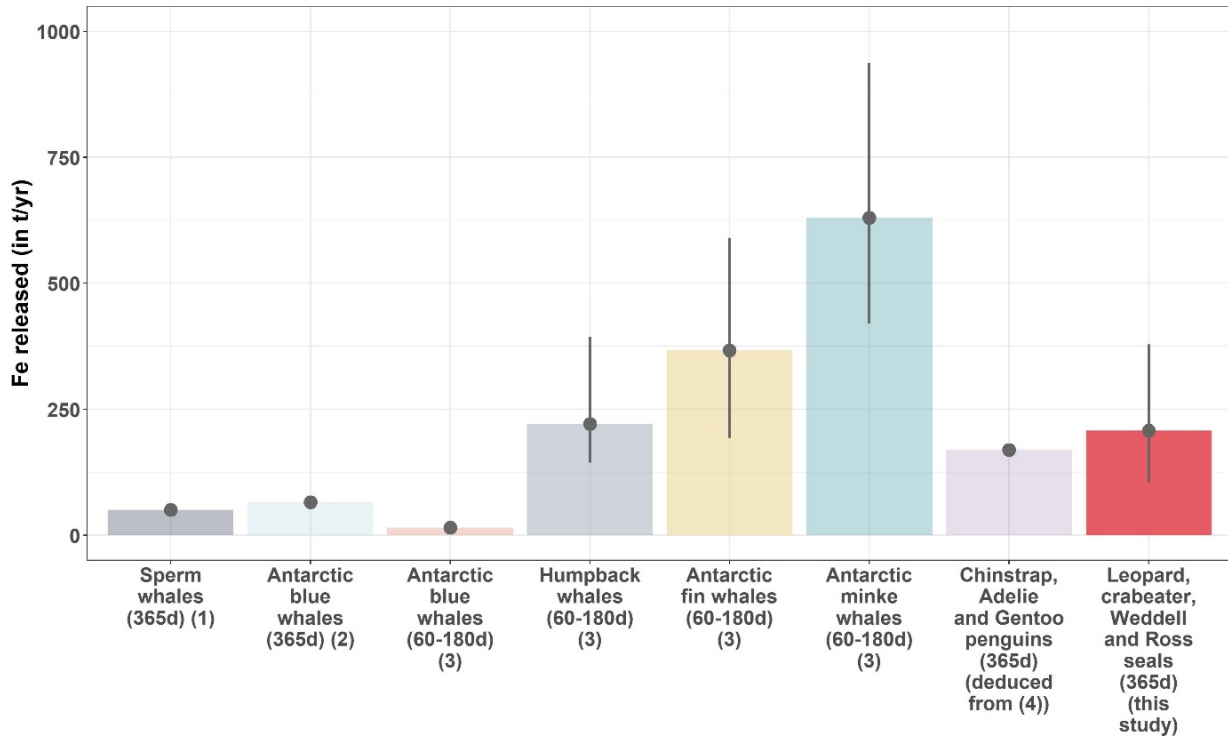


Fig.2 Iron released by different Southern Ocean species of megafauna. Data is from literature and present study:(1) Lavery et al. (2010), (2) Lavery et al. (2014), (3) Savoca et al. (2021), (4) Sparaventi et al. (2021). The number of days during which species were considered present in the Southern Ocean and thus for the estimates (in the literature and present study) are indicated in brackets. Estimates from (4), originally calculated for the reproduction period only, have been raised to annual estimates using a simple cross product. Central point represents mean estimates and lower and upper bar the 2.5 and 97.5 percentiles, respectively. Percentiles were not reported with estimates in (1), (2) and (4). Detailed numbers are provided in Online Resource 2

Sobol sensitivity indices show that population abundance A is the most influential model parameter, followed by the mean energy content of the diet E , the mean iron concentration of the diet x_{Fe} , the metabolic multiplier β and individual body mass BM (Fig. 3). In contrast, the assimilation efficiency AE and iron release rate r_{Fe} have very little influence on the model output.

