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Lola Gilbert

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PhD Thesis

**BROWN NUANCES IN THE BIG BLUE: EXPLORING FACETS
OF MARINE MAMMALS' ROLE IN NUTRIENT CYCLING**

Lola Gilbert



Under the supervision of Dr Jérôme Spitz and Dr Tiphaine Jeanniard-du-Dot

La Rochelle Université 2020-2023



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**Brown nuances in the big blue: exploring facets of marine
mammals' role in nutrient cycling**

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Peer-reviewed publications

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Gilbert, L., Spitz, J., and Jeanniard-du-Dot, T. (2023). Pack-ice seals contribute to biological transfers of iron in the Southern Ocean. *Polar Biology*, (0123456789). DOI:[10.1038/s41467-023-41532-y](https://doi.org/10.1038/s41467-023-41532-y)

Chouvelon, T., **Gilbert, L.**, Caurant, F., Méndez-Fernandez, P., Bustamante, P., Brault-Favrou, M., and Spitz, J. (2022). Nutritional grouping of marine forage species reveals contrasted exposure of high trophic levels to essential micro-nutrients. *Oikos*, 2022(7), e08844. DOI:[10.1111/oik.08844](https://doi.org/10.1111/oik.08844)

Gilbert, L., Jeanniard-du-Dot, Spitz, J. *et al.* Differential concentrations of essential nutrients in forage fish prey and predator's feces and implications for nutrient cycling. In prep.

Gilbert, L., Spitz, J., and Jeanniard-du-Dot, T. *et al.* Essential nutrient release by two colonies of Antarctic fur seals (*Arctocephalus gazella*) on and around the Kerguelen Islands. In prep.

Conferences

Oral presentations

Gilbert, L., Jeanniard-du-Dot T., and Spitz, J., Cetaceans release nutrients in the photic zone: large-scale estimates from contrasted ecosystems highlight the relative contribution of different ecological groups. 24th Biennial Conference on the Biology of Marine Mammals (Society for Marine Mammalogy) 2022, Palm Beach, Florida, USA.

Gilbert, L., Spitz, J., and Jeanniard-du-Dot T., Ecosystem services from small cetaceans' populations: the contribution of small cetaceans to nutrient flows in European coastal

waters. Smart urban coastal sustainability days (EU-CONEXUS) 2021, La Rochelle, France. (*virtual attendance*)

Poster presentations

Gilbert, L., Spitz, J., Jeanniard-du-Dot T., Bousquet, N., and Authier, M. Dealing with several sources of uncertainty in modelling of community level processes. International statistical ecology conference (ISEC) 2022, Cape Town, South Africa. (*virtual attendance*, but in person attendance to the "French hub" organised by the [GRD-Ecostat](#))

Workshops

Green whale science & research symposium - Whales and Dolphins Conservation (WDC)

Participation (virtual) to two symposium (2021, 2022).

Utilising the ECS 'Hivemind' to Expand Knowledge of Small Cetacean Ecosystem Functioning - 34th European Cetacean Society (ECS) Conference 2023, O'Grove, Galicia, Spain

Gilbert, L., Jeanniard-du-Dot T., Spitz, J. Exploring the contribution of cetaceans to the cycling of essential nutrients worldwide: highlighting the role of small delphinids. Presentation and participation as invited participant, *virtual attendance*.

International Whaling Commission (IWC) - Convention on Migratory Species (CMS) 2nd workshop on cetaceans and ecosystem functioning 2023, Bonn, Germany

Gilbert, L., Spitz, J., Jeanniard-du-Dot T., . Composition of cetacean communities world-wide shapes their contribution to ocean nutrient cycling. Presentation and participation as invited participant.

Teaching experience

Practical courses - Animal biology

BSc (2nd year), Animal dissection (frog) and microscope observation. 2020-2021 (24-h), 2021-2022 (18-h).

Practical courses - Plant biology and physiology

BSc (1st year), microscope observation and microscopic slide preparation. 2020-2021 (15-h), 2021-2022 (15-h).

BSc (2nd year), seed reserve physiology and scientific reasoning to follow seed germination. 2020-2021 (24-h), 2021-2022 (18-h).

Courses followed

General courses

Professional and Scientific Communication and Networking in Multidisciplinary Environment. EU-Conexus PhD Summer School, Zadar, Croatia, 2021.

Research Integrity in scientific professions. University of Bordeaux, 2022 (*virtual attendance*).

Second year doctoral student symposium. La Rochelle Université, 2022 (Best Poster Price).

Speciality courses

Good practices for a reproducible research in numerical ecology. Cesar-FRB/GDR Ecostat, Montpellier, France, 2021.

Introductory distance sampling workshop. University of St Andrews, Scotland, 2022 (*virtual attendance*).

Foreword

This PhD thesis contains independent article manuscripts as its main chapters. This format allows easier writing of articles ready for publication, but implies redundancy in introduction and discussion of some of the chapters, which can sometimes also feel disconnected. However, we have taken particular care in the introduction to present the different chapters in detail, explaining their links and our general approach. We hope that this will make the document easier to read as a whole.

The thesis includes five chapters. The first two have been published in peer-reviewed scientific journals at the time of writing. The third will be submitted for publication in the weeks following the manuscript deposit. The fourth may require additional analytical material, but should be submitted for publication in 2024. The fifth chapter was written on a different format. It presents a study that was conceived and started during this PhD thesis, but does not include results.

Bonne lecture!

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Acronyms

APIS Antarctic Pack-Ice Seal. 54

HC hierarchical clustering. 81, 82, 91, 92, 94, 97, 102, 118

HNLC High Nutrient Low Chlorophyll. 38, 48, 112, 115, 154

HPI hard part index. 80, 81, 91

MWW Mann-Whitney-Wilcoxon. 81–83, 89, 90, 92, 95–97, 118, 125

PCA principal component analysis. 81, 82, 94, 102

SCAR Scientific Committee on Antarctic Research. 54

SO Southern Ocean. 47–51, 54, 57–59, 62–66, 68–71, 73, 74, 100, 101, 110, 115, 154

SST sea surface temperature. 26, 29

General introduction

0.1 Marine mammals and their ecosystems

0.1.1 Marine mammals: top predators in the world's big blue

Marine mammals are found in every oceans, from the poles to the equator. With more than 130 species, they include cetaceans, from the smallest porpoise, the vaquita (*Phocoena sinus*), to the largest animal on earth, the blue whale (*Balaenoptera musculus*), the amphibious pinnipeds (*e.g.* seals, fur seals), odobenids (walruses *Odobenus rosmarus*), sea otters (*Enhydra lutris*), sirenians (dugongs and manatees) and the polar bear (*Ursus maritimus*) (Jefferson et al. 2008, Wursig and Perrin 2009). Except for a few species living exclusively in freshwater, all of them depend to varying degrees on the marine environment (Jefferson et al. 2008, Wursig and Perrin 2009) and all belong to the marine megafauna (Estes et al. 2016, Tavares et al. 2019). Marine mammals as a group feed on all trophic levels, from plants (sirenians), to zooplankton (*e.g.* blue whales), benthic invertebrates (*e.g.* walruses, sea otters), small to large fish or cephalopods (*e.g.* pinnipeds, most toothed cetaceans), or other mammals (*e.g.* some populations of orcas *Orcinus orca*, polar bears) (Jefferson et al. 2008, Trites and Spitz 2018a, Wursig and Perrin 2009).

In the current era of the Earth's sixth mass extinction, megafauna species are at risk from habitat loss and fragmentation, direct harvesting and human conflicts (Enquist et al. 2020, Estes et al. 2011 and references therein), including marine mammals, even though most of them benefit from protected status. Of the species mentioned above, the vaquita is on the brink of extinction due to entanglement in fishing gear (Jaramillo-Legorreta et al. 2019, Taylor et al. 2017), blue whales are struggling to recover from industrial whaling (Savoca et al. 2021), and the polar bear is facing drastic changes in its habitats due to global warming (Hamilton and Derocher 2019, Prop et al. 2015, Regehr et al. 2010). The need to protect these charismatic animals, however, goes beyond the patrimonial and emotional aspects.

Strong theoretical and empirical evidences suggest that they have a structuring effect on ecosystems and that their loss could alter ecosystem functioning (Baum and Worm 2009, Bowen 1997, Estes et al. 2016, Heithaus et al. 2008). While herbivorous sirenians have been shown to shape the seagrass meadows on which they graze (Preen 1995), for

most other species this ecological importance is largely related to their prey consumption (Bowen 1997, Haro et al. 2020, Heithaus et al. 2008, Rupil et al. 2022). Their ecological effects are referred to as top-down processes because changes in their populations affect their prey populations, which in turn can cascade down the food web to herbivorous species and primary producers (Baum and Worm 2009, Hairston et al. 1960, Heithaus et al. 2008). The large body mass, high abundance and high metabolic rates of marine mammals make them particularly prone to triggering such trophic cascades (Borer et al. 2005, Doughty et al. 2016, Estes et al. 2016). The impact of consumption on their prey population can be direct (*i.e.* influence on prey size, population structure and/or abundance) or indirect (*i.e.* influence of prey behaviour in response to the predation risk) (Heithaus et al. 2008, Kiszka et al. 2015). For example, gray whales (*Eschrichtius robustus*) in the Bering Sea are determinant to the population structure, efficiency and abundance of amphipods (Berge et al. 2012, Coyle et al. 2007), which are also preyed on by other trophic levels (Berge et al. 2012). Seals in the Baltic Sea have a strong sequential influence on populations of both large (cod) and small (herring and sprat) fish stocks (Österblom et al. 2007). In the Southern Ocean, orcas and leopard seals (*Hydrurga leptonyx*) shape the habitat use of ice-obligate penguins, which avoid entering the water at night to lower predation risks (Ainley and Ballard 2012).

One of the well-known example of a marine mammal-related trophic cascade is the one generated by sea otters on the Pacific coast of Alaska (Estes and Palmisano 1974, Reisewitz et al. 2006, Springer et al. 2003). Sea otters feed in part on sea urchins on rocky seabeds (Estes and Palmisano 1974). Sea urchins, on the other hand, are grazers of kelp, a macro-algae that can grow to tens of metres in length, forming underwater forests which constitute an important habitat for other marine species (*e.g.* crustaceans, fish) (Estes et al. 1989). Where sea otters are present, they tend to prey on the larger sea urchins, leaving fewer and smaller urchins in their environment and allowing kelp forests to form and thrive. However, without sea otters, urchin populations can reach high numbers and overgraze the kelp to the point of local eradication, affecting populations of fish and their predators (*e.g.* seagulls or eagles) (Estes et al. 2016, Reisewitz et al. 2006). While this structuring effect of sea otter presence was first demonstrated following the over-exploitation of sea otters for their fur (Estes and Palmisano 1974), more recent changes following their recovery have involved other marine mammal species and further demonstrated it (Springer et al. 2003). Some populations of killer whales in these regions feed on marine mammals. As populations of large whales were reduced by whaling,

they shifted their diets to include higher proportions of sea otters and Steller sea lions (*Eumetopias jubatus*). This led to a severe decline in their populations, with consequences for habitat structure and coastal heterogeneity, particularly the presence of kelp forests (Springer et al. 2003).

Such top-to-bottom trophic cascades from marine mammals are rare, because of their complexity and because they occur at spatio-temporal scales that preclude experimentation in most cases, especially in the oceans. Most are still controversial (e.g. DeMaster et al. 2006) because, at these scales, multiple inherent factors may be involved in the observed ecosystem changes. However, together with the empirical and theoretical evidences on the effects of predators on terrestrial ecosystems (more amenable to experimentation), effects of marine top predators such as marine mammals on the functioning of their ecosystems is widely accepted (Heithaus et al. 2008).

The ecological effect of prey removal by marine mammals as top predators has long been studied, although other facets of their role in the ecosystems were also identified (see examples below) (Bowen 1997, Katona and Whitehead 1988). This focus has helped establishing it as a functionally important, if not unique, role of marine mammals in ecosystems in the minds of the general public, including conservation policy makers or people who may interact with them in their daily activities, such as fishermen. And yet, predation is not limited to the removal of prey from their environment. Marine mammals do more than just eat. Like most animals on the planet, they eat, poop and pee.

0.1.2 Marine mammals: nutrient recyclers?

While the natural mechanism of defecation and urination may seem inconsequential, it has recently been highlighted as an important facet of the role of marine mammals in ecosystem functioning, starting with the large whales of the Southern Ocean (Lavery et al. 2010, Nicol et al. 2010). Large whale populations in the Southern Ocean (blue whales, fin whales *Balaenoptera physalus* and sperm whales *Physeter macrocephalus*) were heavily exploited following the rapid development of industrial whaling in the early 20th century (Hofman 2017). Baleen whales in this region feed almost exclusively on krill (Nicol and de la Mare 1993), a small shrimp-like crustacean that plays a central role in the energy transfers of the Southern Ocean relatively simple trophic web (Mori and Butterworth 2006, Nicol and de la Mare 1993). Whale populations were so drastically reduced that it was hypothesised that the elimination of whale predation on krill would result in a surplus of krill, estimated to be between 150 and 420 million tons (Laws 1977, Savoca et al. 2021).

This increase in krill biomass would in turn have had a positive effect on populations of smaller krill predators such as minke whales (*Balaenoptera acutorostrata*), penguins or Antarctic fur seals (*Arctocephalus gazella*) (Laws 1977). The growing krill fisheries would also have benefited from this newly available krill biomass (Nicol and de la Mare 1993). This krill surplus hypothesis illustrates the common belief that predators influence ecosystem function primarily through their prey consumption. However, this hypothesis has never been universally accepted (Emslie et al. 2013, Ruegg et al. 2010, Trathan et al. 2012). While some populations of penguins and Antarctic fur seals increased, others did not (Boveng et al. 1998, Dunn et al. 2016, Hoffman et al. 2022, Hucke-Gaete et al. 2004, Ruegg et al. 2010, Trivelpiece et al. 2011). In addition, krill biomass did not increase as much as expected and in some regions it even decreased significantly (Atkinson et al. 2004, Smetacek 2008).

Several hypotheses have been formulated to explain this "krill paradox" (Smetacek 2008). It could be related to a decrease in primary productivity caused by changes in climate conditions affecting sea ice (Atkinson et al. 2004, Kawaguchi and Nicol 2009, Surma et al. 2014, Trathan et al. 2012, Trivelpiece et al. 2011), which in turn prevented krill from thriving (bottom-up process). It could also be due to an initial increase in krill biomass, which led to an increase in krill grazing pressure on phytoplankton and a subsequent decrease in primary production (top-down process) (Smetacek 2008). Alternatively, krill mesopredator populations (minke whale, penguins, fur seals) may have absorbed the krill surplus with their growing populations (Smetacek 2008).

Smetacek (2008) proposed an other hypothesis based on krill consumption of large whales, their large production of feces, and iron. Iron, an essential nutrient for most living organisms, is involved in the photosynthetic reaction used by primary producers, including phytoplankton in the oceans. In the Southern Ocean, it is in such low concentrations that it is the primary limiting factor for phytoplankton growth during the productive seasons (Boyd and Law 2001, Boyd et al. 2000). Any addition of iron to the surface waters can therefore trigger a local burst of phytoplankton, which in turn can stimulate the entire food web. Smetacek (2008) suggested that large whales may have stimulated the trophic web on which they depend by releasing large quantities of iron-rich feces near the surface as a result of their large consumption of krill (Fig. 0.1), and that the severe depletion of large whale stocks in the Southern Ocean may have consequently reduced this iron recycling pathway, with consequences for the overall productivity of the ecosystem (Smetacek 2008).

By this time, the Southern Ocean ecosystem had undergone such intense and sequential changes over a large spatio-temporal window that it is difficult to confidently confirm or refute any of the hypotheses put forward to explain the observed krill paradox. Nevertheless, several studies tested Smetacek's whale iron fertilisation hypothesis to assess its plausibility. Southern whale feces were found to be up to ten million times more concentrated in iron than typical Antarctic surface waters (Nicol et al.



Figure 0.1: Blue whale *Balaenoptera musculus* defecating near the surface. Photo credit: Ian Wiese

2010, Ratnarajah et al. 2014), and Southern Ocean phytoplankton species incubated with whale feces showed a positive response (Smith et al. 2013). In addition, the ratio of iron to carbon in baleen whale muscle compared to feces suggests that whales are indeed actively defecating iron (Ratnarajah et al. 2014). While these studies demonstrated the potential for whale feces to be an effective fertiliser for Southern Ocean surface waters, Surma et al. (2014) and Willis (2014) demonstrated through ecosystem modelling that the large-scale ecological relevance of iron fertilisation by whales is a plausible hypothesis to explain the krill paradox. Lavery et al. (2014) also showed that Antarctic blue whales stimulate primary production using a fishery surplus-yield model that incorporates iron defecation.

This process may not be limited to baleen whales feeding on krill. Post-whaling sperm whales, mostly feeding on deep-sea squids, release 50 tons of iron per year into the surface waters of the Southern Ocean (Lavery et al. 2010). Feces of Southern right whales (*Eubalaena australis*), New Zealand fur seals (*Arctocephalus forsteri*) and Hooker's sea lions (*Phocarctos hookeri*) from sub-Antarctic islands are also highly concentrated in a range of essential trace nutrients (*i.e.* nutrients with known biological functions and needed only in low concentrations), including iron (Wing et al. 2014, 2017). Finally, this fertilisation process likely also involve urine, which also contains nutrients. For example, urine is the main excretory pathway for metabolic nitrogen, a major nutrient component of key biological molecules (*e.g.* proteins, DNA) and therefore required in larger quantities than trace nutrients by all living organisms. Marine mammal urine can hardly be sampled directly, but nutrient release from both feces and urine can be modeled. In the Gulf of Maine (Northwest Atlantic), Roman and McCarthy (2010) estimated that whales and

seals may release as much nitrogen as the rivers in the same area using a bioenergetic framework. In addition, the waters in the fecal plumes left after whale defecation are significantly enriched in nitrogen and phosphorus compared to surrounding waters (Roman and McCarthy 2010, Roman et al. 2016), and incubation experiments showed that (i) dissolved nitrogen and phosphorus leach from fecal pellets over several hours, and (ii) dissolved nitrogen from feces increase productivity (Roman et al. 2016).

Such nutrient recycling mediated by defecation and urination had previously been identified as a possible ecologically relevant facet of the role of cetaceans (Katona and Whitehead 1988). They calculated that sperm whales around the Galapagos Islands could provide about 8% of the nitrogen used by primary production in the area by feeding at depth and defecating at the surface. And yet this facet of marine mammals' role in ecosystem functioning was unexplored until it was brought to the forefront in the case of large whales in the Southern Ocean, with subsequent studies suggesting that it may be ecologically relevant.

0.2 Nutrient cycling, marine mammals and their ecosystems

0.2.1 Nutrient cycling, an essential component of ecosystem functioning

The fact that all living organisms require a wide range of essential nutrients (Lavelle et al. 2005) - the smallest building blocks of organic matter - may make their recycling an obvious determinant of ecosystem functioning. Historically and on many occasions, however, humans were unable to predict and anticipate the consequences of changes in natural nutrient cycling processes, and have only recognised their importance in ecosystem dynamics after they have been significantly altered, usually to their own detriment. The exploitation and alteration of the Southern Ocean ecosystem is one such example among many, from the global issue of degraded soils due to intensive agriculture combined with inappropriate nutrient fertilisation (Parr and Hornick 1992), to the green tides caused by the vast quantities of manure resulting from intensive livestock production (Charlier et al. 2008). The disturbance of wild habitats and wildlife assemblages has also highlighted their important contribution to nutrient cycling and ecosystem functioning. For example, the severe reductions in large mammal populations have altered soil quality, which is

critical for plant growth and thus the terrestrial food web, in open grasslands and forests, and for herbivores as well as predators (Berzaghi et al. 2019, Monk and Schmitz 2022, Schmitz et al. 2010, Wang et al. 2018, Wardle and Bardgett 2004). The most pervasive, global and irreversible man-made disruption of a natural nutrient cycle is probably that of carbon, which, together with the biodiversity crisis, is now the greatest threat to the prosperity of human societies on Earth. All these examples highlight the need to improve our understanding of the importance of nutrient cycling in ecosystem functioning. The ecological relevance of nutrient cycling mediated by threatened wildlife should not be dismissed.

Nutrient cycling processes in oceanic environments are challenging to study because of their inherently fluid nature in three dimensions and their scale of variation. This is true both horizontally (*e.g.* currents running across entire ocean basins) and vertically, as reaching the ocean floor is a serious technological challenge. Nutrients can enter the oceans from the atmosphere, winds, rain and rivers (Bakun 1997, Fasham 1984). They are transported by currents, and those that have sunk at depth can be returned to the upper layers by vertical mixing processes such as upwellings (*i.e.* wind-driven movements of dense and nutrient-rich deep water towards the surface ocean, sometimes in the presence of a topographic barrier) (Bakun 1997). However, biological recycling and transfer of nutrients is also important.

At the scale of the planet, the oceans are known to significantly contribute to atmospheric dioxygen production and carbon fixation. The oceans are known to largely contribute to global atmospheric dioxygen production and carbon fixation. This is modulated by the biological activity of unicellular primary producers, the phytoplankton, through photosynthesis (Falkowski 1997). These primary producers are at the base of the marine light-based trophic web, so any change in their production will affect all trophic levels up to top predators. As organic matter is transferred along the light-based trophic web, a part is also transferred to deeper waters in the form of excreta, dead cells, fecal pellets or carcasses (Fasham 1984, Turner 2015). The activity and abundance of primary producers is therefore also determinant for food webs at depths, as these are based on the use of detrital organic matter produced above them (Fasham 1984). These processes form the "biological carbon pump" (Fig. 0.2), as they allow some atmospheric carbon to be sequestered in the ocean floor through this sinking detrital organic matter, possibly in large quantities (Thompson et al. 2017) and for geological periods of time (Ducklow et al. 2001, Falkowski 1997).

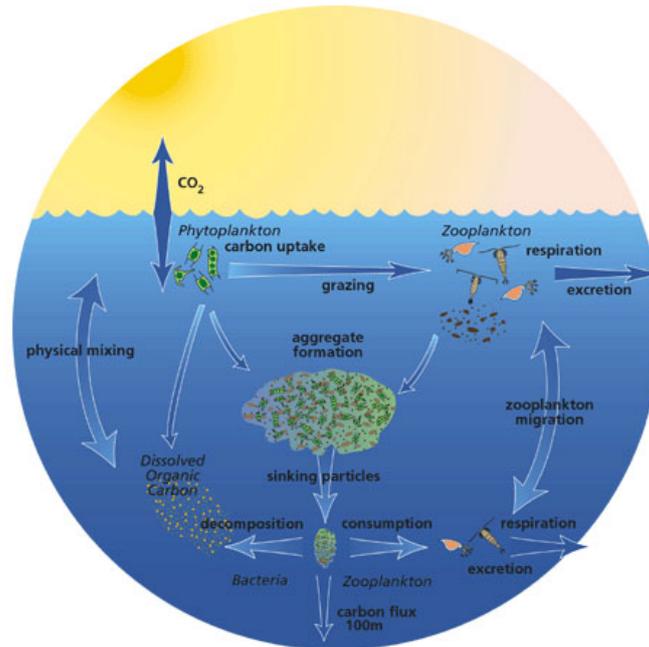


Figure 0.2: Schematic illustration of processes involved in the biological carbon pump (credit [United States Joint Global Ocean Flux Study \(JOGFS\)](#))

The ability of phytoplankton to grow and thrive is determined by light - which confines them to the upper water layer where sunlight can penetrate (the euphotic zone) - temperature, and the presence of nutrients essential for their growth, such as the nitrogen and iron mentioned above. Processes that retain or introduce nutrients in the euphotic zone, whether physical or biological, are therefore critical to the productivity of marine ecosystems. They determine the strength of the biological pump (*i.e.* how much carbon is taken up by phytoplankton), while the biological activity within the water column determines its efficiency (*i.e.* how much carbon is effectively transferred to the seafloor) (Turner 2015 and references therein). Beyond carbon considerations, this body of research has highlighted the complexity of biological nutrient cycling processes and their importance to the functioning of oceans and the planet's climate.

0.2.2 The singular contribution of marine mammals

In the oceans as on land, living organism from unicellular bacteria or phytoplankton to top predators release waste into their environment. Although the ecological relevance of these processes has only been evidenced for a few species, marine consumers from all trophic levels contribute to nutrient cycling in their ecosystems through this pathway. Microbial communities are major contributors because of their global distribution and

capacity for rapid growth (Arrigo 2005, Maldonado et al. 2016, Smith et al. 2021). So is the contribution of zooplankton (Hernández-León et al. 2008, Turner 2015), including krill in the Southern Ocean (Nicol et al. 2010, Ratnarajah and Bowie 2016, Ratnarajah et al. 2014), as they are ubiquitous, graze more than they need to and release most of what they consume ("sloppy feeding", Fasham 1984, Smetacek 2008, Smith et al. 2021). Sea sponges actively recycle and retain nutrients in oligotrophic tropical coral reefs (de Goeij et al. 2017, 2013). The aggregation of filter-feeding freshwater mussels in streams influences their nutrient cycling and productivity, with different patterns depending on the species (Atkinson et al. 2018). Fish and shark-mediated nutrient cycling are also important in different ecosystems (Allgeier et al. 2014, 2013, Roff et al. 2016, Williams et al. 2018).

In the case of marine mammals, the potential ecological importance of their role in nutrient cycling depends on several factors. First, their large size alone increase their relative contribution to ecosystem functioning, including through nutrient cycling pathways (Doughty et al. 2016, 2013, Estes et al. 2011, Hall et al. 2007, Pimiento et al. 2020, Tavares et al. 2019). Combined with their relatively high metabolic rate, this results in a high capacity for nutrient storage (in their own bodies) and a high nutrient cycling rate (through their high consumption rate and subsequent waste release) (Enquist et al. 2020, Tavares et al. 2019). They are also highly mobile and can quickly transport nutrients over large distances and against physical forces (e.g. currents, winds) (McInturf et al. 2019). In addition, some of the largest marine mammals undertake long-distance annual migrations between contrasted ecosystems (Roman et al. 2014, Roman and McCarthy 2010). They intensively feed in nutrient-rich regions and breed in nutrient-poor regions, and as such may transport nutrients between them, a process called the "Great whale conveyor belt" (Pearson et al. 2023, Roman et al. 2014, Roman and McCarthy 2010). Other species such as pinnipeds can transport nutrients between the marine environment where they feed, and terrestrial coastal ecosystems where they establish their breeding colonies (Bokhorst et al. 2019a,b). On the Antarctic Peninsula, marine nutrients from penguins and southern elephant seals (*Mirounga leonina*) colonies are incorporated into terrestrial food webs, stimulating their productivity and diversity and making their presence an important component in shaping coastal ecosystems (Bokhorst et al. 2019a). These cross-realm movements together with their ubiquitous (albeit heterogeneous) distribution in the world oceans, may increase marine mammals impact in ecosystem functioning through nutrient cycling pathways (Pimiento et al. 2020).

Finally, unlike most marine animals, marine mammals are air-breathers. While they are tied to the underwater marine environment to forage and feed, they also have to regularly surface to breathe. And chances are high that this is also when and where they fulfil another simple biological need: getting rid of metabolic and digestive waste through defecation and urination. While it is difficult to make sure that defecation and urination do not occur at depth, marine mammals' metabolism is reduced while diving, presumably to limit oxygen consumption (Kooyman 2009, Kooyman et al. 1981, Murdaugh Jr et al. 1961, Ortiz 2001). In addition, given the hydrostatic pressure at depth, marine mammals are unlikely to expel waste while actively foraging. As any nutrient input in the ocean euphotic zone can stimulate productivity from the bottom up the food web, surface waste release may increase marine mammal relative contribution to marine ecosystem functioning, and more specifically through the release of feces and urine in upper layers of the oceans. Their vertical movement in the water column to feed, breathe and expel wastes adds a vertical dimension to their role as nutrient vectors. Depending on the depth at which they forage, the nutrients they bring to the surface can be recycled if they never left the euphotic zone, or new ones if they were consumed at depth (Lavery et al. 2010, Martin et al. 2021).

Consequently, the contribution of marine mammals to nutrient cycling is singular, and suggests that the functional role of marine mammals in ecosystem extend beyond prey removal to nutrient egestion and excretion.

0.2.3 Marine mammals nutrient cycling pathways

The contribution of marine mammals to ecosystem nutrient cycling is likely not limited to their defecation and urination of nutrient-rich material fertiliser to primary producers. This nutrient-rich matter can be a direct food source for species at low trophic levels, from zooplankton to fish (Roman et al. 2016, Sazima et al. 2003). For example, tropical reef fish species associate with spinner dolphins (*Stenella longirostris*) to feed on their feces and spews, detecting the events before they occur by observing the dolphins' behaviour (Sazima et al. 2003). Sizes of fish groups were found positively correlated to dolphin group sizes (Sazima et al. 2003). As most of the fish involved in this behaviour are herbivorous, it represents an alternative trophic pathway for the nutrients contained in the dolphins' waste products to re-enter the food web.

In addition, avoidance (e.g. sheltering) or protective behaviours to mitigate predation risks (e.g. schooling) of fish towards marine mammals (Bampoh et al. 2021, Heithaus

et al. 2008, Kiszka et al. 2015, Monk and Schmitz 2022, Nottestad et al. 2002), could potentially affect nutrient cycling processes in their ecosystems (Bampoh et al. 2021, McInturf et al. 2019, Monk and Schmitz 2022, Wootton et al. 2023). Such changes in the behaviour and distribution of marine mammal prey may influence the distribution of nutrients in the living biomass at a given time (nutrient stock), while at the same time influence the nutrient deposition patterns generated by their prey (nutrient fluxes) (Allgeier et al. 2017, McInturf et al. 2019, Vanni 2002).

Marine mammal bodies can also be sources of organic matter when they die, and therefore mediate nutrient transfers between different trophic compartments of the ecosystem. For example, the fall of large whale carcasses to the seafloor provides local nutrient-poor benthic environments with tens of tons of organic matter (Smith et al. 2015, Smith 2002) (Fig. 0.3. These whale falls represent "nutrient islands" on the seafloor and are successively exploited and colonised by a range of organisms, with over 100 species identified as whale fall specialists and observed nowhere else (Smith et al. 2015, 2019). In addition, the carbon contained in their large carcasses can be sequestered on the ocean floor and remain out of the atmosphere for a long time (Pershing et al. 2010), similar to carbon sinking from the biological carbon pump. Pinnipeds also transfer marine nutrients through their bodies on their terrestrial colonies when they die there, in addition to their wastes (Smith 2008).



Figure 0.3: Gray whale *Eschrichtius robustus* skeleton on the sea floor 1.5 year after its fall, with some associated fauna. Photo from Smith et al. (2015)

Some marine mammals can also physically alter their environment and facilitate the suspension of nutrients from shallow water sediments into the water column, whether during foraging (gray whales *Eschrichtius robustus* or walrus feeding on benthic prey; Bowen 1997, Roman et al. 2014), or as a prey capture strategy (bottlenose dolphins *Tursiops truncatus* in the Caribbean region; Fig. 0.4; Kiszka et al. 2022, Ramos et al. 2022). Marine mammals movements up and down the water column can also promote water stirring and nutrient diffusion far below the wind-driven water layer and against physical forces (Lavery et al. 2012a, Smetacek 2008).

Marine mammals therefore likely influence and actively participate in the function and



Figure 0.4: Aerial observations (drone and satellite imagery) of bottlenose dolphins' *Tursiops truncatus* mud rings. Bottlenose dolphins disturb sediments to capture fish in the Caribbean region and thereby stimulate nutrient re-suspension. Figure from Ramos et al. (2022), see the original article for the associated legend

structure of their ecosystems through multiple pathways related to nutrient cycling and transfer.

0.3 A growing interest for whales in the context of climate change

While all marine mammals contribute to nutrient cycling, most studies so far focused on large whales, identified as ecosystem engineers through the *whale pump*, *great whale conveyor belt* and *whale falls* (Pershing et al. 2010, Roman et al. 2014, Roman and McCarthy 2010). Their role in nutrient cycling through the release of feces and urine has been identified as a potentially important ecosystem service to humankind (Pearson et al. 2023, Roman and McCarthy 2010). If whales help to stimulate primary production through this pathway, they may (i) stimulate productivity at higher trophic levels (Lavery et al. 2014, Roman and McCarthy 2010) largely exploited by humans, and (ii) stimulate the biological carbon pump (Chami et al. 2019, Lavery et al. 2010, Martin et al. 2021, Turner 2015). This last point, although only sporadically quantified and with a high levels

of uncertainty (Pearson et al. 2023), was received with great enthusiasm both in the scientific community and among the general public (Meynecke et al. 2023).

These "whale carbon" pathways (Fig. 0.5) were raised as new arguments in favour of whale conservation, since allowing whale populations to recover from whaling would provide a natural way to remove carbon dioxide from the atmosphere (Chami et al. 2019). Whale poo ambassadors are flourishing and advertising these processes (see [the-whale-poo-ambassadors](#)), setting up "Whale poo seamulation" to "learn how whales can help the planet" (see [whalepoo-seamulation](#)). Whale conservation has been considered for inclusion in climate change policies (Pearson et al. 2023), with whale ecological services and whales themselves being monetised (Chami et al. 2019). Some research groups are also working on creating artificial whale feces to mimic the fertilisation process and restore ecosystems (Vaughan 2022).

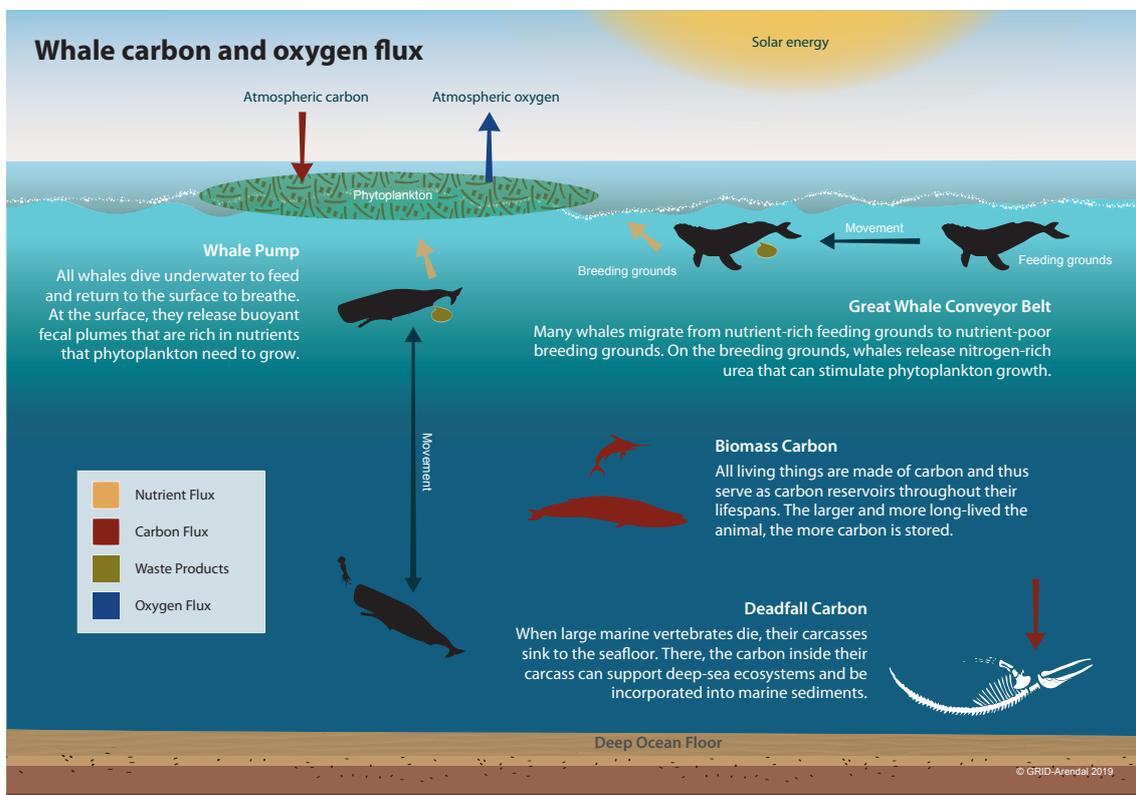


Figure 0.5: **Conceptual illustration of the "whale carbon" pathways.** Creator: GRID-Arendal (<https://www.grida.no/resources/14276>), published under [CC-NC-BY-SA 4.0](#)

Despite the enthusiasm generated by the charming idea of thriving whale populations as one of the pathways to mitigate human-caused climate change, we know little about these processes. Our knowledge is limited in terms of (i) geographical coverage, as this

principle has only been sporadically exported from the Southern Ocean, (ii) nutrients, as mostly iron, nitrogen and phosphorus were included, and (iii) marine mammal taxa involved, as only the whale contribution has been identified as structuring enough for the functioning of ecosystems to represent a potential mechanism to mitigate climate change.

However, gaps in our knowledge of marine mammals' role in nutrient cycling can significantly distort our understanding of their role and importance in ecosystem functioning. It is therefore necessary to assess the contribution of marine mammal-mediated nutrient cycling to ecosystem functioning, beyond their importance in the carbon cycle, to fully assess the impact of population decrease before they occur.

0.4 Exploring facets of marine mammal's role in nutrient cycling

0.4.1 Research hypotheses and scope

In this work, we aimed to investigate unexplored facets of marine mammals-mediated nutrient cycling, to improve our ability to assess their role in ecosystem functioning. Our general hypothesis was that while the ecosystem role of marine mammals is largely determined by their removal of prey, their role in nutrient cycling may also have structuring effects on ecosystem functioning. We limited our scope to cetaceans and pinnipeds. We hypothesised that the role of marine mammals in nutrient cycling may be important for ecosystem functioning beyond that of large whales. We also hypothesised that marine mammals contribute to nutrient cycling wherever they occur, *i.e.* in most of the world oceans, but that their contribution is likely to be spatially heterogeneous. Finally, we hypothesised that the contribution of marine mammals to nutrient cycling extend to numerous nutrients involved in ecosystem functioning processes.