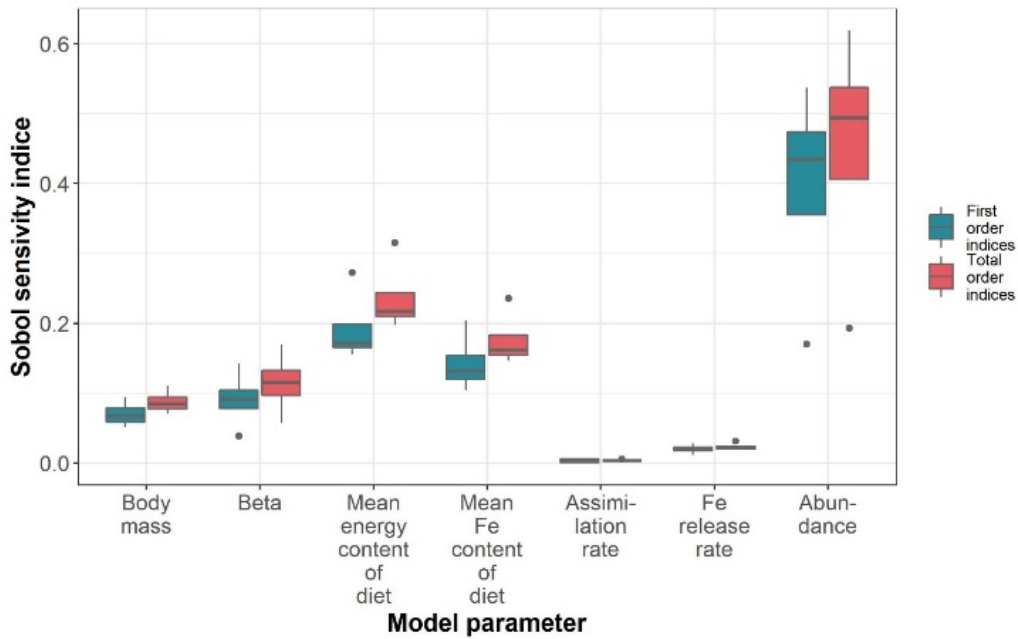


Fig. 3 Estimates of first-order and total order Sobol sensitivity indices of the bioenergetic model parameters. The seven parameters input used to estimate iron released by leopard, crabeater, Weddell and Ross seals in the Southern Ocean included seal body mass, species-specific metabolic multiplier beta, mean energy content of the diet, mean iron (Fe) content of the diet, assimilation efficiency or assimilation rate, iron release rate and population abundance. Boxplots display the median with solid black line in each box, lower and upper hinges correspond to the 25th and 75th percentile, respectively; upper and lower whiskers extend respectively from the hinges to the largest and lowest values no further than 1.5 times the inter-quartile range, and data beyond the end of whiskers are plotted as points

Discussion

Although ice seals play an important role in trophic networks of the SO, their role in recycling iron, and the cascading effects this may have on ecosystem structure and productivity, are still unknown. Using the best available data on population abundance, diets, metabolism and prey composition, we provided the first estimates of total iron released in faeces of pack-ice seals inhabiting the SO. Based on these quantitative results, we can assess the relative contribution of the four species to the biological cycling of this key limiting nutrient at individual and population levels, and within the broader community of SO air-breathing megafauna. Knowledge of the ecology of these pack-ice seals allows us to go further and discuss functional aspects of their contribution.

Uncertainties

As in any modelling exercise, our results carry uncertainties linked to the inherent variability of the system we are trying to model, and to biases in the model structure. While the

uncertainty associated with each parameter can be considered individually, they were combined in our model through the use of Monte-Carlo simulations. Most of the intrinsic variability and uncertainty was inferred. We may have under- or over-estimated them, but we leaned towards the conservative side.

The most influential parameter was population abundance estimate, as expected given the size of the populations and the large confidence intervals associated with each estimate. Global abundance estimates for highly mobile and marine predators are challenging to obtain, even more so given the spatial extent, remote location and climatic conditions of the SO. The data used here are from the more recent large-scale coordinated effort to estimate the abundance of these pack-ice seals throughout their range (Southwell et al. 2012). Even though it was in the early 2000s, it can be considered the best available data.

The mean energy content and iron concentration in the seals' diet also have a significant influence on our final model outputs. As mentioned earlier, seal diets vary individually, seasonally and spatially. In addition, prey energy content and iron concentrations also vary with life stage, season, location or body part (Kim et al. 2014; Ruck et al. 2014; Ratnarajah et al. 2016b). For example, we could not directly account for the belly-biting behaviours of leopard seals that tend to consume only muscle and viscera when preying on pinnipeds or penguins (D. Krause, personal comm.). Liver, part of the viscera, highly concentrates iron, but we only considered the muscle iron concentration as a conservative choice. As we applied a relatively high standard deviation to these parameters to account for all these interconnected sources of variability, they influence the output of our model the most after population abundance.