We focused on one pathway of nutrient cycling, namely their contribution through the release of nutrient-rich feces and urine into their environment. Although the importance of released nutrients for ecosystem functioning underpinned our research, we did not formally quantify this influence. Its importance to ecosystem functioning is determined by the fate of the released nutrients in the recipient ecosystem, *i.e.* how much is taken up by primary producers or low trophic levels and how much sinks, and how long they remain available in the euphotic zone, in deep water layers or, in the case of pinnipeds, in terrestrial ecosystems. We focused on the first steps of these processes (*i.e.* food intake

followed by defecation and urination) as a necessary prerequisite for identifying what, where and under what conditions should be investigated next.

We aimed to assess the quantities of nutrients released by marine mammals and the quality of the "fertiliser" they produce in terms of the relative composition of the nutrient cocktails they deposit. We undertook a functional approach, taking into account the different behaviours of the species, the importance of their diet and prey in these processes, and placing this information in the context of local ecosystems. Our work integrates different spatio-temporal and functional scales, from whole communities across different ocean realms or taxonomic groups in a large ocean basin, to a few species in an ocean, or to a population, a few colonies or individuals in a specific area. We also integrated multiple nutrients.

0.4.2 Thesis outline

Chapters 1 and 2 propose wide-scale approaches. Chapter 1 investigates the contribution of cetacean communities to the recycling of multiple nutrients in different oceans around the world, and includes small cetaceans and deep-diving species together with baleen whales. Chapter 2 focuses on one ocean, the Southern Ocean, and fills in a taxonomic gap in our understanding of the role of marine mammals to nutrient cycling there. Most studies have indeed focused on large whales in the Southern Ocean, but none has looked at the contribution of phocid seals around the Antarctic continent so far. Chapter 2 thus investigates the contribution of four seal species to the cycling of iron in the Southern Ocean, broadening the view of the contribution of the marine predator community by placing it alongside that of whales and penguins. We focused on iron in this chapter because of the importance of this specific nutrient in the Southern Ocean food web and nutrient cycles.

Chapters 3 and 4 were designed based on findings from chapters 1 and 2, both based on bioenergetic models. The relative richness of different nutrients in the wastes produced by marine mammals is mainly determined by the composition of their prey. However, data on the multi-nutrient composition of prey are scarce, especially at large (world- or ocean-wide) scales. Smaller-scale studies are therefore conducted in Chapters 3 and 4 spatially (Kerguelen Plateau), temporally (breeding season) and taxonomically (1 species). Both chapters are focused on the Antarctic fur seal (*Arctocephalus gazella*) around the Kerguelen Archipelago (southern Indian Ocean), and make use of a multi-nutrient composition dataset of fecal samples (scats) collected during their breeding season on

land in the Austral summer.

Chapter 3 explores the fine-scale variability in the multi-nutrient composition of Antarctic fur seal scats along with the composition of a range of forage fish around the Kerguelen Islands. While our multi-nutrient composition data for fish expanded our initial database, it also allowed us to investigate the indirect role of prey species in nutrient cycling by providing different nutrients to predators. Chapter 4 builds on findings from previous chapters, and investigates the amounts of nutrients released by two colonies of Antarctic fur seals in the Kerguelen Islands for several essential nutrients, both at sea and on land. We adapted a bioenergetic framework to use fecal multi-nutrient composition data instead of prey multi-nutrient composition data to examine nutrient deposition patterns without the bias associated with diet and prey composition. We also used different estimation methods to assess how the fine-scale variability in deposition patterns affected the total amounts of deposited nutrients at the colony and population levels.

Chapter 5 describes an ongoing study initiated as part of this thesis to assess the influence of fur seal nutrient deposition on coastal ecosystem functioning around their colonies. The fieldwork was carried out in winter 2022-2023 (Austral summer). The data and samples have not yet been analysed, but the chapter introduces the study and its objectives, and describes the data collection protocol and the next steps of analysis that remain to be completed. This study was designed to explore sea-to-land nutrient transfers and was an opportunity to gain experience in starting and developing a project, from initiating a collaboration to setting up a sampling protocol and preparing and conducting a field campaign.

The thesis then concludes with a general discussion that summarises the main findings and their limitations, places these findings in a wider context and suggests some perspectives for future research.

Composition of cetacean communities worldwide shapes their contribution to ocean nutrient cycling

Defecation by large whales is known to fertilise oceans with nutrients, stimulating phytoplankton and ecosystem productivity. However, our current understanding of these processes is limited to a few species, nutrients and ecosystems. Here, we investigate the role of cetacean communities in the worldwide biological cycling of two major nutrients and six trace nutrients. We show that cetaceans release more nutrients in mesotrophic to eutrophic temperate waters than in oligotrophic tropical waters, mirroring patterns of ecosystem productivity. The released nutrient cocktails also vary geographically, driven by the composition of cetacean communities. The roles of small cetaceans, deep diving cetaceans and baleen whales differ quantitatively and functionally, with contributions of small cetaceans and deep divers exceeding those of large whales in some areas. The functional diversity of cetacean communities expands beyond their role as top predators to include their role as active nutrient vectors, which might be equally important to local ecosystem dynamics.

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1.1 Introduction

The importance of cetaceans in marine ecosystem functioning has long been limited to their role as top predators and their top-down impact at lower trophic levels through prey consumption (Baum and Worm 2009). However, a growing body of research suggests that their importance in ecosystem dynamics extends to their role in fine-scale nutrient cycling processes (Kiszka et al. 2022, Lavery et al. 2014, Ratnarajah et al. 2018, Roman et al. 2014, Savoca et al. 2021). The cycling of essential nutrients, such as nitrogen (N) or iron (Fe), is a key dynamic component of ecosystem functioning, from their initial uptake by primary producers to their transfer up the food web and their re-mineralisation. As air-breathing mammals, cetaceans urinate and defecate at the surface when they breathe or rest. This triggers patchy, transient nutrient enrichment events in the euphotic zone (Roman and McCarthy 2010, Roman et al. 2016), which could locally stimulate marine productivity.

The euphotic zone tends to be naturally depleted in nutrients essential to phytoplankton growth, at the base of light-based trophic webs, resulting in conditions of suboptimal productivity in most of the world's oceans (Falkowski et al. 1998, Moore et al. 2013). Productivity limitation is rarely due to the paucity of only one nutrient (Koch and Trimborn 2019, Moore and Read 2008). Trace nutrients (*i.e.* with low concentrations in the environment), such as Fe, copper (Cu) or manganese (Mg), are essential cofactors of metalloenzymes involved in photosynthesis and respiration, or structural elements in proteins (Coale 1991, Koch and Trimborn 2019, Schroeder et al. 1966). As such, they are as important in ecosystem functioning as major nutrients (N, phosphorous (P)), even if in substantially lower concentrations (Moore et al. 2013). Oceans also consist of heterogeneous habitats with different intrinsic nutrient characteristics and associated nutrient limitation conditions (Moore et al. 2013). At large spatial scales, primary productivity per unit area is two to ten times greater at high latitudes than at low latitudes (Longhurst et al. 1995). Most low latitude systems are characterised by an intense water column stratification due to the elevated average temperatures (Bopp et al. 2013), and phytoplankton biomass is primarily limited by nitrogen availability (Moore et al. 2013). In contrast, higher latitudes are characterised by strong seasonal changes in their dynamics, and trace nutrient paucity is the primary factor limiting phytoplankton biomass (Moore et al. 2013). At smaller spatial scales, neritic waters (*i.e.* coastal waters from the continental shelf) fed by terrestrial inputs tend to be eutrophic and have higher

productivity per unit area than oceanic waters, which tend to be oligotrophic in the absence of major physical processes of nutrient enrichment (*e.g.* upwelling) (Longhurst et al. 1995, Moore et al. 2013). Phytoplankton productivity is also the first biological process involved in the ocean carbon pump: carbon dioxide dissolved in surface waters is partly transferred to organic matter through photosynthesis, and partly sequestered in sediments via sinking particles and carcasses, passive advection and vertical migration of animals (Stukel and Ducklow 2017). A thorough assessment of nutrient cycling in the euphotic zone is therefore essential to understanding the mechanisms regulating trophic web productivity and atmospheric carbon sequestration in the world's oceans, including nutrient cycling mediated by animals.

The ecological importance of animal-driven nutrient biological cycling is increasingly recognised and has been demonstrated in many ecosystems (*e.g.* Allgeier et al. (2013), Atkinson et al. (2017), Poulsen et al. (2018), Subalusky et al. (2018)). Cetaceans are singular nutrient vectors in the oceans as (i) their waste products are greatly concentrated in nutrients compared to surface waters (Nicol et al. 2010, Ratnarajah et al. 2014, Roman and McCarthy 2010, Roman et al. 2016), (ii) they are highly mobile, and can transfer nutrients against physical forces and between habitats of different nutrient regimes (McInturf et al. 2019, Subalusky and Post 2019), (iii) deep diving species can transfer nutrients from the ocean depths, where they feed, to the surface, mediating a nutrient pump known as the “whale pump” (Lavery et al. 2010, Roman and McCarthy 2010), (iv) some species can form large aggregations and create “hotspots” and “hot moments” of nutrient biological cycling (Ryan et al. 2023, Subalusky and Post 2019), and, finally, (v) they are tied to the euphotic zone for breathing, where they release their wastes. On a large spatiotemporal scale, the gross nutrient enrichment caused by cetacean waste release is likely minor compared to that caused by physical processes (*e.g.* upwelling, weathering of shelf sediments) (Smith et al. 2021), or to the biological cycling by microfauna (microbial community, microzooplankton) (Maldonado et al. 2016). However, it could be important in supporting certain ecosystem processes locally (Subalusky and Post 2019), disproportionately so in some contexts (Enquist et al. 2020), although it is particularly challenging to investigate in the ocean realm.

In controlled laboratory conditions, nutrients leaching from cetacean wastes stimulate phytoplankton growth and productivity (Roman et al. 2016, Smith et al. 2013). It is thus likely that nutrients released by cetacean communities *in natura* act as fertilizers and are - at least partially - being re-injected in marine ecosystems via phytoplankton

uptake. Nutrients that are not directly taken up by primary producers might also be partially retained in the euphotic zone, and influence ecosystem productivity through indirect pathways. The microbial community (heterotrophic bacteria and viruses) could uptake some nutrients from cetacean wastes (Ratnarajah et al. 2018, Shatova et al. 2016), and detritivore species of zooplankton could feed directly on fecal particles (Roman and McCarthy 2010). Microbial communities facilitate the rapid recycling of nutrients in the euphotic zone (microbial loop), and their dynamics are closely linked to those of primary producers (Christie-oleza et al. 2017). Zooplankton also play an important role in nutrient biological cycling (Ratnarajah and Bowie 2016), and could facilitate the recycling of cetacean-released nutrients into organic matter, which in turn might affect the productivity and structure of communities at higher trophic levels (Roman and McCarthy 2010). Thus, the importance of cetacean-released nutrients in ecosystem functioning might not be limited to the fraction taken up directly by primary producers.

Estimating the total amount of nutrients that cetaceans release is, therefore, a good starting point for investigating their role in nutrient biological cycling, and has been a commonly used approach to date. However, the role of cetaceans in nutrient cycling in ocean surface waters and the importance of these processes in ecosystem functioning are still poorly understood on a worldwide basis. Previous studies were generally limited to single species - mostly large baleen whales, single location – mostly the Southern Ocean, and one nutrient -mainly iron or nitrogen (Lavery et al. 2010, 2014, Roman and McCarthy 2010, Roman et al. 2016). Cetacean communities worldwide include species ranging from small porpoises to large rorquals. Cetacean species can be classically divided into three main guilds: small cetaceans (porpoise and dolphin species less than 4 m long and feeding in the epipelagic zone); deep divers (toothed cetaceans feeding in the meso- and bathypelagic zones, such as sperm whales, beaked whales, pilot whales and Risso's dolphin *Grampus griseus*); and baleen whales (cetacean species in which baleen plates take the place of true teeth and feeding in the epipelagic zone mainly on krill or small preys). These species have different metabolisms, behaviours, foraging ecologies and population sizes, and the composition of cetacean communities is likely to be different in contrasted environments. Hence, the diversity of the cetacean community could shape the spatial and temporal variability in the amount and quality of nutrients delivered by cetaceans to surface waters. Given the central role of phytoplankton in the productivity, regulation and resilience of marine ecosystems, the narrow understanding of the cetacean contribution to ocean nutrient cycling needs to be widened to a comprehensive view at

broader taxonomic, spatial and nutrient-type scales.

This study provides a quantitative estimation of nutrients released by cetaceans at the community level in fourteen contrasted areas around the globe, for two major nutrients (N, P) and six trace nutrients (Fe, Cu, Mn, selenium (Se), zinc (Zn) and cobalt (Co)), and for a total of thirty-eight cetacean species. Our approach is based on a bioenergetic consumption-egestion/excretion model using prey nutrient concentrations, cetacean diets, metabolic parameters and cetacean abundance estimates from wide-scale multispecies surveys. We estimate both the quantities of nutrients released in cetacean wastes and the relative composition of these wastes. We show (i) how the cetacean community's contribution to nutrient cycling varies geographically from subarctic to tropical regions, and (ii) how the species composition of cetacean communities can shape these processes. We discuss the potential importance of cetacean nutrient release in ecosystem functioning in light of the functional characteristics of ecosystems and cetacean species. Taken together, the results of this work suggest that small cetaceans, deep-divers and baleen whales play different roles in nutrient biological cycling at both global and local scales and that diversity in the cetacean community may be important locally in shaping patterns of productivity and diversity in their ecosystems.

1.2 Materials and Methods

1.2.1 Bioenergetic model

We used a bioenergetic model of individual consumption previously applied to marine mammal populations (Barlow et al. 2008, Lockyer 2007, Spitz et al. 2018), and adapted it to estimate the nutrient consumption and egestion of populations (Roman and McCarthy 2010). The model estimates $Q_{tot,n}$, the yearly amount of nutrient n (in $t \cdot year^{-1}$) released by a given cetacean species in a specific area using 1.1 below, in which the BMR is the Basal Metabolic Rate of individuals ($BMR = \beta \times 293.1 \times BM^{3/4}$ in $kJ \cdot day^{-1}$, with body mass BM in kg and β a species-specific metabolic multiplier accounting for additional cost of daily activities (Kleiber 1975, Spitz et al. 2018, 2012)), E is the mean diet energy content (in $kJ \cdot kg^{-1}$ fresh weight), AE the digestive assimilation efficiency, x_n the average concentration of nutrient n in the diet (in $mg \cdot kg^{-1}$ fresh weight), r_n the release rate of nutrient n , t the number of days of presence in an area within the year and A the population abundance:

$$Q_{tot,n} = \frac{BMR}{AE \times E} \times x_n \times r_n \times A \times t \times 10^6 \quad (1.1)$$

The model calculations were carried out in fourteen areas where large-scale, multi-species cetacean population abundance estimates were available (Supplementary Data 4). Thirty-eight cetacean species were included.

The supplementary data in this chapter consisted of large Excel tables with several sheets and many pages. Printing them on paper would require several hundred pages for each printed document. To avoid this, we refer readers to the downloadable versions linked to the published article here <https://www.nature.com/articles/s41467-023-41532-y#additional-information>.

1.2.2 Model uncertainty

All parameters are associated with a certain degree of uncertainty and/or inherent natural variability. To account for it, we combined Monte-Carlo simulations and bootstrapping (10^4 simulations and drawings, respectively) to simulate vectors of possible values for each parameter based on a given basal value and distribution (Table 1.1). Six model parameters ($B\bar{M}$, β , AE , r_n , A , t) were sampled from parametric statistical distribution based on published information (Table 1.1). Two (E and x_n) were estimated based on the diet of each species and the composition of prey items: uncertainty was quantified using the bootstrap. We found high ranges of variations for some model parameters (Supplementary Data 4), which ultimately impacted uncertainty in the model output.

1.2.3 Model parameters

The mean body mass $B\bar{M}$ used in the model resulted from body length to body mass regression equations (Trites and Pauly 1998). For species not listed in Trites and Pauly (1998), we either used other published reference or the mean body mass of a morphologically similar species (Supplementary Data 4). We considered a standard deviation of 20% of using a normal (Gaussian) distribution to account for intra-species variability and uncertainty (Table 1.1).

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). Variability for β was simulated using a truncated normal distribution (Table 1.1), with different base values

Table 1.1: Parameter settings of the bioenergetic model used to estimate nutrient released through cetacean waste products using Monte-Carlo simulations ($n = 10^4$)

Parameters	Monte-Carlo simulation setting
Body mass BM	$\sim \mathcal{N}(\bar{B}M, 0.2 \times \bar{B}M)$
Beta β	$\sim \mathcal{N}(\bar{\beta}, 0.2 \times \bar{\beta}, a = 1, b = 5)$
Assimilation efficiency AE	$\sim \mathcal{N}(0.85, 0.05, a = 0.8, b = 0.95)$
Nutrient release rate r_n	$\sim \mathcal{U}(0.2, 0.4)$ for N and P for migratory baleen whale species in their breeding grounds 0 for Fe, Cu, Mn, Se, Zn, Co for migratory baleen whale species in their breeding grounds $\sim \mathcal{U}(0.7, 0.9)$ in all other cases
Population abundance A	$\sim \log \mathcal{N}(\log(\frac{\bar{A}}{\sqrt{1+(C\bar{V}_A)^2}}), \sqrt{1+(C\bar{V}_A)^2})$
Number of days of presence t	$\sim \mathcal{U}(120, 240)$ for migratory baleen whale species in their feeding grounds 365 in all other cases

depending on species. We used three base values $\bar{\beta}$: 2, 3, and 4. We associated a $\bar{\beta}$ of 2 to species with low cost of living (e.g. sperm whales), and a $\bar{\beta}$ of 4 to species with high cost of living (e.g. harbour porpoise). We defined three functional and ecological groups of cetaceans: baleen whales, deep divers and small cetaceans, partly guiding the choice of $\bar{\beta}$. We also considered that the consumption of energy-rich food indicates high-energy needs and consequently a relatively high cost of living (Spitz et al. 2012).

To account for the additional cost of lunge-feeding (Savoca et al. 2021), was increased by 0.5 for lunge-feeding baleen whale species. Individual daily rations estimated by our model for these species (Supplementary Data 3) fall between previously published estimates (Savoca et al. 2021). For all species, we set the truncated normal distribution with minimum and maximum values of 1 and 5 to obtain physiologically plausible ranges (Table 1.1).

The mean assimilation efficiency of energy AE is typically $\sim 80\%$ in cetacean bioenergetic models (Barlow et al. 2008, Roman and McCarthy 2010, Spitz et al. 2018). Yet, experimental studies gave values in the range of 73–93% for cetaceans (Kriete 1995, Mårtensson et al. 1994). To lean on the conservative side, we chose a base value of 85% and set the truncated normal distribution with minimum and maximum of 80% and 95% to avoid non-physiologically plausible values (Table 1.1).