The individual body mass BM , the metabolic cost of activities multiplier β , the assimilation efficiency AE and iron release rate r_{Fe} carry little uncertainty compared to the other parameters. BM , β and AE are well known for pinnipeds (e.g. Hoelzel (2009); Trites and Spitz (2018)). Furthermore, some of our intermediary output parameters, such as daily prey intake,

including as a percent of body mass (Table 3), are within the range of those previously published for pinnipeds (e.g. Hoelzel (2009); Trites and Spitz (2018); Nilssen et al. (2019)). This provides confidence in our model outputs (Table 3 and Online Resource 1). r_{Fe} has in contrast never been measured on pinnipeds, but as mammals, adult seals (excluding pregnant and lactating females, see Shero et al. (2022)) are expected to defaecate any iron that they do not require to maintain their body homeostasis (Candela et al. 1984; Ratnarajah et al. 2014). Its small influence on the final output variability was expected, as it is close to one.

Finally, most of these uncertainties, except for the partial consumption of specific prey species, were also included in previously published models on air-breathing megafauna taxa (Otero et al. 2018; Ratnarajah et al. 2018), which justifies comparisons between their results and ours for contributions to the global SO system.

Quantitative contribution of pack-ice seals to total iron biological cycling in the SO

Daily individual iron release

Daily amounts of iron released per individual differ between species (Table 3), due to different iron contents in their diet (linked to iron levels in their prey and consumption rate of each prey type) as well as intake levels and released biomass (linked to species' body mass and metabolic requirements). As long-lived top predators, pinnipeds and penguins have higher iron content than lower trophic level prey (e.g. zooplankton). This explains the high mean iron concentration in the diet of leopard seals (including fish and krill but also 21 and 6% of pinnipeds and penguins, respectively). Weddell and Ross seals prey mainly on medium trophic levels (fish and cephalopods) compared to crabeater seals, which feed almost exclusively on krill. In addition, crabeater and Ross seals are the smallest species, and they likely have lower metabolic requirements. As a result, individual crabeater and Ross seals release seven to nine times less iron daily than leopard seals and two to three times less iron than Weddell seals.

Iron release occurs as patchy, transient defecation events, limited to small spatial and temporal scales, and the response of primary producers to this iron supply also begins at these scales. Total faecal iron will affect local primary producers differently depending on its quantity and chemical form, on biochemical conditions (e.g. temperature, light, availability of other nutrients), and on the specific needs of local primary producer communities (Allgeier et al. 2017). However, as a general approach, individual daily iron release rates can provide an indication of the magnitude of the impact of iron fertilisation on local primary productivity (and hence, the trophic web), assuming that the faeces of each species have similar biochemical properties in terms of the speciation of the iron released and the time it remains in surface waters. Thus, our results suggest that the magnitude of the potential impact of leopard seal defecation is greater than that of crabeater, Weddell and Ross seals, given similar biochemical conditions.

Moreover, these results imply that the role of pack-ice seals as iron recycling vectors may (i) vary between seasons and locations, following the variation in the diet of seals (e.g. Lake et al. (2003)) and the variation of iron concentrations in their prey (Kim et al. 2014; Ruck et al. 2014), (ii) vary if these predators switch prey, for example in response to changes in prey availability or changes in their environment (e.g. Wing et al. (2021)). Given the severe changes occurring in the SO (Gutt et al. 2015), this should be considered when assessing SO ecosystem functioning (Wing et al. 2021).

Annual population iron release

Although individual crabeater seals release the least amount of iron daily, they contribute the most to iron release within the pack-ice seal community at the population level (73%, Table 3) because they are by far the most numerous (Southwell et al. 2012) (Table 1). Individual Weddell seals release almost three times more iron than crabeater seals daily, but their population is the second largest (Southwell et al. 2012) (Table 1), so they contribute significantly to total pack-ice seal iron cycling (21%). Despite feeding on higher, iron-enriched

trophic levels, the lower populations of leopard and Ross seals are only small contributors to the global biological cycling of iron in the entire SO (4 and 1% respectively).

Contribution of pack-ice seals to biological iron cycling within the air-breathing SO megafauna community

This study identifies pack-ice seals as major contributors to the biological supply of iron to the SO euphotic zone (Fig. 2). In several aspects, the role of pack-ice seals in iron biological transfers to the SO euphotic zone relates to that of penguins, rather than that of whales. Like penguins (Sparaventi et al. 2021), pack-ice seals are long-lived, year-round residents of the SO with abundant and widely distributed populations; they mostly prey on low (krill) or medium trophic levels (fish and cephalopods). Pack-ice seals are specific in that they are dependent on sea ice for parts of their cycle (Shirihai 2008), which only applies to Adelie penguins. The likely release of large amounts of waste products directly onto the sea ice is an important factor to consider in terms of ecosystem functioning. Sea ice retains nutrients and primary producer biomass (phytoplankton and algae) sometimes in greater amounts than the underlying euphotic zone, and its annual advance and retreat plays a great role in the SO ecosystem (Massom and Stammerjohn 2010). In spring, biological activity along the ice edge is boosted as the melting ice releases iron and algae when light conditions are favourable, which stimulates overall productivity (Massom and Stammerjohn 2010; Lannuzel et al. 2016b). The dependence of pack-ice seals on sea ice also makes their spatial distribution relatively complementary to that of whales (Laws 1977; Hoelzel 2009). Obviously, the scale at which whales, seals or penguins individually release iron is as different as their respective body mass range. Yet, baleen whales are migratory species, most individuals spending only the summer season in the SO and targeting highly productive areas. In addition, while some whale populations have recovered significantly from industrial whaling (e.g. humpbacks (Pallin et al. 2018)), some others still struggle to recover (e.g. blue (Savoca et al. 2021)). In contrast, pack-ice seals, like penguins, have never been subject to any high-level human exploitation (Hofman 2017). It is therefore possible that populations of pack-ice seals (and penguins) have taken on a comparatively larger role in the fertilization of the SO system than they used to.

While we provide another piece to the puzzle of the contribution of SO air-breathing megafauna to iron biological cycling, it is important to note that two important pinniped

species are still missing: Antarctic fur seals *Arctocephalus gazella* and southern elephant seals *Mirounga leonina*, although they spend most of their annual cycle in SO waters. Like whales, their populations have been severely depleted due to exploitation of their blubber (elephant seals) and fur (Antarctic fur seals), with contrasting recovery successes between populations (Laws 1994; Hucke-Gaete et al. 2004). Unlike pack-ice seals, these species are tied to ice-free land to breed and moult (Shirihai 2008). They carry out nutrient transfers from sea to land, which significantly influence the structure of ecosystems around their colonies (Bokhorst et al. 2019). They may also forage in waters around ice-free land for extended periods. As these waters tend to be richer in iron due to land weathering compared to pelagic waters or waters surrounding sea ice, the importance of these seals in stimulating primary productivity is likely to be different than that of pack-ice seals. Yet, their contribution to the biological cycling of iron in the SO has never been quantified and should be investigated in the future.

Functional characteristics of the contribution of pack-ice seals to SO biological iron cycling

Spatial segregation and aggregation

Dispersal ranges of crabeater, Weddell, leopard and Ross seals greatly overlap around the Antarctic continent (Fig. 4), but these four species do not display the same habitat preferences (Fig. 5). Thus, they may deposit their waste in areas with different inherent characteristics in terms of iron supply and demand of the community of primary producers. Crabeater and Weddell seals generally haul out on sea-ice throughout the year, while Ross and leopard seals spend more time in pelagic, ice-free waters outside of the breeding and moulting seasons (Southwell et al. 2012). Crabeater seals primarily use pack-ice (Southwell et al. 2008; Bengtson et al. 2011) whereas Weddell seals are primarily bound to fast-ice and nearby pack-ice, relying on breathing holes to navigate between ice-floes (Shirihai 2008; Thomas and Terhune 2009; Southwell et al. 2012; Davis et al. 2013; Goetz et al. 2017). Whether iron is released on pack-ice or on fast-ice - and thus seals different spatial contributions - has different implications,

given the central role of sea-ice in retaining and releasing iron in SO waters (Lannuzel et al. 2016b; Genovese et al. 2023). Pack-ice, for instance, may grow and melt further offshore, releasing the iron it contains in more limited waters (Lannuzel et al. 2016a) than fast-ice melting in coastal, enriched waters. Ross seal is the most pelagic species, spending most of the year in open pelagic water and returning to pack-ice only for short periods of time to breed and moult (Thomas and Rogers 2009; Arcalis-Planas et al. 2015; Brault et al. 2019). As Ross seals forage in low productivity, open ocean food web where conditions are particularly limiting, the local impact of the iron they release could be more significant. Habitat preferences of leopard seals are still poorly known (Southwell et al. 2012), but overall, they seem to prefer marginal pack-ice areas with extended periods spent in pelagic waters outside of the breeding and moulting seasons (Bengtson et al. 2011; Southwell et al. 2012). They can migrate further north than other species (especially between 90°W and 90°E, Fig. 4) and are regular visitors to subantarctic islands and southern continents (Walker et al. 1998; Nordøy and Blix 2009; Rogers 2009; Krause et al. 2015; Staniland et al. 2018). They can display residency around islands for extended periods (Walker et al. 1998), and could thus contribute to nutrient transfers from sea to land.