The release rates of nutrients r were never measured on cetaceans. For captive pinnipeds, N release rate ranged between 84 and 89% (Keiver et al. 1984, Ronald et al. 1984). Most studies focusing on mammal species suggest high release rates for micronutrients such as Fe, Cu or Mn (Evans 1973, Lawson et al. 1997, Linder 2020). Bioenergetic models estimating nutrient egestion for cetaceans used a release rate of 0.80

for N (Roman and McCarthy 2010), 0.80 for Fe or 0.85 again for Fe but with a range of variation between 0.70 and 0.90 (Lavery et al. 2010, Ratnarajah et al. 2016a). Given the little empirical information available, we defined the release rate as following a Uniform distribution between 0.7 and 0.9, for both major elements (N, P) and trace nutrients (Fe, Cu, Mn, Se, Zn, Co; Table 1.1). As migratory baleen whales fast in their breeding grounds, we considered these species only urinate during their presence there. Excretion of trace nutrients in urine is negligible (Evans 1973, Linder 2020), so we set nutrient release for the migratory species in breeding grounds to zero for trace nutrients and to between 0.2 and 0.4 for N and P (Table 1.1).

For population abundance A , we selected only dedicated large-scale, multi-species surveys using distance sampling protocols and analysis. When the survey design included several spatial blocks, we used mean estimates and coefficients of variation (CV) of blocks to compute the overall mean and CV for each area (Supplementary Data 4). Distinct estimates between habitats were computed where both oceanic and neritic blocks were surveyed. We then used a lognormal distribution with the calculated parameters for Monte Carlo simulations (Table 1.1).

Blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), Sei (*Balaenoptera borealis*), Bryde's (*Balaenoptera edeni*) and humpback (*Megaptera novaeangliae*) whales are known to migrate from their feeding grounds of temperate and subpolar areas to breeding grounds in tropical to sub-tropical areas (Wursig and Perrin 2009). Of the fourteen areas included in this study, six are identified as feeding grounds (Northeast and Northwest Atlantic, Central North Atlantic, California current and Gulf of Alaska), while six are known breeding grounds (Hawaii, French Polynesia, Southwest Indian Ocean, French Antilles, New Caledonia and Wallis & Futuna). To account for migration behaviour, we included a parameter t set between 120 and 240 days (four to eight months) following a uniform distribution in feeding and breeding grounds (Table 1.1). For other areas and species, t was set as a constant at 365 days.

A unique diet was defined per species with no difference between locations and no seasonal variation, using diet composition data from the published literature (119 references in total, Supplementary Data 4). While we are aware that a unique diet could lead to an underestimation of the spatial variability of the final output, we used nine functional prey groups to describe diets to reduce this bias. If populations of the same species in different locations are unlikely to feed on the same prey species, they are likely to have the same trophic ecology, and therefore target prey from the same functional groups.

We preferred information related to the percentage of biomass ingested of prey species or group of prey species (%W) from stomach content analysis (64 references) rather than qualitative information from isotope analysis, list of prey or surface observations (55 references). When not available, qualitative data was used to describe an average diet. We then compiled energy and nutrient content analytical data of 154 prey samples from two studies (Chouvelon et al. 2022b,c). We were limited to these data sets in our analysis, but we artificially extended them by using a kernel-based bootstrap procedure to simulate variation in the composition of each prey group and obtain vectors of energy content (E_{pg}) and nutrient concentration ($x_{n,pg}$) per prey group pg . A distribution for the composition of each prey group (for each nutrient, separately) is estimated from sample values from the compiled data sets and 1^{e4} values are then drawn randomly from this estimated distribution. For the prey group *Zooplankton*, there was only one sample which precluded the use of the bootstrap procedure. We instead conducted Monte-Carlo simulations ($n = 1^{e4}$) using a normal distribution with the value of the sample as a mean and a standard variation of 20% for energy and macronutrient content and 40% for micronutrient content. Then, we used these energy and nutrient content values (E_{pg} and $x_{n,pg}$, respectively) and the percentage of prey groups in diets (W_{pg}) to determine the mean energy content (E , 1.2) and the mean iron concentration (x_n , 1.3):

$$E = \sum_{pg} W_{pg} \times E_{pg} \quad (1.2)$$

$$x_n = \sum_{pg} W_{pg} \times x_{n,pg} \quad (1.3)$$

Datasets of prey composition are available under the depository system PANGAEA (Chouvelon et al. (2022a, 2021); <https://doi.pangaea.de/10.1594/PANGAEA.937345> and <https://doi.pangaea.de/10.1594/PANGAEA.940861>). Further details and references for the setting of parameters are provided in [Supplementary Data 4](#).

1.2.4 Differences between areas, habitats and cetacean groups

Dimensions of parameters and outputs ($n = 1^{e4}$) resulting of the Monte Carlo simulations and bootstrap precluded the use of standard statistical test of significance when comparing outputs for two groups (either areas, habitats, or taxonomical groups). Instead, we assessed unilateral binary relations by calculating the percentage of values from one group superior to the other group. We considered difference was significant when this percentage was

$\geq 95\%$ or $\leq 5\%$. To describe results, we either directly mentioned this *p-value* if it was $\leq 5\%$ or expressed $(1 - p\text{-value})$ when it was $\geq 95\%$ and adapted the direction of the binary relation of interest, so the result of our test (called *p*) could be expressed as in classic statistical tests (*i.e.* significant difference when $p \leq 0.05$). For example, if a test investigating whether nutrient release in area A is greater than nutrient release in area B and the result resulted in a 0.99 value, we concluded that nutrient release in area A is significantly greater than nutrient release in area B with $p = 0.01$.

1.2.5 Sensitivity analysis

We conducted a sensitivity analysis to determine parameters' influence on the final output value and uncertainty (Saltelli et al. 2008). We adopted a global approach, so that the effect of one parameter could be estimated when all other inputs were varying. It enables the identification of interactions, and does not require the model to be linear and additive (Cariboni et al. 2007). We used the Sobol variance-based approach where the variance of the output can be decomposed into the contributions imputable to each input factor.

1.2.6 Nutrient release and ecosystem productivity

Surface chlorophyll concentration and sea surface temperature (SST) were extracted for our study areas (year 2021, <https://oceancolor.gsfc.nasa.gov>). We computed their mean values over each of our 14 studied area and tested their relationships with cetaceans-released nutrients levels using linear models, this for the 8 nutrients.

1.2.7 Relative composition of cetacean waste products

We estimated the stoichiometry of the waste products regardless of the amounts released by each species by calculating how much of each nutrient was released per kilogram of food ingested, and then by normalizing values per nutrient across species. Minimum, mean, lower and higher quantiles and maximum were calculated for small cetaceans, deep divers and baleen whales. We investigated the cetacean taxonomic influence on the composition of the nutrient cocktail released using Principal Component Analysis on summary statistics (quantiles and mean) of the relative composition of each species.

1.3 Results

Model estimates (per area, habitat, taxa and taxa within habitats, waste relative composition) and Sobol sensitivity indices are provided in [Supplementary Data 1](#), and results of statistical tests for differences (between areas, habitats and taxa) are available in [Supplementary Data 2](#).

1.3.1 Cetaceans release greater quantities of nutrients in temperate areas

The contribution of cetacean populations to nutrient cycling (annual quantity of nutrient released per surface unit) varies geographically from 2.1 kg.km⁻².yr⁻¹ (95% confidence interval - hereafter [CI 95%], *i.e.* [1.4 ; 3.1]) to 152.2 [96.9 ; 234.1] kg.km⁻².yr⁻¹ for the major nutrient N, and from 2.6 [1.2 ; 5.0] mg.km⁻².yr⁻¹ to 162.5 [80.8 ; 292.0] mg.km⁻².yr⁻¹ for the trace nutrient Co (Fig.1.1). French Polynesia in the Pacific Ocean has the lowest release values for all nutrients, while the central North Atlantic Ocean shows the highest values, up to 77 times higher than French Polynesia's, for Fe release (Fig. 1.1). All tropical or sub-tropical areas (Gulf of Mexico, Hawaii, French Polynesia, New Caledonia, Wallis & Futuna, French Antilles and Guyana) show relatively low nutrient inputs from cetacean communities (2 to 10 times greater than French Polynesia, the baseline – poorest - area). In contrast, temperate and sub-Arctic areas (Gulf of Alaska, central North and Northeast Atlantic oceans) show high nutrients inputs from cetaceans (29 to 77 times greater than our baseline area). The Southwest Indian Ocean shows a relatively high nutrient release from cetaceans compared to other low-latitude areas (8 to 10 times greater than in French Polynesia). Among temperate areas, cetacean's nutrient release in the Mediterranean Sea is the lowest with fold-change ratios from 9 to 17, even when compared to areas at similar latitudes (California current and Northwest Atlantic, fold-change ratios from 8 to 45, Fig. 1.1).

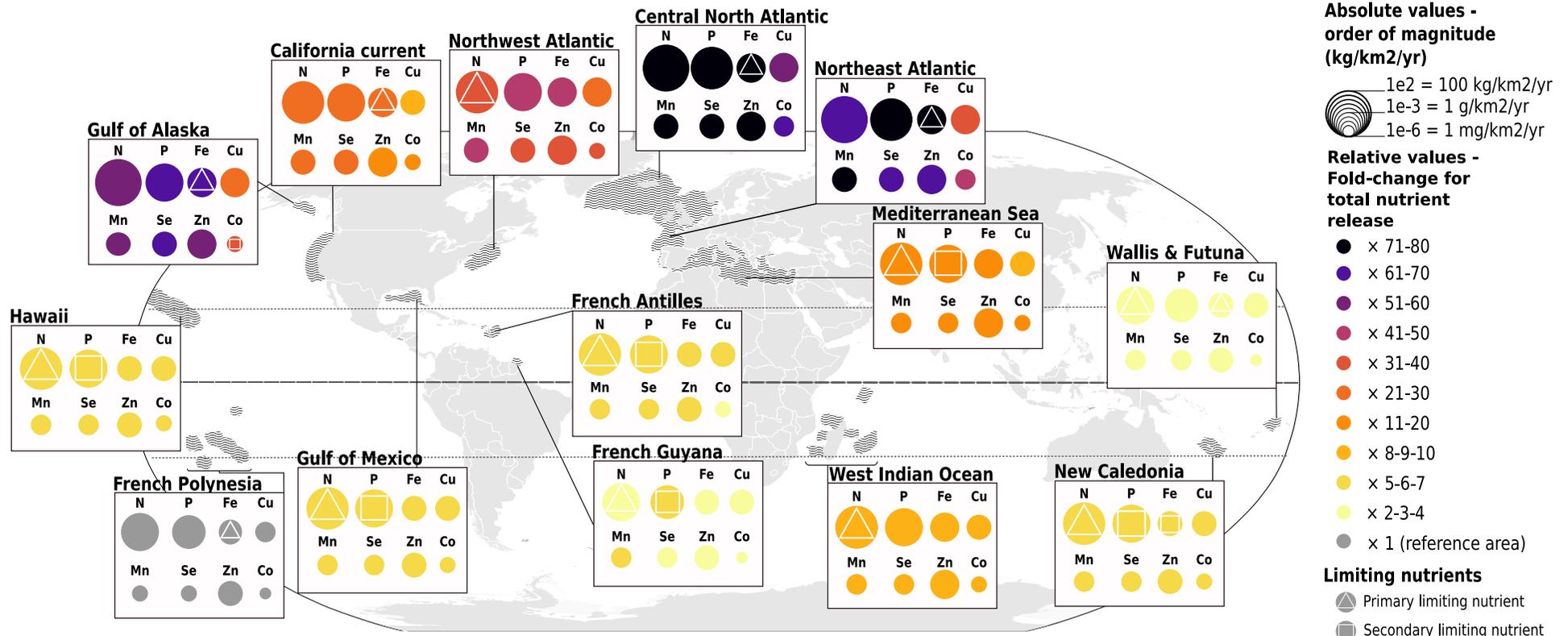


Figure 1.1: **Nutrient loads released by cetacean communities in 14 contrasted areas show quantitative and qualitative variations around the globe.** Results are from the bioenergetic model supplemented with an original dataset of abundance estimates, diet composition, prey composition and metabolic data. Model was set up with Monte-Carlo simulations combined with a bootstrap procedure with $n = 1e4$. Dark grey shaded areas define locations surveyed for population abundance estimates used in the model. In each area (*i.e.* box), sizes of the circles are proportional to the order of magnitude of mean absolute estimates in kg/yr/km²; color gradient of the circles indicates values of the fold-change ratio of nutrient release compared to the area of reference (French Polynesia, where absolute values are the lowest), *i.e.* how much more nutrients are released in a given area compared to this baseline one. Shapes in the circles identify primary (triangles) and secondary (squares) limiting nutrients for primary producers in specific areas as taken from Drupp et al. (2011), Moore et al. (2013), Sonnekus et al. (2017), Zhao and Quigg (2014). Vector map adapted from Felipe Menegaz/[CC-BY SA 3.0](https://creativecommons.org/licenses/by-sa/3.0/)

1.3.2 The latitudinal nutrient release pattern correlates with productivity

Mean surface chlorophyll concentration and SST are two correlated indicators of ecosystem productivity commonly use in habitat characterisation. Mean annual SST in the 14 studied areas range from 6.4°C in the central North Atlantic to 29.8°C in Wallis & Futuna, and the annual mean surface chlorophyll concentration from 0.06 mg.m⁻³ in French Polynesia to 1.20 mg.m⁻³ in the Northeast Atlantic Ocean (Fig. 1.2). Amounts of nutrients released by cetacean communities in the 14 studied areas are negatively correlated with the sea surface temperature (R^2 from 0.80 to 0.89 and p -value $\leq 1.5 \times 10^{-5}$), and positively correlated with mean surface chlorophyll concentration (R^2 from 0.65 to 0.89 and p -value $\leq 8.1 \times 10^{-4}$; Fig. 1.2, Table 1.2). Slopes of these relationships vary between nutrients, but they are steeper with mean surface chlorophyll concentrations than with SST. For instance, the relationship between mean surface chlorophyll concentrations and nutrients is more than 5 times stronger for Fe than for Cu.

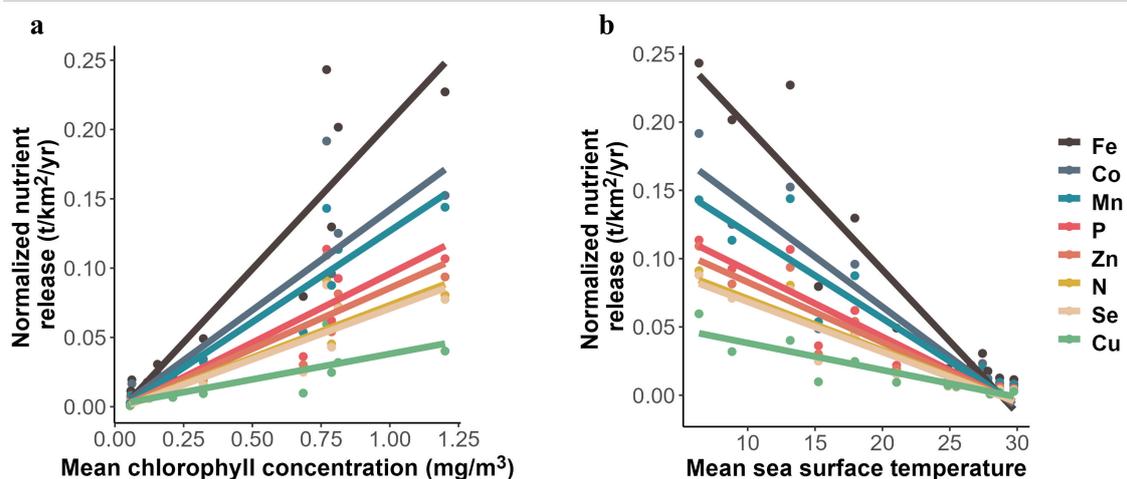


Figure 1.2: **Cetacean communities' nutrient release correlates with indexes of ecosystem productivity.** Mean estimates of nutrient loads released by cetacean communities in 14 contrasted areas were normalized per nutrient and plotted against two indicators of ecosystem productivity: a) the mean surface chlorophyll concentration b) and the mean sea surface temperature estimated from satellite data on <https://oceancolor.gsfc.nasa.gov>. Mean nutrient release estimates result of a bioenergetic model supplemented with an original dataset of population abundances, diet composition, prey composition and metabolic data and set up with Monte-Carlo simulations combined with a bootstrap procedure with $n = 10^4$. French Guyana area was removed for the left plot as the chlorophyll concentration estimate was driven by the water turbidity due to the Amazon River plume. Linear models were run for each nutrient and each slope was statistically significant (see Table 1.2)

Table 1.2: Linear regressions between absolute levels of nutrient release by cetacean communities and indicators of productivity (mean chlorophyll concentration Chlo and sea surface temperature SST)

Nutrient	covariate	slope	R ²	p-value
N	Chlo	0.08	0.82	2.3 ^{e-5}
P	Chlo	0.10	0.85	7.0 ^{e-6}
Fe	Chlo	0.21	0.85	7.7 ^{e-6}
Cu	Chlo	0.04	0.65	8.1 ^{e-4}
Mn	Chlo	0.13	0.89	1.1 ^{e-6}
Se	Chlo	0.07	0.81	2.4 ^{e-5}
Zn	Chlo	0.09	0.81	2.7 ^{e-5}
Co	Chlo	0.14	0.79	5.4 ^{e-5}
N	SST	0.004	0.88	8.2 ^{e-7}
P	SST	0.005	0.88	7.4 ^{e-7}
Fe	SST	-0.01	0.89	4.6 ^{e-7}
Cu	SST	0.002	0.80	1.5 ^{e-5}
Mn	SST	-0.006	0.87	1.0 ^{e-6}
Se	SST	0.004	0.88	6.1 ^{e-7}
Zn	SST	0.004	0.88	8.0 ^{e-7}
Co	SST	-0.01	0.86	1.5 ^{e-6}

1.3.3 Quantity of cetacean-released nutrients differ in neritic and oceanic waters but differences are not consistent between areas

Annual densities of cetacean-released nutrients are significantly higher in oceanic than in neritic waters in the Northeast Atlantic Ocean ($p \leq 4.0^{e-4}$, p referring to our calculated p-value as detailed in Methods), while the opposite is found for the Gulf of Alaska, the French Antilles and Guyana ($p \leq 1.0^{e-4}$; Fig. 1.3). There is no significant difference in the quantities of all nutrients released between both habitats in the central North Atlantic Ocean and the Mediterranean Sea ($p \geq 2.2^{e-1}$ and 7.5^{e-2} , respectively). In the Northwest Atlantic Ocean area, Cu release is significantly greater in oceanic than in neritic waters ($p = 1.0^{e-3}$), while the difference is not significant for other nutrients ($p \geq 7.4^{e-2}$). In the Southwest Indian Ocean, nutrient release in oceanic waters is significantly greater than in neritic waters for all nutrients ($p \leq 4.5^{e-2}$) except P ($p = 1.1^{e-1}$), Fe ($p = 8.2^{e-2}$) and Mn ($p = 1.8^{e-1}$).