Patterns of animal aggregation could also locally shape the iron supply rate, a key parameter controlling primary productivity (Howarth 1988; McInturf et al. 2019). Ross and leopard seals are mostly observed alone when hauled-out (Bengtson et al. 2011; Southwell et al. 2012), while Weddell seals are most likely to form groups of up to 20 individuals on fast-ice (Southwell et al. 2012). Crabeater seals can form large groups on pack-ice (Bengtson et al. 2011; Joiris and D’Hert 2016) but are mostly observed alone or in pairs (Gales et al. 2004; Southwell et al. 2012). More noteworthy, they can form large aggregations of up to 350

individuals when foraging (Gales et al. 2004; Gottfried 2014; Joiris and D’Hert 2016). These four seal species could therefore affect iron supply at different spatial and temporal scales.

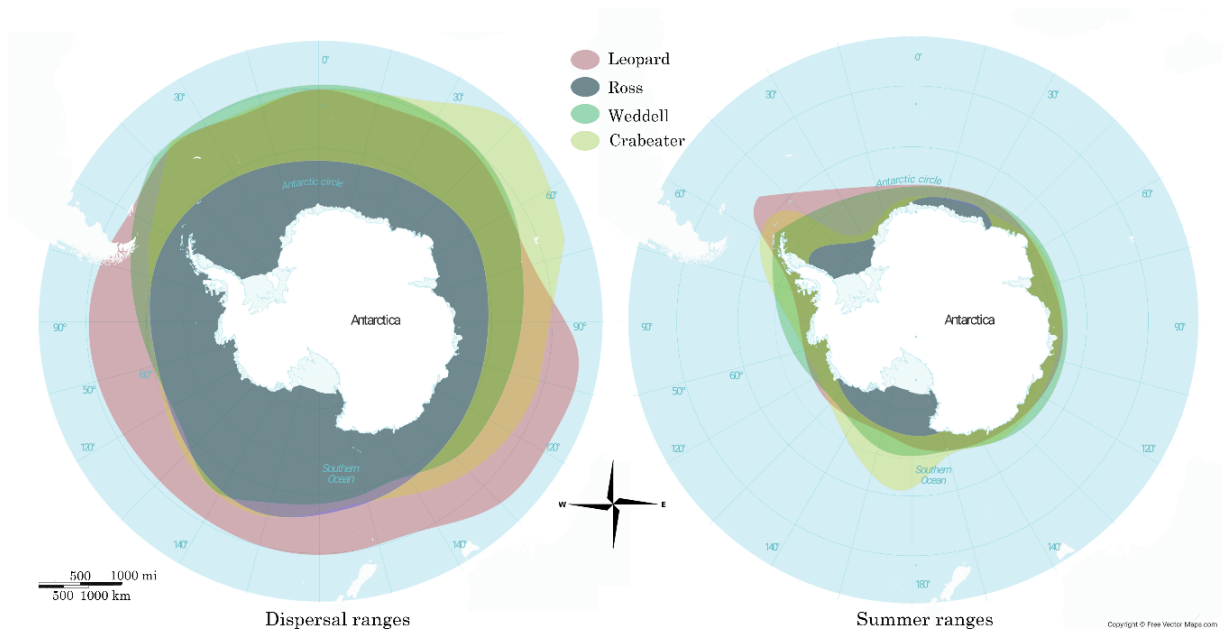


Fig. 4 Dispersal and summer ranges of leopard, Weddell, crabeater and Ross seals in the Southern Ocean (adapted from Shirihai (2008), original map by FreeVectorMaps.com)

In addition to these species-specific aggregation patterns, there may be some overlap between the four species, particularly in summer (Fig.4) in highly productive areas (e.g. Ross and Weddell seas). These areas are also targeted by other megafauna taxa, i.e. penguin colonies and aggregations of feeding whales (Herr et al. 2022). As all individuals take advantage of the increased productivity, they synchronously participate in maintaining iron levels in the euphotic zone when conditions are favourable for primary producers. Until now, studies have focused on the role of single species or group of species from the same taxa in iron biological cycling in the SO. However, the localized and sequential aggregation of communities of air-breathing predators likely have a synergistic impact. The rapid recycling of iron they mediate on these hot spots and during these key periods could extend seasonal productivity by maintaining higher levels of bioavailable iron when compared to the influence of external inputs (Boyd et al. 2017; McInturf et al. 2019). While challenging, studying such

complex biochemical transfers at community levels and at fine spatial and temporal scales would significantly further our understanding of SO ecosystems functioning.