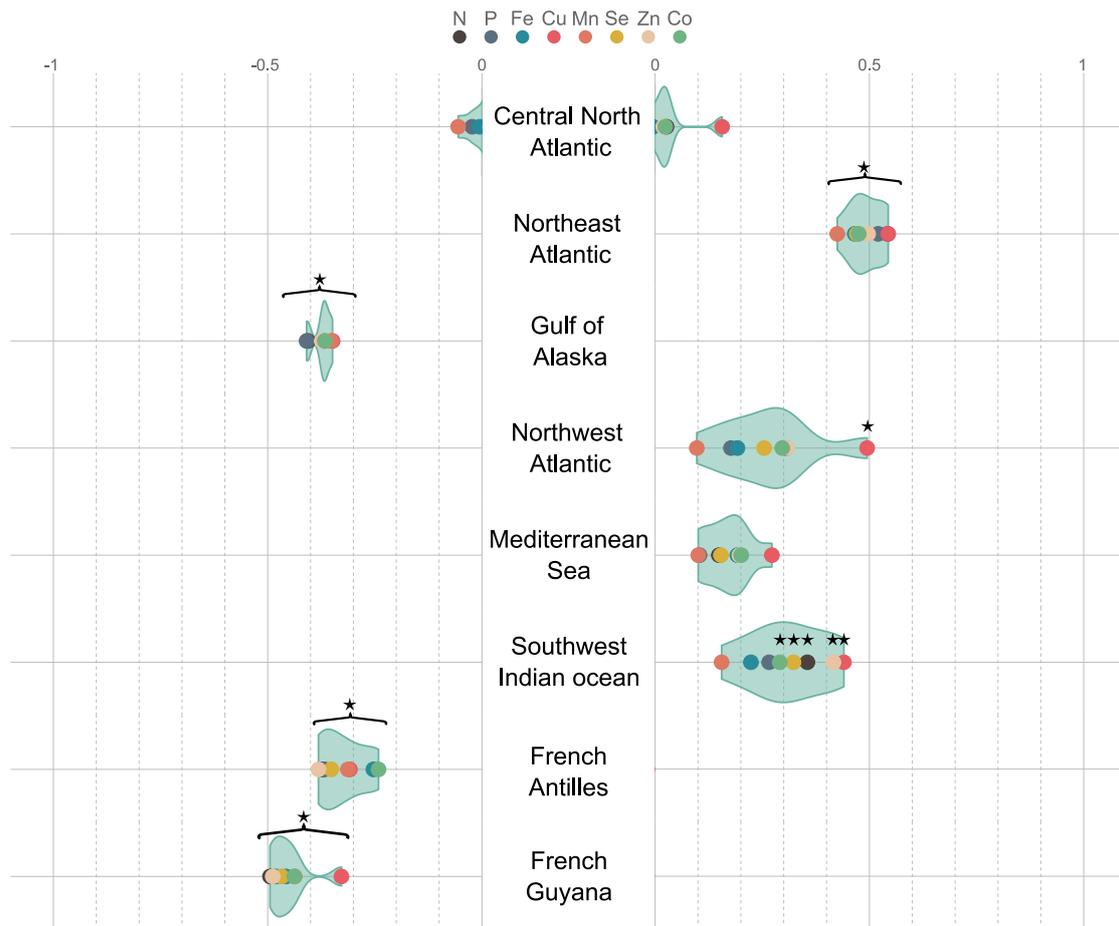


Figure 1.3: **Cetaceans do not release equivalent amounts of nutrients in different habitats, depending on areas.** Differences between mean levels of nutrients released by cetacean communities in neritic and oceanic habitats, with levels of nutrient release per unit area and per year normalized per nutrient and per area. When values are negative (left panel), nutrient release is greater in neritic than oceanic habitat, and when values are positive (right panel), nutrient release is greater in oceanic than in neritic habitat. Habitat differences between nutrient release per unit area and per year estimates were assessed based on unilateral binary relations between estimates (see Methods), and significant differences between habitats are indicated with a black star (test results are provided in [Supplementary Data 2](#)). Mean nutrient release estimates result of a bioenergetic model supplemented with an original dataset of population abundances, diet composition, prey composition and metabolic data and set up with Monte-Carlo simulations combined with a bootstrap procedure with $n = 10^4$. Green shades are violin plots, indicating the distribution of difference estimates

1.3.4 Relative compositions of cetacean-released nutrient cocktails differ between ecosystems

In tropical and sub-tropical areas, relative proportions of nutrients within the same area are of similar range (differences in fold-change ratios are between 1 and 3, see homogeneous

colours in Fig. 1.1). However, in temperate northern areas, nutrients can be over- or under-represented in the total load compared to the relative composition of the nutrient cocktail released in tropical areas. For example, in the Northeast Atlantic Ocean, cetaceans release 35 times more P and Fe than Cu (fold-change ratios of 72 and 37, respectively, Fig. 1.1). In the central North, Northeast and Northwest Atlantic oceans, the Gulf of Alaska and the California current, cetacean wastes are depleted in Cu and Co (lowest fold-change ratios in each area, between 9 and 54), while being enriched in Fe, P and Mn (highest fold-change ratios in each area, between 28 and 77) compared to tropical areas. Within a specific area, the relative composition of the nutrient cocktail released can differ between oceanic and neritic habitats (Fig. 1.3), e.g. in the Northwest Atlantic Ocean the difference between standardized release levels is around 0.5 for Cu while it is around 0.1 for Mn. Cetacean wastes are enriched in Cu in areas where cetaceans release more nutrients in oceanic habitats (highest difference compared to other nutrients in the Northeast & Northwest Atlantic oceans, and the Southwest Indian Ocean, Fig. 1.3).

1.3.5 Relative contributions of baleen whales, deep divers and small cetaceans populations to whole community-released nutrients differ quantitatively and qualitatively

Multivariate analyses on the relative composition of wastes showed a segregation of nutrient release profiles among the three cetacean groups, *i.e.* small cetaceans, deep divers and baleen whales, mainly driven by the differential composition in Cu, P and Mn (Fig. 1.4). Deep divers release waste matter significantly richer in Cu (9.5 [2.6; 18.5] mg.Cu.kg⁻¹ of food ingested) than small cetaceans (3.5 [0.6; 10.6] mg.Cu.kg⁻¹ of food ingested, $p = 2.2 \times 10^{-2}$) and baleen whales (2.9 [0.6; 7.0] mg.Cu.kg⁻¹ of food ingested, $p = 1.4 \times 10^{-2}$; Fig. 1.5). No other significant difference for nutrients considered separately was found despite slight variations (*e.g.* higher P and Mn content in matter released by small cetaceans, $p \geq 4.2 \times 10^{-1}$).

These qualitative differences at species levels combined with release rates and population abundances result in differences in the relative contribution of baleen whales, deep divers and small cetaceans to total nutrient loads released by communities in the different studied areas (Fig. 1.6). Baleen whales contribute over 90% of cetacean-released nutrients in the Gulf of Alaska, about half (46-55%) in the Northeast Atlantic Ocean and 37 to 65% in the central North Atlantic Ocean. Their contribution is significantly

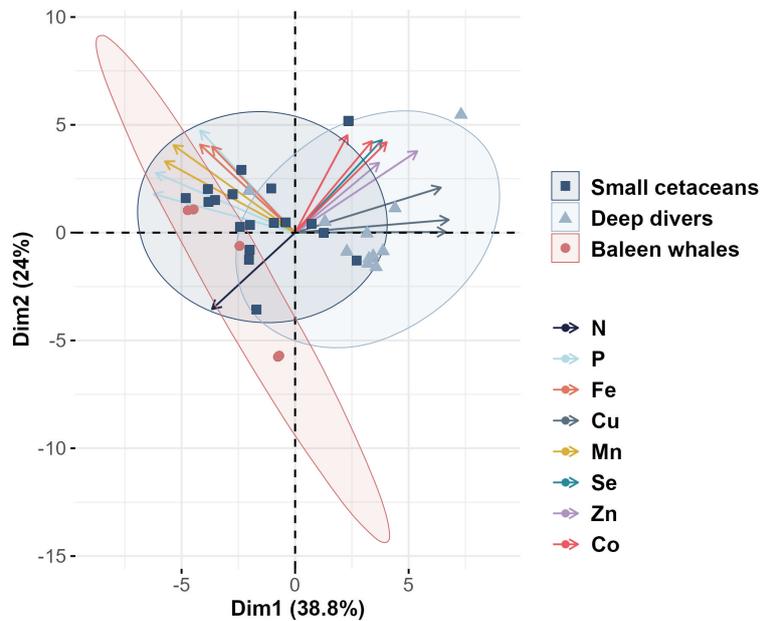


Figure 1.4: **Principal component analysis (PCA) reveals distinction between the relative nutrient composition of wastes released by small cetaceans, deep divers and baleen whales.** Individual nutrient released per kilogram of food ingested daily was estimated using a bioenergetic model supplemented with an original dataset of diet composition, prey composition and metabolic data and set up with Monte-Carlo simulations combined with a bootstrap procedure with $n = 10^4$, normalized per nutrient and computed for 38 cetacean species belonging to small cetaceans (dark blue ellipse and square points), deep divers (light blue ellipse and triangle points) or baleen whales (red ellipse and circle points). Each point represents a species. Contribution of variables (lowest 2.5% quantile, mean and highest 97.5% quantile, for all nutrients) to the first two principal components are plotted as arrows on the biplot, colour indicates the nutrient. Only variable with $\text{cos}^2 > 0.5$ were plotted

greater than that of small cetaceans and deep divers for all nutrients only in the Gulf of Alaska ($p \leq 3.0 \times 10^{-4}$, [Supplementary Data 2](#)), and than that of deep divers for N in the Northeast Atlantic Ocean ($p = 1.3 \times 10^{-2}$). In the California current, Northwest Atlantic Ocean and Mediterranean Sea, baleen whales contribute to total nutrient release less (30-41%, 22-35% and 17-26%, respectively) than small cetaceans (51-64%, 35-50% and 50-74%, respectively), except for Cu in the California current (49% released by baleen vs 30% by small cetaceans) and in the Northwest Atlantic Ocean (22% released by baleen whales vs 19% by small cetaceans; [Fig. 1.6](#)). Differences between the two groups are significant only in the Mediterranean Sea for N, P, Fe, Mn and Zn ($p \leq 4.0 \times 10^{-4}$, [Supplementary Data 2](#)). Deep divers are the least contributing group in the Gulf of Alaska, California current, Mediterranean Sea and Northeast Atlantic Ocean, but they contribute to 22-62% of the total loads in the central North and Northwest Atlantic oceans, where

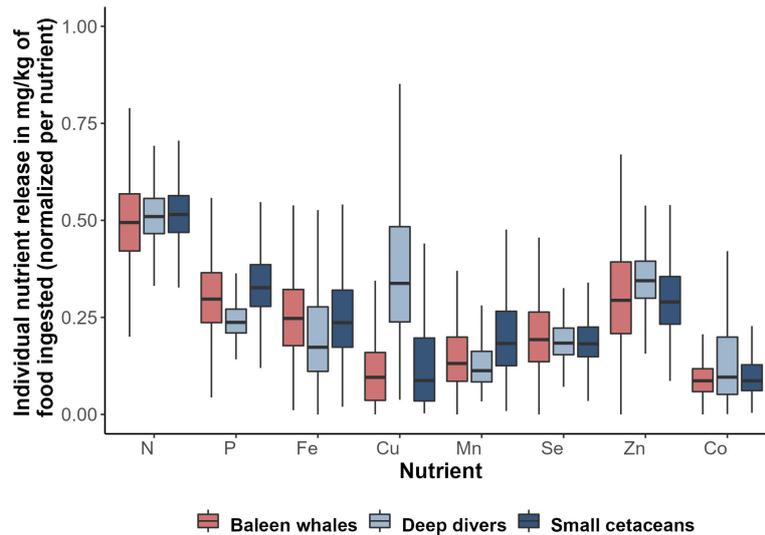


Figure 1.5: **Relative nutrient composition of wastes produced by small cetaceans, deep divers and baleen whales.** Individual nutrient released per kilogram of food ingested daily was normalized per nutrient and computed for 38 cetacean species, as estimated using a bioenergetic model supplemented with an original dataset of diet composition, prey composition and metabolic data and set up with Monte-Carlo simulations combined with a bootstrap procedure with $n = 1e^4$. For all nutrient except copper (Cu; with our calculated p -value $p = 2.2e^{-2}$ for comparison with small cetaceans) there is no significant difference between the relative composition of each taxon. 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 not plotted

their contribution is not significantly different from that of baleen whales for all nutrients ($p \geq 9.2e^{-2}$) but P ($p = 4.3e^{-2}$) in the central North Atlantic Ocean (Fig. 1.6). Baleen whales are minor contributors to nutrient cycling in tropical Gulf of Mexico and Hawaii (0-4%, $p \leq 2.3e^{-3}$), where some species are present year-round and thus observed during abundance surveys (surveys are usually conducted in the summer season, when migrating species are in their foraging grounds). small cetaceans are the main contributors for all nutrients (62-74%, $p \leq 4.0e^{-2}$) but Cu (50%, $p \geq 6.2e^{-2}$), Se and Co (58-61%, $p \geq 5.1e^{-2}$ with baleen whales) in the Mediterranean Sea, and for all nutrients (74-85%, $p \leq 3.4e^{-2}$) but Cu and Co (42-68%, $p \geq 1.1e^{-1}$) in French Guyana. The contribution of deep divers is significantly the greatest in the cetacean community for all nutrients in New Caledonia (75-93%, $p \leq 2.3e^{-2}$), for N, P, Cu, Se, Zn in Hawaii (66-79%, $p \leq 3.4e^{-2}$), for N, Cu, Se and Zn in French Antilles (72-89%, $p \leq 4.8e^{-2}$), for Cu, Zn and Co in French Polynesia (70-87%, $p \leq 3.3e^{-2}$) and for Cu in the Southwest Indian Ocean (82%, $p = 1.0e^{-1}$). The most significant variations in relative contributions to the release of different nutrients

are observed for Cu, for which the contribution of deep divers rises compared to other nutrients (*e.g.* from 31% for Fe to 62% for Cu in the central North Atlantic Ocean, or from 42% for Fe to 70% for Cu in Wallis & Futuna; [Fig. 1.6](#)). Deep divers contribute to more than 50% of Cu release by cetacean communities in 10 out of 14 areas, and to more than 70% in 7 of these areas. The relative contribution of small cetaceans is also the greatest for Mn and the lowest for Cu, in all areas.

Sobol sensitivity indices show that model outputs are most sensitive to population abundance (a fixed population abundance would reduce the output variance by up to 64%), followed by the metabolic multiplier β (6-11% of output variance depending on nutrients), individual body mass (3-7% of output variance), and to a lesser extent by the mean energy content of the diet (2-5% of output variance; [Fig. 1.7](#)). Diet mean nutrient content is more influential for trace nutrients than for major nutrients (*e.g.* fixing this parameter would reduce the output variance by 30% for Fe but only by 2% for N). The assimilation efficiency and nutrient release rates show little influence on the model output.

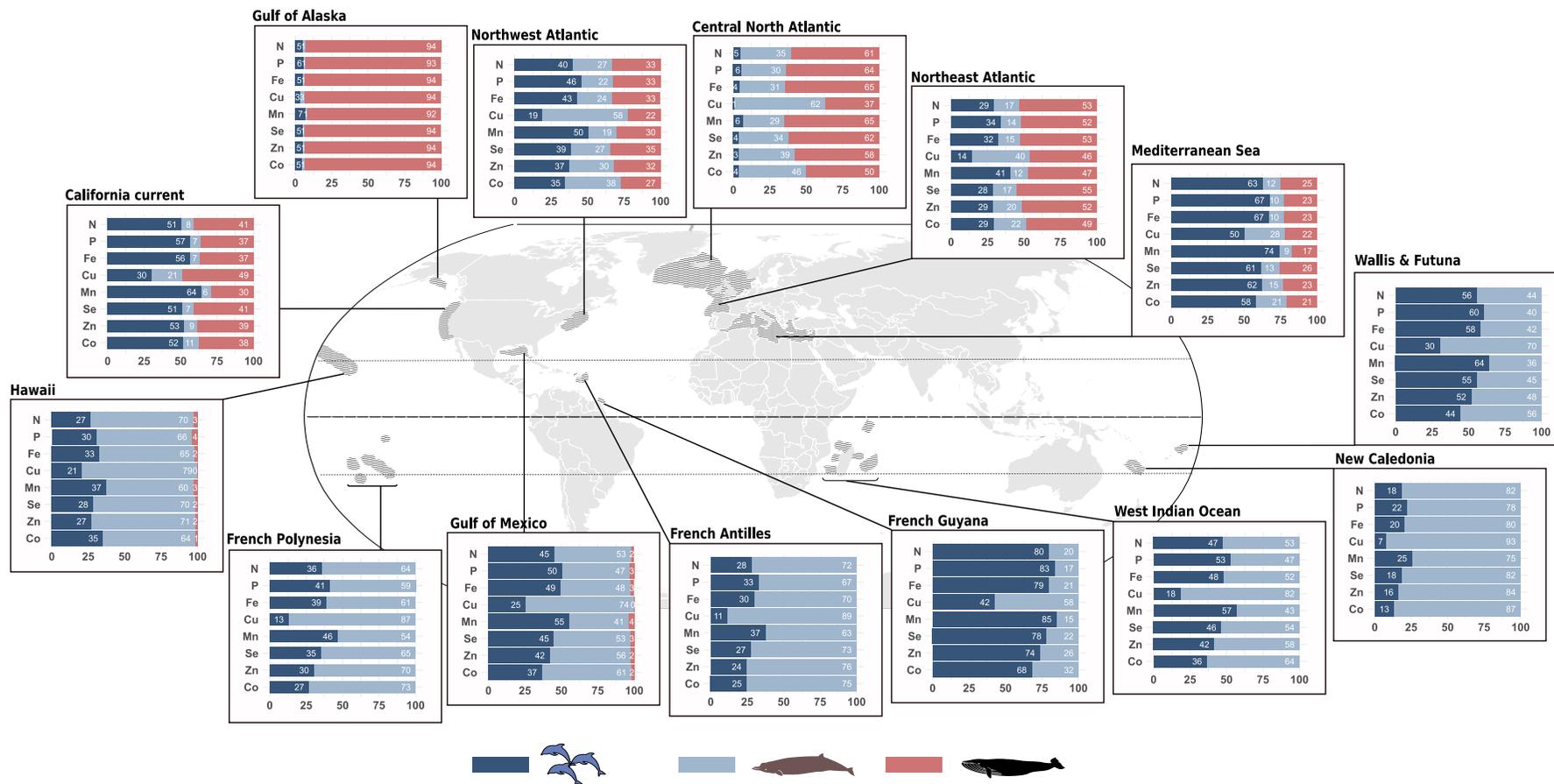


Figure 1.6: **Different cetacean taxa show different contributions to nutrient cycling worldwide.** Respective contribution (in %) of baalen whales (red), deep divers (light blue) and small cetaceans (deep blue) to loads of nutrients released by whole cetacean communities in 14 contrasted areas. Results are from the bioenergetic model supplemented with an original dataset of abundance estimates, diet composition, prey composition and metabolic data. Model was set up with Monte-Carlo simulations combined with a bootstrap procedure with $n = 1e4$. Vector map adapted from Felipe Menegaz/[CC-BY SA 3.0](https://creativecommons.org/licenses/by-sa/3.0/)