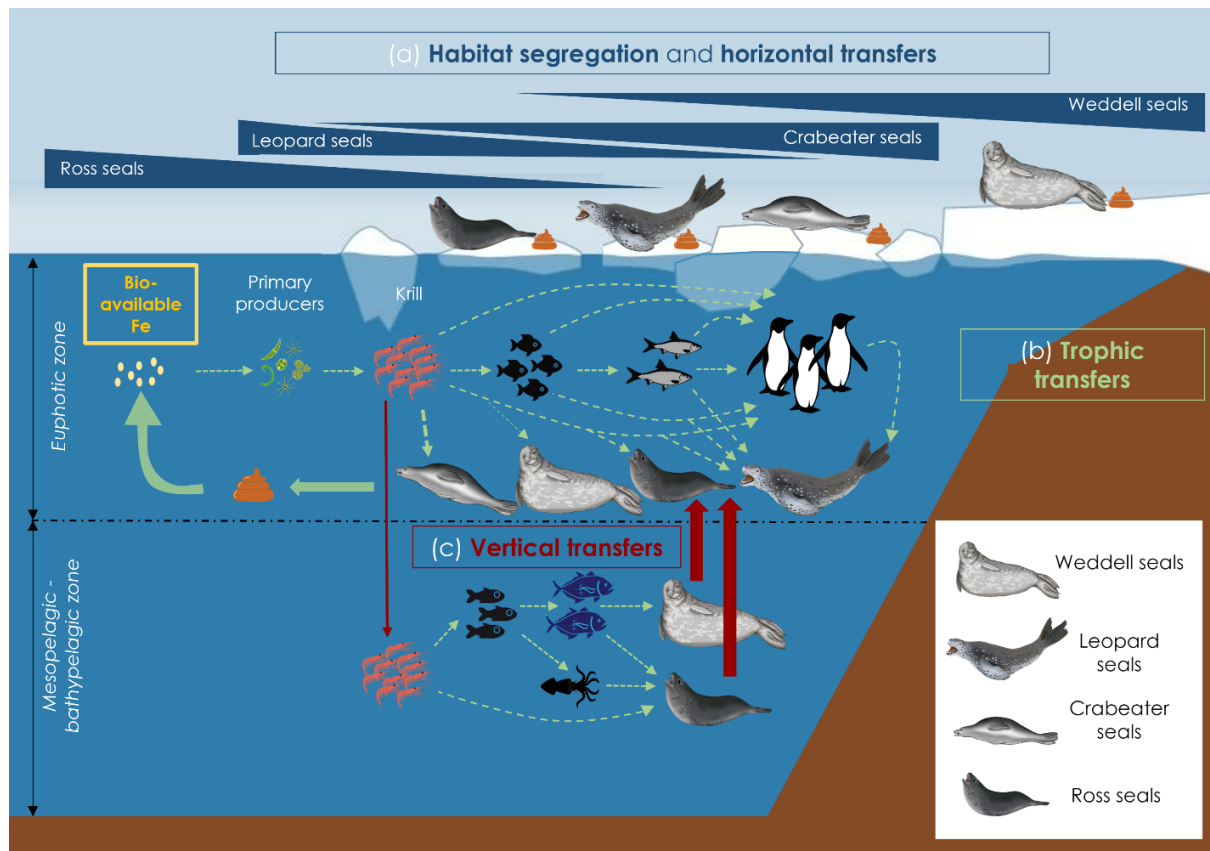


Fig. 5 Conceptual diagram showing functional traits of the contribution of leopard, crabeater, Weddell and Ross seals to iron (Fe) cycling in the Southern Ocean through **a** habitat segregation and horizontal transfers (blue triangles indicating relative time spent in habitats including fast-ice, pack ice and open pelagic waters for each species), **b** trophic transfers of iron operated through the consumption of prey at different trophic levels (green arrows) and **c** vertical transfers, operated through the consumption of prey in meso-benthopelagic zones and subsequent release of iron-rich waste back in the euphotic zone (red arrows)

Horizontal iron transfers

Pack-ice seals are highly mobile predators. They can travel several kilometres on a single dive (e.g. Weddell seals (Thomas and Terhune 2009; Davis et al. 2013)) and up to 11 500 km within 10 months (e.g. Ross seals (Arcalis-Planas et al. 2015)). Thus, they can transfer iron from where they forage to anywhere along their path after digestion, between habitats (fast-ice, pack-ice, open water) or within a single habitat (e.g. Weddell seals (Southwell et al. 2012)) (Fig. 4 and 5). As the nutrient dynamics associated to the relatively narrow and stationary fast-ice does not compare to that of the highly dynamic and constantly drifting pack-ice (Massom and Stammerjohn 2010), the consequences of iron release in either of these habitats are likely to

differ, and transfers between them can be of ecological importance. Defecation on sea-ice also makes iron return to surface waters entirely dependent on weather conditions and sea-ice melting. In the case of multi-year ice, it can be years.

Vertical iron transfers

To fully understand the role of megafauna in supporting primary production, the release of new and recycled iron in the euphotic zone need to be teased apart (Lavery et al. 2010; Martin et al. 2021). Recycled iron is initially assimilated by primary producers within the euphotic zone, transferred between trophic levels through grazing and predation, and returned in the euphotic zone to be available again to primary producers. Released iron is considered new when it originates from outside - or was transported out - of the euphotic zone, through trophic transfers and/or sedimentation. The four SO species of pack-ice seals feed on different prey (Fig. 5, Table 2). Consequently, they have different foraging strategies, and are likely to contribute differently to new versus recycled iron transfers in the water column. Leopard and crabeater seals are primarily shallow divers, foraging mostly between 10 to 50 m depths (Shirihai 2008; Nordøy and Blix 2009; Southwell et al. 2012). They mostly operate horizontal transfers of recycled iron. Weddell and Ross seals, while exploiting different habitats (fast-ice and open pelagic areas, respectively), forage in deeper waters, between 100 and 300 m (Southwell et al. 2012; Davis et al. 2013). Both prey on demersal to bathypelagic species of myctophids, to some extent (Casaux et al. 1997, 2006; Southwell et al. 2012). Ross seals prey largely on squid (Southwell et al. 2012) while Weddell seals are the only species known to forage in benthic habitats on benthopelagic fish (e.g. channichthyids) (Casaux et al. 1997, 2006). Therefore, they operate vertical transfers of iron, benefiting organisms in the euphotic zone. Daily migration of prey between shallow and deep waters or prey feeding in benthic habitats may also indirectly contribute to these vertical transfers (e.g. Schmidt et al. (2011))) even when prey are captured in the euphotic zone, which adds another layer of complexity to these processes.

Trophic iron transfers and turnover rate

As previously mentioned, the trophic level of pack ice seals affects their individual daily iron release rates, but it also affects the turnover rate of the iron released. Nutrient turnover is the time between the initial uptake of a nutrient into living biomass and its re-release into the environment in a bioavailable form. The turnover rate of iron released by small, low trophic levels (e.g. microbial community, phytoplankton grazers or secondary consumers) is thus faster than the turnover rate of iron released by animals feeding on higher trophic levels (e.g. top predators). However, a rapid nutrient turnover can support a greater primary production than a slower one, even at low concentrations (Benitez-Nelson and Buesseler 1999), so that turnover rate is another functional feature to consider in iron biological cycling. As predators, pack-ice seals (and other megafauna species) occupy a medium-to-high trophic level, which implies a lower contribution to iron biological cycling compared to small organisms (microzooplankton and heterotrophic microbial community) (Maldonado et al. 2016). Yet, as megafauna species do not all feed at the same trophic level, the turnover rate of the iron they release is another functional trait that differentiates their relative contribution.

The four species of pack-ice seals all consume krill, although in different proportions (Table 2, Fig. 5). With its large biomass, low trophic level, circumpolar distribution and seasonal persistence, krill plays a key role in the biochemical iron cycling (Nicol et al. 2010; Ratnarajah et al. 2014, 2018; Ratnarajah and Bowie 2016). The level of krill consumption can thus be an indicator of the impact of the seal species on iron turnover. Weddell and leopard seals have the highest trophic positions (Zhao et al. 2004; Brault et al. 2019), although leopard seals feed on both large and long-lived predators and on small fish and krill. On average, the iron released in these two seal species faeces has thus a slower turnover rate than that of crabeater seals that feed primarily on krill (Zhao et al. 2004; Brault et al. 2019). In this respect, the role of crabeater seals in biotically-mediated iron transfers relates to that of baleen whales and krill-feeding penguin species. Thus, crabeater seals are not only the main contributors to total iron release among the pack-ice seal community, they also contribute to a more efficient iron

cycling. This further highlights the significance of iron transfers operated by pack-ice seals in the functioning of SO ecosystems, and the central role of krill in the SO biochemical cycling of iron.