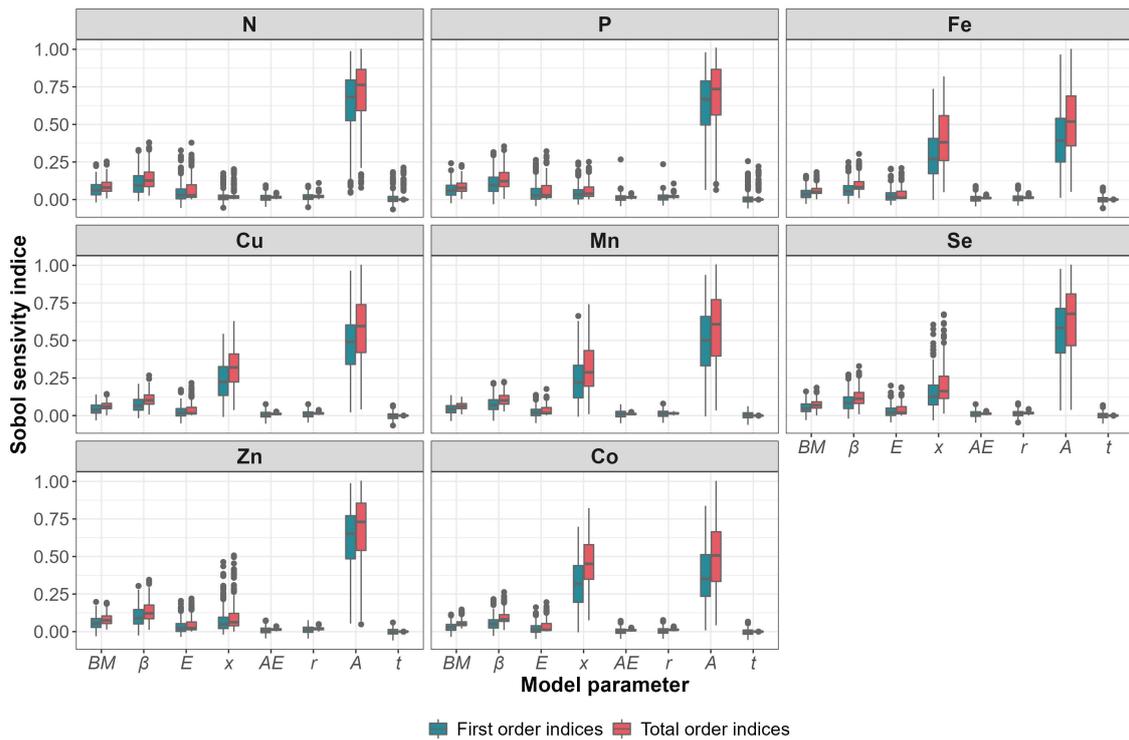


Figure 1.7: **Sensitivity of the bioenergetic model output to uncertainty in model inputs.** Ranges of estimates of Sobol indices (first-order, in blue, and second-order, accounting for interactions between parameters, in red) calculated for each species of cetacean included in the model, in each habitat of each area. BM is the body mass, β is as species-specific metabolic multiplier, E is the mean energy content in the diet, x the mean nutrient content in the diet, AE the mean assimilation of energy rate, r the nutrient release rate, A the population abundance and t the number of days of presence. The bioenergetic model was set up with Monte-Carlo simulations combined with a bootstrap procedure with $n = 10^4$. 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 not plotted

1.4 Discussion

Cetacean communities release significantly more nutrients through their wastes in temperate latitudes than in tropical latitudes, mirroring patterns of ecosystem productivity (Figs. 1.1 and 1.2). This illustrates a well-known bottom-up process: as predators depend on lower trophic levels, cetacean populations reflect the state of their environment (Moore 2008). Our results highlight how this bottom-up effect creates a ‘nutrient virtuous cycle’: the more productive the trophic base, the more nutrients are recycled through animal-

mediated processes (Smetacek 2021). In addition, this study provides insights into the specific role of small cetaceans, deep divers and baleen whales in marine nutrient cycling, and shows that the role of small cetaceans and deep divers should not be overlooked. In most meso- to eutrophic areas, their relative contribution is up to that of baleen whales for most studied nutrients, even above in the Mediterranean Sea (Fig. 1.6). In tropical and subtropical waters, the productivity is too low to support populations of feeding baleen whales, leaving small cetaceans and deep divers as the only cetacean species involved in nutrient biological cycling in a large part of the world's oceans.

However, the varying amounts of nutrients returned to ecosystems by cetaceans cannot be considered proportional to their importance in ecosystem functioning, as the potential top-down effect of cetaceans on productivity does not necessarily scale with the bottom-up effect of primary productivity on cetacean populations. First, not all cetacean-released nutrients are equally likely to elicit a response from primary producers, depending on local demand. In most tropical and subtropical regions, where N and P are the primary limiting nutrients (Fig. 1.1), it is the N and P fractions of cetacean wastes that are likely to scale with ecosystem response. On the other hand, N and P released in cetacean wastes in High Nutrient Low Chlorophyll (HNLC) areas (*e.g.* Southern Ocean or large regions of the Pacific Ocean) only add to their already high concentrations in these waters, whereas the released Fe could enhance the growth and productivity of primary producers, and thus be more likely to influence ecosystem functioning. It is interesting to note that the relationship between levels of cetacean-released nutrients and local productivity indicators is the strongest for Fe (Fig. 1.2, Table 1.2), identified as either primary or secondary limiting nutrient in half of the fourteen areas included in the study, and in a large part of the world's oceans (Fig. 1.1). At the finer habitat scale, oceanic species of diatoms in temperate, meso- to eutrophic regions require higher Cu concentrations compared to their neritic counterparts, especially in iron-limited areas, due to the role of Cu in Fe acquisition (Guo et al. 2010, Peers and Price 2006). Interestingly, nutrient loads released by cetaceans are richer in Cu in oceanic habitats than in neritic ones (Fig. 1.3). This is likely due to deep divers, largely associated to deep oceanic waters, that release waste products enriched in Cu (Figs. 1.4–1.6). Although not all cetacean-released nutrients are equally relevant to ecosystem functioning, the simultaneous release of nutrients within a highly concentrated cocktail could facilitate the supply of nutrient-ratios optimal for primary producers (Allgeier et al. 2017) and have a synergistic effect by limiting the risk of co-limitation (Shatova et al. 2017).

Furthermore, cetacean-mediated nutrient cycling is probably as important in ecosystem functioning as their relative contribution to shaping the nutrient background in their environment. Primary producers may rely more on animal-mediated nutrient cycling in oligotrophic ecosystems than in meso- to eutrophic ecosystems, which benefit from other sources of supply (Allgeier et al. 2017, Subalusky and Post 2019). The contribution of cetacean communities to nutrient and ecosystem dynamics may be greater where nutrient sources are limited and water column stratification is intense, *i.e.* tropical systems and oceanic waters. This further highlight the potential importance of small cetaceans and deep divers in nutrient biological cycling in the world's oceans. In temperate, meso- to eutrophic areas, the ecological relevance of cetacean-led nutrient cycling is likely more context-dependant (Allgeier et al. 2017) and relative to other nutrient inputs. In the Northwest Atlantic Ocean, our estimate of cetacean N release ($75 [52; 112] \text{ kg.N.km}^{-2}.\text{yr}^{-1}$; [Supplementary Data 1, Table 1.3](#)) is lower than that of Roman and McCarthy (2010) for cetaceans in the Gulf of Maine (around $190 \text{ kg.N.km}^{-2}.\text{yr}^{-1}$; [Table 1.3](#)). These estimates are still of a similar order of magnitude than supplies from physical processes (*e.g.* river discharge and atmospheric deposition, [Table 1.3](#)). In the Mediterranean Sea, cetacean-released N ($52,300 [35,250; 74,800] \text{ t.N.yr}^{-1}$) is equivalent to the natural N background of the Rhône or the Ebro river ($52,339 \text{ t.yr}^{-1}$ and $51,018 \text{ t.N.yr}^{-1}$, respectively), while cetacean-released P ($5700 [3,700; 8,300] \text{ t.P.yr}^{-1}$) is above natural weathering P input of the Rhône, Ebro, Pô and Evros rivers combined (Malagó et al. 2019) ($2,782 \text{ t.P.yr}^{-1}$; [Table 1.3](#)). In the California current area, N released by cetaceans ($49,300 [30,900; 75,800] \text{ t.N.yr}^{-1}$) is 5 times greater than the input from local rivers ($10,000 \text{ t.N.yr}^{-1}$) and 6% of the input from seasonal upwelling ($800,000 \text{ t.N.yr}^{-1}$) (Howard et al. 2014). This demonstrates the potential ecosystemic value of cetacean-mediated nutrient cycling, although comparison is possible only for a few areas and nutrients.

Table 1.3: Nitrogen and phosphorous released by cetacean communities in different study areas (in bold) compared to estimates of nitrogen and phosphorous inputs from other processes and sources

Area	River	Nutrient	Process	Amount (t/yr)	Reference
Mediterranean Sea	Rhône	N	Natural background	52,339	Malagó et al. (2019)
Mediterranean Sea	Rhône	N	Erosion	24,427	Malagó et al. (2019)
Mediterranean Sea	Ebro	N	Natural background	51,018	Malagó et al. (2019)
Mediterranean Sea	Ebro	N	Erosion	14,607	Malagó et al. (2019)
Mediterranean Sea	Pô	N	Natural background	38,978	Malagó et al. (2019)
Mediterranean Sea	Pô	N	Erosion	27,755	Malagó et al. (2019)
Mediterranean Sea	Evros-Maritsa	N	Natural background	22,987	Malagó et al. (2019)
Mediterranean Sea	Evros-Maritsa	N	Erosion	6,676	Malagó et al. (2019)
Mediterranean Sea		N	Cetacean waste products release	5,650 [3,740; 8,320]	This study
Mediterranean Sea	Rhône	P	Natural weathering	883	Malagó et al. (2019)
Mediterranean Sea	Rhône	P	Erosion	9,812	Malagó et al. (2019)
Mediterranean Sea	Ebro	P	Natural weathering	932	Malagó et al. (2019)
Mediterranean Sea	Ebro	P	Erosion	6,275	Malagó et al. (2019)
Mediterranean Sea	Pô	P	Natural weathering	635	Malagó et al. (2019)
Mediterranean Sea	Pô	P	Erosion	8,262	Malagó et al. (2019)

Table 1.3: (continued)

Area	River	Nutrient	Process	Amount (t/yr)	Reference
Mediterranean Sea	Evros-Maritsa	P	Natural weathering	332	Malagó et al. (2019)
Mediterranean Sea	Evros-Maritsa	P	Erosion	2,961	Malagó et al. (2019)
Mediterranean Sea		P	Cetacean waste products re-lease	5,700 [3,700; 8,300]	This study
Gulf of Maine (103,000 km ²)	All rivers	N	Total N	11,2	Roman and McCarthy (2010)
Gulf of Maine (103,000 km ²)		N	Atmosphere	130,260	Roman and McCarthy (2010)
Gulf of Maine (103,000 km ²)		N	Cetacean waste products re-lease	19,6	Roman and McCarthy (2010)
Extended Gulf of Maine (451,985 km ²)		N	Cetacean waste products re-lease	34,400 [23,530; 50,600]	This study
California current		N	Upwelling	750	Howard et al. (2014)
California current	All rivers	N	Total N	10	Howard et al. (2014)
California current		N	Cetacean waste products re-lease	49,270 [30,880; 75,820]	This study

Characteristics of cetacean-released nutrient cocktails – such as absolute quantities and relative nutrient composition, both quantified here, but also nutrient turnover rates in ecosystems, nutrient allochthonous/autochthonous status, and nutrient biochemical properties (sinking rate, chemical speciation) – also shapes their importance in ecosystem functioning. The scale at which individual small cetaceans, deep divers and baleen whales release nutrients is as different as their respective body mass ranges and metabolism, which suggests differences in the magnitude of the ecosystem response to defecation by the three taxa. Small cetaceans and deep divers, however, have higher consumption rates per unit body mass ([Supplementary Data 3](#)) and therefore release more nutrients per unit of cetacean biomass than baleen whales. This means that for an equivalent total biomass, a population of small cetaceans would release more nutrients than a population of whales. In addition, our results show differences in the relative composition of waste products released by small cetaceans, deep divers and baleen whales. Primary producer communities respond differently when fertilised with nutrient cocktails of different composition (Coale 1991, Morel and Price 2003, Shatova et al. 2017). Thus, ecosystem response to defecation by the three taxa could vary both quantitatively and qualitatively, given similar conditions in the recipient ecosystem. The composition of the potential fertiliser released reflects individuals' diet and the nutrient content of their prey (*i.e.* nutrient concentrations and bio-availability) (Evans 1973), which in turn depends on prey taxa and habitat (Chouvelon et al. 2022b,c). For example, Cu is a constituent of hemocyanin, the respiratory pigment of cephalopods and crustaceans. The high consumption of cephalopods by deep diving species (*e.g.* pilot whales *Globicephala*) results in higher levels of Cu in their diet (Chouvelon et al. 2022b) - and thus their waste products ([Supplementary Data 1 & 3](#), [Figs. 1.4 and 1.5](#)), compared to other species. Bony fish have high P contents, which is reflected in higher P levels estimated in the waste of small cetaceans. This illustrates the potential consequences of prey switching (in response to changes in prey quality and/or availability) on the nutrient biological cycling mediated by cetaceans in marine ecosystems. The fact that model outputs are more sensitive to diet nutrient concentration for trace nutrients than for major nutrients is likely due to their higher variability in the composition of functional prey groups (Chouvelon et al. 2022c). Variations in the relative composition of released nutrient loads between taxa, areas and habitats could be underestimated here, due to extrapolations made to apply the model to numerous species in numerous areas. Particularly, we assumed a fixed diet per species, and the compositional dataset for preys compiled samples from a unique area (Northeast Atlantic). While we limited the extent of

these bias using bootstrapping and functional prey groups to describe diets (see Methods), these parameters should be more precisely and locally set for future replication of our approach at finer spatial scales. This could be especially informative in revealing fine-scale patterns of nutrient deposition.

Nutrients released by each taxon also differ in their turnover rates, *i.e.* the time between the assimilation of nutrients in organic matter and their return to ecosystems in a bioavailable form. Even at low concentrations, a rapid turnover can support a greater fraction of primary producers than a slower one (Benitez-Nelson and Buesseler 1999), and thus have a greater impact on the trophic web structure and productivity. Most species of baleen whales feed entirely or partially on zooplankton (Supplementary Data 4), *i.e.* either direct grazers of primary producers or predators of grazers. Thus, the turnover of nutrients released by baleen whales feeding on zooplankton is short compared to that of small cetaceans or deep divers feeding on fish and/or squid species, at much higher trophic levels. In regions such as the Gulf of Alaska or the Northeast and central North Atlantic oceans, where baleen whales are major contributors to the nutrient load released by the cetacean community (Fig. 1.6), the rapid turnover of the nutrients they release could further increase their importance in maintaining primary productivity levels.

Moreover, the origin of the released nutrients, *i.e.* inside the euphotic zone (true recycling) or outside of the euphotic zone (new supply), will affect their potential contribution to ecosystem productivity (Martin et al. 2021). Recycled nutrients might help to maintain primary productivity levels, but new nutrients might stimulate new production. Baleen whales and small cetaceans mostly feed in the euphotic zone (Wursig and Perrin 2009) and mediate the recycling of autochthonous nutrients within it. Deep divers, on the other hand, forage in deeper water layers, routinely below the euphotic zone (around 200 m depth) and as far down as the bathypelagic zone, at depths of up to 3,000 m depth, depending on species. They operate a vertical nutrient transfer, bringing allochthonous nutrients back to the euphotic zone through their wastes¹⁵. In Hawaii, New Caledonia, the French Antilles or French Polynesia, 60 to 80% of the nutrients released by the cetacean community are newly introduced to the euphotic zone through this nutrient pump (Fig. 1.6). This highlights the importance of the nutrient supply provided by deep divers in these oligotrophic regions, where water stratification is intense and growth conditions for primary producers are especially limiting.

An issue that remains unresolved is whether wastes produced by the different cetacean species have the same biochemical properties. The chemical speciation of released nutrients

and how they are retained in the euphotic zone, *i.e.* how much and for how long, are likely to be primary determinants of the ecological importance of the functional characteristics discussed above. Collecting waste from small cetaceans and deep divers is even more challenging than it is already for baleen whales, but experimental designs using products collected from stranded animals may help to reveal their distinctive properties. Such studies could be particularly instructive and would shed new light on current findings and discussions.

Finally, the scale of annual estimates over broad regions obscures the variations in spatial and temporal patterns of nutrient deposition. The actual relative contribution of small cetaceans, deep divers and baleen whales is unlikely to be constant throughout the year. Baleen whales migrate annually between oligotrophic breeding grounds, where they fast, and meso- to eutrophic temperate or polar regions, where they take advantage of the high productivity season to feed intensively (Wursig and Perrin 2009). In contrast, small cetaceans and deep divers feed at a fairly constant rate throughout the year and, although their distribution may vary slightly between seasons (*e.g.* Laran et al. (2017)), they do not perform long-range migrations. Taking the central North Atlantic Ocean area as an example, the relative contribution of baleen whales to Fe release increases from 65% over a year to 86% over a four-month presence period. With the additional contributions of small cetaceans and deep divers over the same period, this means that 76% of the Fe released in a year is actually released in just four months, during the high productivity season. In subtropical and tropical areas, however, nutrient release rates and taxa relative contributions are likely to be fairly constant throughout the year, reflecting the stability of environmental conditions in these regions. The temporal component of these nutrient release patterns is thus important to bear in mind.

Similarly, cetaceans do not uniformly release nutrients across the large areas in which they live. Different species tend to have different habitat preferences and more or less patchy distributions, so they are likely to release their waste in areas with different intrinsic characteristics. Moreover, the size of their aggregations influences the intensity of the nutrient uptake and release events (McInturf et al. 2019, Subalusky and Post 2019). As such, their aggregation behaviours when they forage, travel, socialise or rest near the surface will determine whether they disperse or concentrate nutrients in their environment. For example, deep divers are thought to disperse when foraging at depth (Jensen et al. 2011), but several species form aggregations near the surface, where they release their waste, presumably concentrating nutrients in their environment. These

aggregations can range from a few individuals (*e.g.* beaked whales) to a dozen (*e.g.* sperm whales *Physeter macrocephalus* or Risso's dolphins *Grampus griseus*) or even a few hundred (*e.g.* pilot whales). In contrast, aggregations of baleen whales are more likely to occur when foraging (*e.g.* supergroups of fin whales *Balaenoptera physalus*; Ryan et al. 2023) than when resting, probably facilitating the dispersal of nutrients ingested in nutrient hotspots. Small cetaceans, on the other hand, are commonly observed in groups both when foraging and when resting or socialising near the surface. Although they are less likely to generate nutrient concentration or dispersal patterns, they still facilitate horizontal transfers. This can be particularly important for ecosystem functioning when the intrinsic nutrient characteristics of the donor and recipient ecosystems are significantly different (Subalusky and Post 2019), *e.g.* diurnal movements of spinner dolphins *Stenella longirostris* between offshore waters, where they feed, and lagoons, where they rest, in the Maldives and the Chagos archipelagoes (Letessier et al. 2022).