Limits and future directions

The complete elucidation and quantification of the role of marine top predators in supplying iron to the euphotic zone is a lengthy task given the numerous processes and parameters involved. Estimating how much total iron these predators release is an essential first step. Trace element analysis of scats from the four pack-ice seal species, collected from different locations and seasons, could help to validate our estimates. However, the amount of total iron estimated here to be released by pack-ice seals should not be assumed to be fully recycled, i.e. taken up by phytoplankton to be re-integrated into the trophic network. The fate of iron released in waste products, in terms of how much is retained in the euphotic zone and how much sinks, and the subsequent contribution of predators to primary productivity, likely depends on its chemical speciation. Iron in the faeces of pack-ice seals could be dissolved (labile or colloidal) or particulate, eventually bound to organic or inorganic ligands, and is probably in several of these forms (e.g. Ratnarajah et al. (2017)). Yet, estimating the relative composition of the iron released in faeces by means of a bioenergetic model is today too speculative and is beyond the scope of this study. Further investigations into the chemical speciation of iron in these faeces would help to quantify its relative bioavailability to primary producers or heterotrophic bacteria, and thus to quantify the true contribution of these seals to overall productivity of the system.

Moreover, we limited our calculation to the release of iron for its pivotal role as a primary limiting nutrient in the SO, and comparison between taxa can only be conducted on the basis of iron release. However, SO megafauna waste products contain a wide range of micronutrients associated with biochemical and physiological functions shared by most forms of life (Ratnarajah et al. 2014; Wing et al. 2014, 2017, 2021; Shatova et al. 2016; Sparaventi et al. 2021). The alleviation of a primary nutrient limitation or co-limitation can trigger new limiting effects by other nutrients (Koch and Trimborn 2019). Micronutrients released along with iron in seal, penguin and whale faeces could be of interest for primary producers, as

suggested by the synergetic effect of guano addition compared to simple iron fertilization observed in lab experiments (Shatova et al. 2017). Hence, the role of other micronutrients in productivity and community structure should not be overlooked (Coale 1991; Hassler et al. 2012b). The contribution of marine predators to nutrient transfers in SO ecosystems and trophic webs does not solely apply to iron, even though formally identifying and quantifying the impact of multiple nutrients leaching from animal products remains a complex task (Subalusky and Post 2019). Extending our knowledge of the complex SO ecosystem functioning and of the role of megafauna in fertilizing their own habitat would thus require to extend the present study to include synergistic impacts of several key nutrients.

It is also worth noting that, although not relevant to the study of processes regulating primary productivity, the proportion of nutrients being transferred towards deep waters may be important to the functioning of benthic ecosystems.

Conclusions

Our results provide quantitative and functional arguments to extend the role of pack-ice seals in ecosystem functioning from simple predators to significant actors in the biochemical cycling of iron, placing them alongside other megafauna taxa such as whales and penguins. Leopard, crabeater, Weddell and Ross seals all make different quantitative contributions in terms of iron released at individual and population levels. In addition to their different quantitative contributions, differences in the functional traits of the four species, such as habitat use, social and foraging behaviour, suggest that each species may contribute to maintaining contrasting biochemical conditions throughout the SO euphotic zone, with possible impacts in sustaining biodiversity in the ecosystems (Marzetz et al. 2017). These behavioural traits also distinguish these predators as active iron vectors compared to physical, abiotic and passive processes of iron supply (McInturf et al. 2019; Subalusky and Post 2019), and are therefore important functional characteristics of their role in the biological cycling of iron in the SO.

Supplementary Information

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Author contributions

LG, TJDD and JS designed the study; LG performed the data analysis with contributions of JS and TJDD on parameter settings; LG, JS and TJDD wrote the manuscript.

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Data and code availability

No original data were used nor generated for this study which mobilised data from the literature for the setting of parameters in our bioenergetic model. References are provided in the manuscript (Methods and Table 1 and 2). Statistics of estimates used to generate Figure 1 are provided in Table 1 and ESM 1, with additional information on estimates for other input or output parameters of the model in the latter. Statistics for Sobol sensitivity index reported

on Figure 3 are provided in ESM 1. Figure 4 was made based on Shirihai (2008), with the base map originating from <https://freevectormaps.com>. Figure 5 mobilised data from the literature (references in the Discussion) and was made by the authors. Data and code to generate results presented in the present study are available in the public Github repository <https://github.com/Lola-san/FeSthOpinn.git>.

Declarations

Competing interests The authors disclose no conflict of interest.

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