To conclude, this study provides a broad, worldwide view of cetacean contribution to nutrient biological cycling. Cetacean-mediated nutrient cycling in ocean surfaces varies geographically, quantitatively and qualitatively, and at different spatial and temporal scales. Variations are largely driven by the specific composition of cetacean communities. The complexity of the processes involved renders the role and importance of cetacean-mediated nutrient biological cycling in ecosystem functioning difficult to decipher, but we identified characteristics of both cetacean species and local ecosystems that could matter. Differences in the characteristics of recipient ecosystems, cetacean wastes, and patterns of nutrient deposition accumulate over space and time. Together, they shape the role of small cetaceans, deep divers and baleen whales in ocean nutrient cycling, and determine the importance of these processes in ecosystem functioning. There is still a long way to go in quantifying cetacean contribution to the marine biological carbon pump, but it is difficult to fathom this ecosystem service being replaced by large-scale artificial fertilisation, once considered as a geo-engineering solution to obtain carbon credits (Güssow et al. 2010). Furthermore, the different functional traits of small cetaceans, deep divers and baleen whales mean that the loss of a given population can hardly be substituted by an equivalent biomass of another taxon without altering the role of the community. Thus, the functional diversity of the cetacean community, largely known for their role as top predators, also applies to their role as active nutrient vectors, and may be equally important for local ecosystem dynamics. In the current era of climate change, biodiversity loss, trophic and habitat simplification, our results support the importance of maintaining and restoring

healthy, diverse and abundant cetacean populations in the world's oceans.

Data and code availability

No original data were used nor generated for this analysis which mobilised data from the literature for the setting of a majority of parameters in our bioenergetic model. Sources are provided in the manuscript and in [Supplementary Data 4](#). The latter also includes means and coefficient of variations used to define population abundances and the diet description used for each species using functional groups of prey. The external datasets of prey composition are available at <https://doi.pangaea.de/10.1594/PANGAEA.937345> and <https://doi.pangaea.de/10.1594/PANGAEA.940861> (see Methods). Oceanographic data was downloaded at <https://oceancolor.gsfc.nasa.gov/l3/order/> in March 2022. The download procedure was indicated in a ReadMe file in the corresponding data folder, on the Github repository attached to the study (<https://github.com/Lola-san/Cetacean.excretion.global.git>). Other data used as an input in our model are also available at this link. The data generated in this study are provided in [Supplementary Data 1](#). Source data are provided with this paper.

The code to reproduce the full analysis, originally performed using R Statistical Software (v.4.1.2) (R Core Team 2021), are available on Github (<https://github.com/Lola-san/Cetacean.excretion.global.git>).

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

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

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2.1 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 (Allgeier et al. 2017, Doughty et al. 2016, Ratnarajah et al. 2018, Wing et al. 2014, 2017). Grazing and predation by fauna, and the subsequent release of waste (feces 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, Otero et al. 2018, Ratnarajah et al. 2014, Sparaventi et al. 2021, Wing et al. 2014). 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 fecal 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, Sparaventi et al. 2021, Wing et al. 2014, 2021, 2017). 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 feces, 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 (Lis et al. 2015, Nodwell and Price 2001, 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 feces (Shatova et al. 2017, Smith et al. 2013). 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 (Goetz et al. 2017, Krause et al. 2015, Staniland et al. 2018). However, their role as vectors of limiting micronutrients has received little attention despite iron concentrations in their feces ($950.8 \pm 148.9 \text{ mg.Fe.kg}^{-1}$ 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 feces 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 feces (*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.

2.2 Material and methods

2.2.1 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 $\text{kJ}\cdot\text{day}^{-1}$) 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. 2018, 2012). For an individual i :

$$ADMR_i = \beta_i \times BMR_i = \beta_i \times 293.1 \times BM_i^{3/4} \quad (2.1)$$

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

$$R_i = \frac{ADMR_i}{AE \times E_i} \quad (2.2)$$

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

$$Fe_{d,i} = R_i \times x_{Fe,i} \times r_{Fe} \quad (2.3)$$

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 $\text{t}\cdot\text{yr}^{-1}$):

$$Fe_{tot} = Fe_{d,i} \times 365 \times A \times 10^6 \quad (2.4)$$

2.2.2 Setting model parameters

Five of the seven parameters in our model (BM , β , AE , r , A) were attributed mean values given 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 2.1).

Body mass BM

The average seals' body mass BM (in kg) for each species were taken from ranges found in the literature (Table 2.1). 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 (Hoelzel 2009, Williams et al. 2001), 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 2.1). 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, Mårtensson et al. 1994, Ronald et al. 1984). 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 2.1).

Table 2.1: Bioenergetic parameters' setting information based on literature values

Parameter	Leopard seal <i>H. leptonyx</i>	Crabeater seal <i>L. carcinophagus</i>	Weddell seal <i>L. weddellii</i>	Ross seal <i>O. rossii</i>	References
BM (kg)	$\sim \mathcal{N}(350, 0.2)$	$\sim \mathcal{N}(200, 0.2)$	$\sim \mathcal{N}(300, 0.2)$	$\sim \mathcal{N}(160, 0.2)$	^a
β	$\sim \mathcal{N}(3, 0.5, 2, 3.5)$	$\sim \mathcal{N}(2, 0.5, [1.5, 3])$	$\sim \mathcal{N}(2, 0.5, [1.5, 3])$	$\sim \mathcal{N}(2, 0.5, [1.5, 3])$	^b
AE	$\sim \mathcal{N}(0.9, 0.05, [0.80, 0.95])$	^c			
E (kJ.kg ⁻¹)	$\sim \mathcal{N}(12.1, 0.2 \times 12.1, [0.2 \times 12.1])$	$\sim \mathcal{N}(5.1, 0.2 \times 5.1, [0.2 \times 5.1])$	$\sim \mathcal{N}(5.4, 0.2 \times 5.4, [0.2 \times 5.4])$	$\sim \mathcal{N}(4.8, 0.2 \times 4.8, [0.2 \times 4.8])$	see Eqs. (2.5) and (2.6) & 2.2
x_{Fe}	$\sim \mathcal{N}(165, 0.2 \times 165, [0.2 \times 165])$	$\sim \mathcal{N}(10.1, 0.2 \times 10.1, [0.2 \times 10.1])$	$\sim \mathcal{N}(22.6, 0.2 \times 22.6, [0.2 \times 22.6])$	$\sim \mathcal{N}(15.6, 0.2 \times 15.6, [0.2 \times 15.6])$	see Eqs. (2.5) and (2.6) & Table 2.2
r_{Fe}	$\sim \mathcal{U}(0.7, 0.9]$	$\sim \mathcal{U}(0.7, 0.9]$	$\sim \mathcal{U}(0.7, 0.9]$	$\sim \mathcal{U}(0.7, 0.9]$	^d
A (No.)	$\sim \mathcal{N}(35500, 22925, [10900 - 102600])$	$\sim \mathcal{N}(5869400, 1229325, [3699400 - 8616700])$	$\sim \mathcal{N}(633000, 278500, [221000 - 1335000])$	$\sim \mathcal{N}(78500, 47950, [39400 - 231200])$	^e

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: $\sim \mathcal{N}(\text{mean}, \text{standard deviation}, [\text{lower limit}, \text{upper limit}])$, if only one number in brackets, it is the lower limit

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

^bCastellini et al. (1992), Hoelzel (2009), Renouf and Gales (1994)

^cAshwell-Erickson and Elsner (1981), Fisher et al. (1992), Goodman-Lowe et al. (1999), Keiver et al. (1984), Lawson et al. (1997), Martensson et al. (1994), Mårtensson et al. (1994), Ronald et al. (1984), Rosen and Trites (2000), Stanberry (2003)

^dCandela et al. (1984), Lavery et al. (2010), Ratnarajah et al. (2014)

^eSouthwell et al. (2012)

Iron release rate r_{Fe}

Adult mammals (excluding pregnant and lactating females) release most consumed micronutrients - including iron - through feces, 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 0.90 (Table 2.1).

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 2.1).

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 2.2). 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 Casaux et al. 2009, Forcada et al. 2009, Hall-Aspland and Rogers 2004) (Table 2.2).

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

Table 2.2: 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} ($\text{kJ}\cdot\text{g}^{-1}$)	Mean iron content $x_{Fe,pg}$ ($\text{mg}\cdot\text{kg}^{-1}$ wet weight)	% in diet (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

^aArmstrong and Siegfried (1991), Kjørboe (2013), Martensson et al. (1996), Ruck et al. (2014)

^bBarbante et al. (2000), Caroli et al. (1998), Kim et al. (2014), Nicol et al. (2010), Palmer Locarnini and Presley (1995)

^cChouvelon et al. (2022b,c), Tierney et al. (2002)

^dChouvelon et al. (2022b,c), Goutte et al. (2015), Honda et al. (1987)

^eChouvelon et al. (2022b,c), Croxall and Prince (1982)

^fChouvelon et al. (2022b,c), Lourenço et al. (2009)

^gForcada et al. (2009)

^hJulshamn and Grahl-Nielsen (2000), Noda et al. (1995), Yamamoto et al. (1987)

ⁱForcada et al. (2009)

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

prey samples from 9 studies and 300 prey samples from 17 studies (see Table 2.2 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 (Tables 2.1 and 2.2):

$$E = \sum_{pg} W_{pg} \times E_{pg} \quad (2.5)$$

$$x_{Fe} = \sum_{pg} W_{pg} \times x_{Fe,pg} \quad (2.6)$$

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. Jerez et al. 2013b, Kim et al. 2014, Ruck et al. 2014, Yamamoto et al. 1987). 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.

2.2.3 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 -value ≤ 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 results 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).

2.2.4 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/FeSth0pinn.git>).

2.3 Results

Statistics associated to all parameters of the model as a result of Monte-Carlo simulations (Table 2.1) and calculations from the bioenergetic model (Eqs. (2.1)–(2.6), Table 2.2) are available in Chapter 2 - Supplementary Data 1.

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 (largest and most metabolically active species; Table 2.1) (Table 2.3). 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 2.3). 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. 2.1).

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 [12 - 105] 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. 2.1, Table 2.3). Together, these four species release 208 [104 - 378] t.Fe.yr⁻¹ through their feces (Fig. 2.2). 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. 2.2 and references therein, Chapter 2 - Supplementary Data 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] t.Fe.yr⁻¹)

Table 2.3: 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

Model parameter	Leopard seal	Crabeater seal	Weddell seal	Ross seal
Average daily metabolic rate (kJ.day ⁻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.day ⁻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]	152 [60 - 316]	44 [12 - 105]	3 [1 - 8]

and Antarctic fin whales (367 [193 - 590] t.Fe.yr⁻¹), respectively.

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. 2.3). In contrast, the assimilation efficiency AE and iron release rate r_{Fe} have very little influence on the model output.

2.4 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 feces of pack-ice seals inhabiting the SO. Based on these quantitative results,

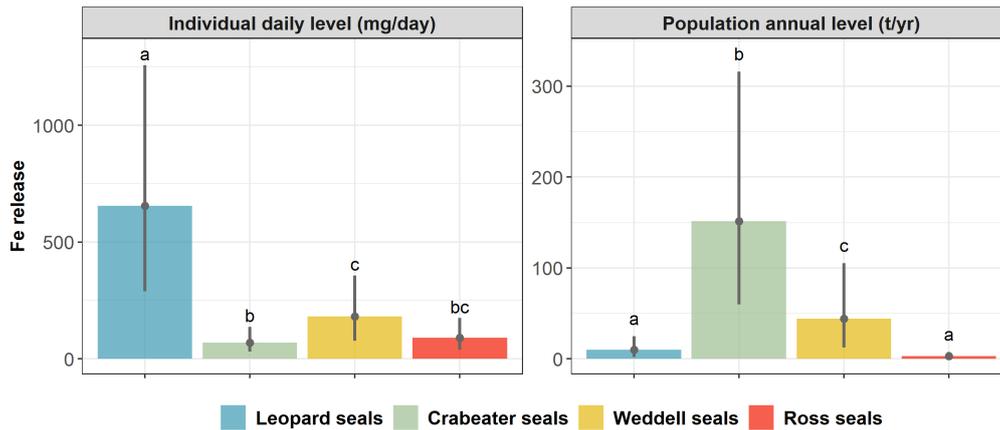


Figure 2.1: **Iron released in the feces of Southern Ocean leopard, crabeater, Weddell and Ross seals.** Individual, daily level (left panel, vertical axis in mg per day) and populational annual level (right panel, vertical axis in tonne per year), as estimated by means of a bioenergetic model. Central 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 Section 2.2.3): 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 ($p > 0.05$)

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.

2.4.1 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

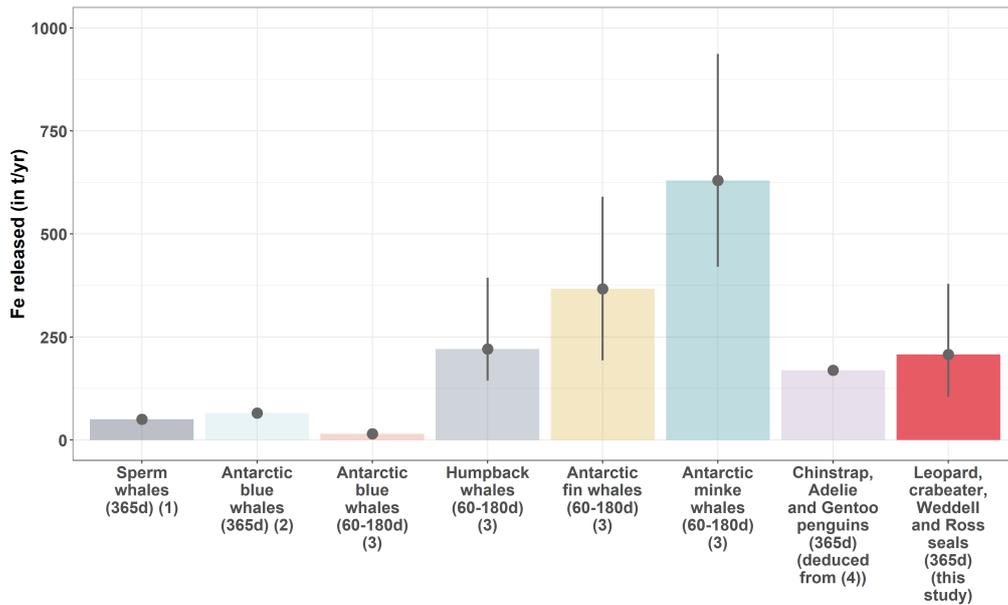


Figure 2.2: **Iron released by different Southern Ocean species of megafauna.** Data is from literature and present study:(1) Lavery et al. (2010), (2) Lavery et al. (2014), (3) Savoca et al. (2021), (4) Sparaventi et al. (2021). The number of days during which species were considered present in the 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 [Chapter 2 - Supplementary Data 2](#)

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, Ratnarajah et al. 2014, 2016b, Ruck et al. 2014). 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

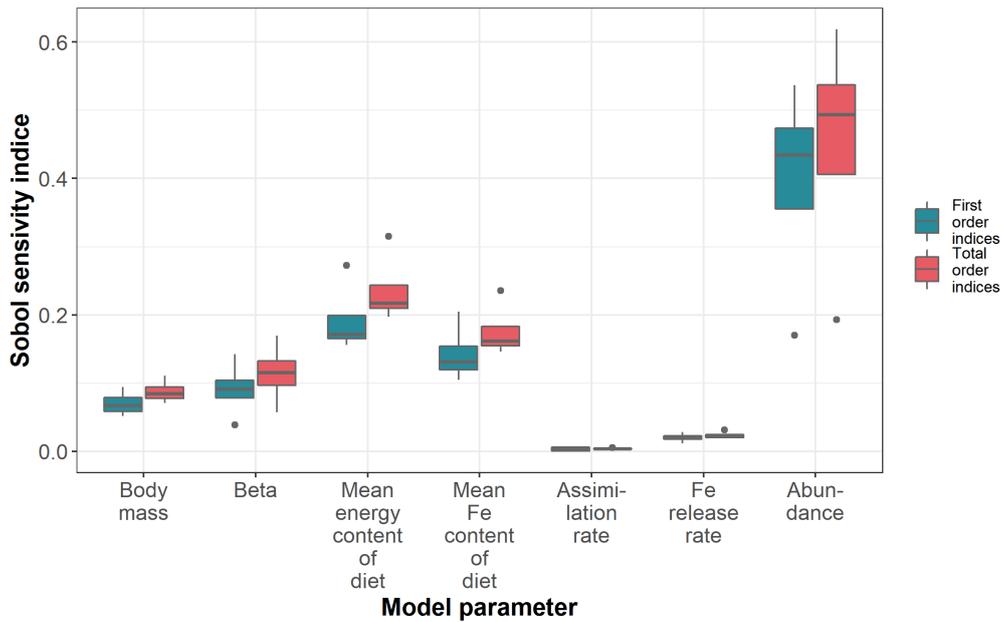


Figure 2.3: **Estimates of first-order and total order Sobol sensitivity indices of the bioenergetic model parameters.** The seven parameters input used to estimate iron released by leopard, crabeater, Weddell and Ross seals in the Southern Ocean included seal body mass, species-specific metabolic multiplier 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

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 2018b). Furthermore, some of our intermediary output parameters, such as daily prey intake, including as a percent of body mass (Table 2.3), are within the range of those previously published for pinnipeds (e.g. Hoelzel 2009, Nilssen et al. 2019, Trites and Spitz 2018b). This provides confidence in our model outputs (Table 2.3 and Chapter 2 - Supplementary Data 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 defecate 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.

2.4.2 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 2.3), 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 fecal 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 feces 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 2.3) because they are by far the most numerous (Southwell et al. 2012; Table 2.1). 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 2.1), 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. 2.2). 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 (Lannuzel et al. 2016b, Martensson et al. 1996). The dependence of pack-ice seals on sea ice also makes their spatial distribution relatively complementary to that of whales (Hoelzel 2009, Laws

1977). 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 (Hucke-Gaete et al. 2004, Laws 1994). 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. 2019a). 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.

2.4.3 Functional characteristics of the contribution of pack-ice seals to Southern Ocean biological iron cycling

Spatial segregation and aggregation

Dispersal ranges of crabeater, Weddell, leopard and Ross seals greatly overlap around the Antarctic continent (Fig. 2.4), but these four species do not display the same habitat preferences (Fig. 2.5). 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 (Bengtson et al. 2011, Southwell et al. 2008) whereas Weddell seals are primarily bound to fast-ice and nearby pack-ice, relying on breathing holes to navigate between ice-floes (Davis et al. 2013, Goetz et al. 2017, Shirihai 2008, Southwell et al. 2012, Thomas and Terhune 2009). 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 (Genovese et al. 2023, Lannuzel et al. 2016b). 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 (Arcalis-Planas et al. 2015, Brault et al. 2019, Thomas and Rogers 2009). 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. 2.4) and are regular visitors to subantarctic islands and southern continents (Krause et al. 2015, Nordøy and Blix 2009, Rogers 2009, Staniland et al. 2018, Walker et al. 1998). 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.

In addition to these species-specific aggregation patterns, there may be some overlap

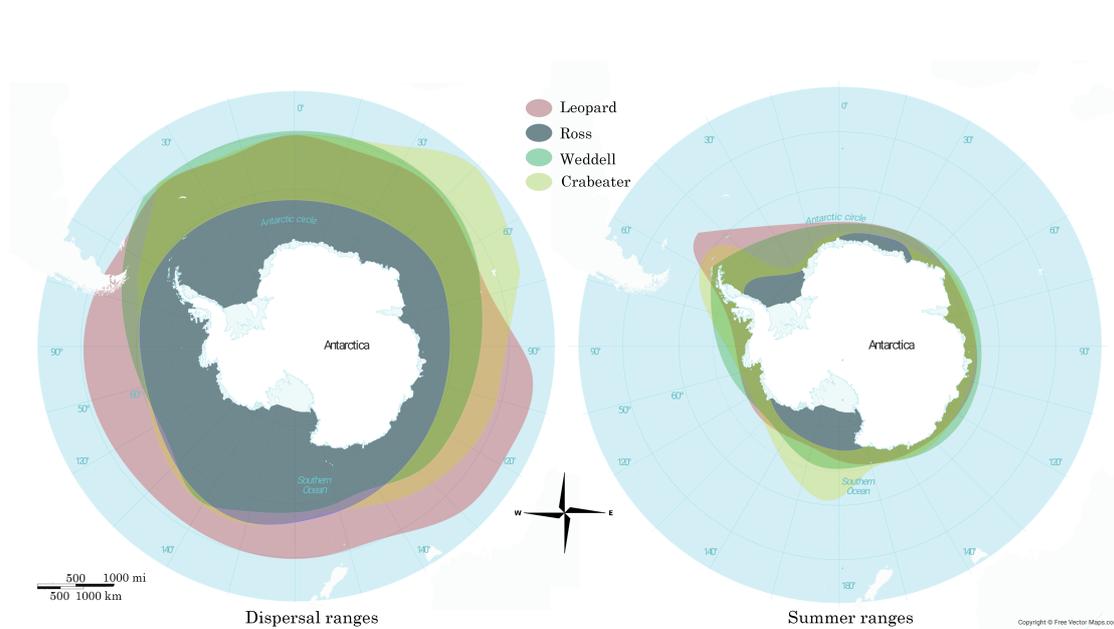


Figure 2.4: Dispersal and summer ranges of leopard, Weddell, crabeater and Ross seals in the Southern Ocean (adapted from Shirihai 2008, original map by [FreeVectorMaps.com](https://www.freevector.com))

between the four species, particularly in summer (Fig. 2.4) 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.

Horizontal iron transfers

Pack-ice seals are highly mobile predators. They can travel several kilometres on a single dive (e.g. Weddell seals; Davis et al. 2013, Thomas and Terhune 2009) and up to 11

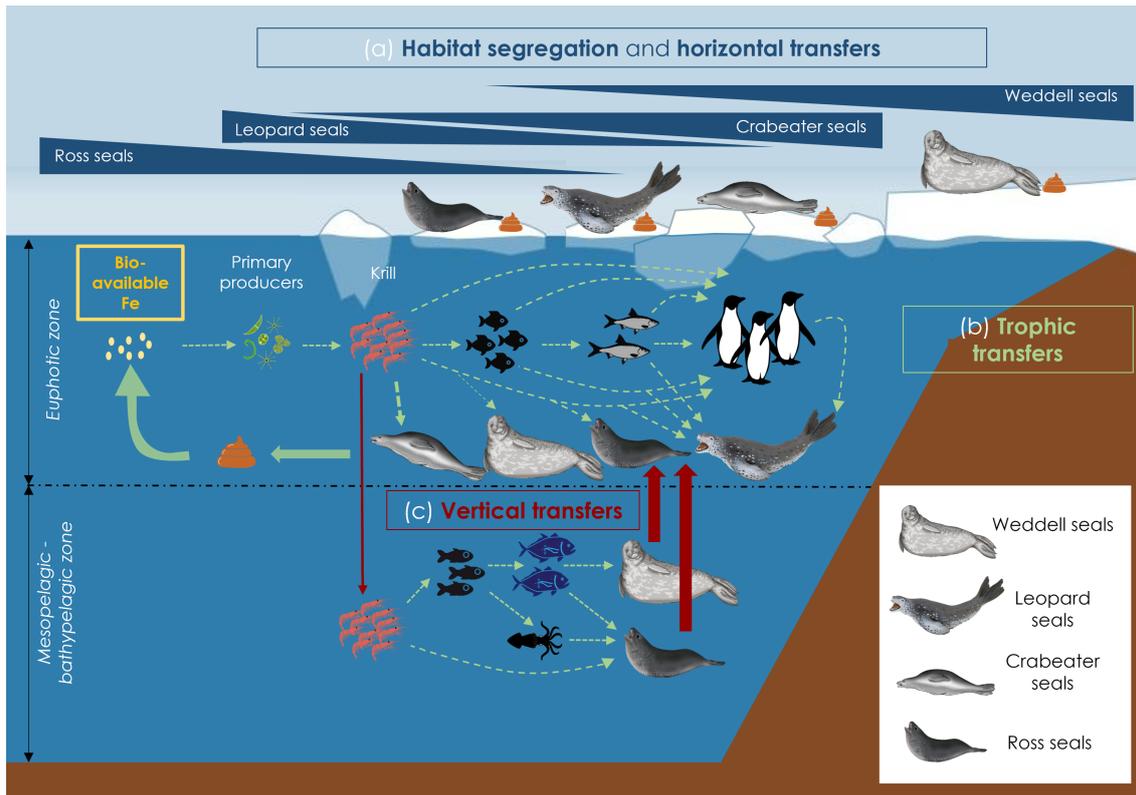


Figure 2.5: **Conceptual diagram showing functional traits of the contribution of leopard, crabeater, Weddell and Ross seals to iron (Fe) cycling in the Southern Ocean** through (a) habitat segregation and horizontal transfers (blue triangles indicating relative time spent in habitats including fast-ice, 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)

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; Figs. 2.4 and 2.5). 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. 2.5, Table 2.2). 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 (Nordøy and Blix 2009, Shirihai 2008, 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 (Davis et al. 2013, Southwell et al. 2012). 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 2.2, Fig. 2.5). 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 and Bowie 2016, Ratnarajah et al. 2014, 2018). 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 (Brault et al. 2019, Zhao et al. 2004), 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 feces has thus a slower turnover rate than that of crabeater seals that feed primarily on krill (Brault et al. 2019, Zhao et al. 2004). 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.

2.4.4 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 feces 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 feces 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 feces 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, Shatova et al. 2016, Sparaventi et al. 2021, Wing et al. 2014, 2021, 2017). 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 feces 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.

2.4.5 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.

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 Tables 2.1 and 2.2). Statistics of estimates used to generate Fig. 2.1 are provided in Table 2.1 and Chapter 2 - Supplementary Data 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 Fig. 2.3 are provided in Chapter 2 - Supplementary Data 1. Fig. 2.4 was made based on Shirihai (2008), with the base map originating from <https://freevectormaps.com>. Fig. 2.5 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/FeSth0pinn.git>.

Differential concentrations of essential nutrients in forage fish prey and predator's feces and implications for nutrient cycling

The rich nutrient content of the feces of amphibious and air-breathing predators (e.g. seals, seabirds) suggests that their defecation may facilitate nutrient recycling at lower trophic levels of the food webs, either in marine ecosystems when they are at sea, or in terrestrial ecosystems when they are on land at their colonies. This biological cycling of nutrients mediated by these predators is largely determined by their diet and the nutrient composition of their prey. Here, we analyse the concentrations of 5 major nutrients and 8 trace nutrients in 34 species of forage fish which could be preyed on by such predator, along with feces (scats) of one of them, the Antarctic fur seal *Arctocephalus gazella*, around the Kerguelen Islands (Southern Indian Ocean). Both fish and scats showed variability in their nutrient concentrations, with greater variability in fur seal scats. Using hierarchical clustering, we show that some fish species are enriched in nutrients found in limited concentrations in Southern Ocean surface waters, such as iron (Fe) and manganese (Mn), while others are enriched in nutrients that may be limiting for primary producers in terrestrial ecosystems, such as phosphorus (P) or calcium (Ca). These fish species could be major contributors to the biological cycling of these nutrients as a result of predation. On the other hand, Antarctic fur seal scats were enriched in trace nutrients compared to fish, with the majority enriched in Fe and to a lesser extent Mn. A smaller group of scats were enriched in major nutrients, particularly P and Ca. This variability in fur seal scats nutrient content suggest some similar variability in the potential response of lower trophic levels to this nutrient supply. In the context of local ecosystem nutrient dynamics, our results provide some insight into the role of fur seal scats as a potential fertiliser in the fur seal environment and the indirect role of different fish species as potential prey in these processes.

This chapter is a manuscript in preparation

3.1 Introduction

Animal-mediated nutrient cycling is increasingly recognised as an important component of nutrient cycling in ecosystems (Subalusky and Post 2019). Not only do they facilitate nutrient recycling in ecosystems via the consumption of prey and the subsequent defecation and urination of undigested matter and metabolic wastes, but they are also active vectors that can spatially transfer nutrients within and between ecosystems, possibly against abiotic forces (McInturf et al. 2019).

In oceans, air-breathing predators such as cetaceans, pinnipeds and seabirds have been shown to significantly contribute to the release of limiting nutrients in surface waters when they deposit their nutrient rich 'fertiliser' while breathing or resting at the surface (Lavery et al. 2010, Otero et al. 2018, Roman et al. 2014, Wing et al. 2014; Chapter 1). As nutrient paucity in surface waters can limit primary producers growth and productivity in large areas of the world's oceans (Moore et al. 2013), these nutrients may be partially returned to organic production through phytoplankton uptake (either directly or after remineralisation by the microbial community), thereby affecting ecosystem functioning and productivity (Roman et al. 2014, Roman and McCarthy 2010). In addition, pinnipeds and seabirds divide their time between foraging at sea and breeding, moulting and resting on land where they also defecate, introducing significant amounts of marine-derived nutrients into coastal ecosystems (Ball et al. 2015, Lavery et al. 2015). These sea-to-land nutrient transfers may be critical for terrestrial ecosystem functioning in areas where external nutrient sources might be scarce, such as on Antarctic and sub-Antarctic islands (Bokhorst et al. 2019a, 2007, Smith 2008). This amphibious lifestyle therefore distinguishes pinnipeds and seabirds as singular nutrient vectors compared to other air-breathing megafauna that remains at sea all lifelong (*e.g.* whales, dolphins).

The importance of specific nutrients in a given ecosystem, and thus the importance of the predator mediated-nutrient cycling, depends on its nutrient background, its biological activity, and its biological nutrient demand. A wide range of nutrients is essential to all forms of life and have the potential to limit productivity if their concentrations in the environment are too low. For example, in the Southern Ocean (SO), iron (Fe) is the primary limiting nutrient, *i.e.* any addition of bioavailable Fe to surface waters is likely to elicit a positive response from primary producers if conditions are favourable (Hassler et al. 2012a). However, manganese (Mn) is co-limiting with Fe in some areas (Browning et al. 2021), and zinc (Zn) and cobalt (Co) concentrations have also been shown to

limit productivity of some Antarctic phytoplankton species (Koch and Trimborn 2019). The nutrient characteristics of ecosystems may therefore differ in different parts of the oceans (Moore et al. 2013), and they may differ even more between oceanic and terrestrial ecosystems. While trace nutrients tend to limit ocean productivity at high latitudes, major nutrients such as nitrogen (N) or phosphorus (P) tend to be the main biochemical limiting factor in high-latitude terrestrial ecosystems (excluding abiotic factors such as light, temperature and water input) (Bokhorst et al. 2019a, Smith 1977, Wasley et al. 2006). Multi-dimensional approaches to animal-mediated nutrient cycling are therefore a necessary step towards a better understanding of nutrient transfers within and between ecosystems.

Multiple nutrients may also interact and co-vary in the environment (Sterner and Elser 2008), either positively (e.g. Fe and Mn, Bucciarelli et al. 2001) or negatively (e.g. Mn and Zn, Hawco et al. 2022) due to their biochemical affinity or physiological processes. This includes different biological compartments, such as predator prey and their waste products. Although studies characterising the role of marine predators in nutrient cycling processes have evidenced the significant influence of predator diet and prey composition on the amounts of nutrient released (or nutrient concentrations in feces), the analysis of the nutrient concentrations in predator feces has rarely been carried out together with the analysis of their prey, and even less so for multiple nutrients. On the other hand, estimating the release of multiple nutrients in waste products using bioenergetic models requires multi-nutrient compositional prey data, which are scarce and likely to vary in space and time (Machovsky-capuska and Raubenheimer 2020).

Yet, prey species enriched in a given nutrient could play a relatively great role in nutrient cycling, as their consumption by predators would result in specifically enriched fecal material. In the SO for example, krill concentrates Fe, and this limiting nutrient can be returned to surface waters after being consumed by marine mammals or seabirds (Ratnarajah et al. 2014, Sparaventi et al. 2021, Wing et al. 2014). Such 'super-contributing' prey can be found for different nutrients in different taxa, including fish and cephalopods, and in all ecosystems (e.g. Chouvelon et al. 2022b,c), but their contribution to predator-mediated nutrient cycling has been largely overlooked. They may also differ depending on which nutrient is of primary interest in a particular ecosystem context. As prey nutrient concentrations are likely to shape the variability of predator-mediated nutrient cycling (outside of traits such as abundance, life stage and behaviour), the lack of prey composition data for a large range of nutrients may hamper our understanding of the role of predators

(and prey) in these processes.

In this context, this study focuses on the multi-nutritional content of a broad range of forage fish species around the sub-Antarctic Kerguelen Archipelago (southern Indian Ocean), and feces (scats) of one of the local top predators, the Antarctic fur seal (*Arctocephalus gazella*). Antarctic fur seals gathers on the shores of the Kerguelen Islands to form breeding colonies for four months in the Austral Summer. During this time, female fur seals alternate between short nursing bouts on land and foraging trips at sea (Jeanniard-du Dot et al. 2017b). The goals of this study were to (i) assess the variability in the nutrient content of potential fish prey and identify potential 'super-contributors' to the biological cycling of specific nutrients around the Kerguelen Islands, (ii) assess the variability in nutrient concentrations in Antarctic fur seal scats and (iii) compare the relative nutrient composition of both biological matrices, *i.e.* potential fish prey and their predators' scats. In this study, we focused on five major (phosphorous P, calcium Ca, sodium Na, potassium K, magnesium Mg) and eight essential trace nutrients (Fe, copper Cu, Zn, Mn, nickel Ni, cobalt Co, selenium Se, arsenic As). However, the multi-nutritional datasets for fish and scat composition also include the essential trace nutrients chromium Cr, molybdenum Mo, strontium Sr, vanadium V, although they were below quantification limits in most samples, as well as potential contaminants (cadmium Cd, lead Pb, and silver Ag). The complete datasets will be made available in InDoRes (for *Inventaire des Données de la Recherche en Environnement et Sociétés*, see <https://www.indores.fr/>), a securised data repository.

3.2 Material & Methods

3.2.1 Fish and scat sampling

We collected 264 individuals of 34 forage fish species (22 of which were previously identified as part of the Antarctic fur seal diet, Cherel et al. 1997, Jeanniard-du Dot 2015, Lea et al. 2002a, 2008) during two ship-based sampling campaigns on and around the Kerguelen Plateau (Table 3.1). The first sampling campaign took place on the eastern slope waters of the Kerguelen Islands (49°05'–49°20'S, 71°15'–72°15'E) on the 25 m-long *La Curieuse* vessel in January 2005, and aimed to sample the mesopelagic fauna. Fishing operations were carried out at night, with an International Young Gadoid Pelagic Trawl (IYGPT) with 12 m × 7 m opening and 10 mm cod-end mesh deployed for 30-min at constant speed, at depth varying from 50 to 425 m (Cherel et al. 2010, Duhamel et al. 2000).

Most samples caught during this campaign (n = 167) were myctophids (n = 119). The second sampling campaign (named 'Poker 2') took place from August to October 2010 on the 77 m-long trawler *FV Austral*. It focused on the demersal fauna and yielded the remaining 97 fish samples. Two hundred stations from shelf and deepsea habitats were sampled during 30-min day trawling operations using a bottom trawl (35 m headline/39 m footrope, reference: G2035013 from Le Drezen: www.ledrezen.com) with a 40 mm cod-end mesh (Duhamel et al. 2017). For both campaigns, fish were sorted on board after initial identification and then kept frozen at -20°C until processing. Identification was again confirmed before sample processing relying on fish external features using published guides (Hulley 1981) and our own reference collection.

We collected 58 Antarctic fur seal fecal samples on two colonies on the Kerguelen Islands, at Cap Noir (49°07' S 70°45' E, 27 samples) and at Pointe Suzanne (49°44' S 70°44' E, 31 samples) during the 2021-2022 austral summer. Samples were collected on the colony in clean plastic bags and were of varying degrees of freshness. Scats were not identified to any individual, so it is unknown whether they were emitted by mature males, females or immature individuals. However, mature females are more numerous in colonies (Guinet et al. 1996, Page et al. 2003), so they are more likely to be from females. Samples were stored at -20°C within 48 hours of collection and until processing.

3.2.2 Sample processing

Each fish was thawed, rinsed with ultrapure water, measured, weighed and ground in the laboratory in a clean and contamination-free setting before being stored at -20°C. All material was carefully rinsed with ultrapure water and ethanol between samples to avoid contamination. Samples were then freeze-dried for a minimum of 72 hours and ground to a fine powder until analysis.

Table 3.1: **Characteristics of forage fish species analysed for nutrient composition.** Species identified as prey of Antarctic fur seals (*Arctocephalus gazella*) are identified with references indicated, location being restricted to around Kerguelen. Preferential habitat is attributed based on our own expertise and data from [FishBase](#) and n is the number of individuals per species. Samples were collected during two field campaigns in 2005 and 2010. SD is standard deviation

Family	Species	Identified as Antarctic fur seal prey	Preferential habitat	n	Standard length (mm) (min -max)	Moisture % (mean \pm SD)
Achiropsettidae	<i>Mancopsetta man-copsetta</i>	no	Demersal	2	21 - 28	73 \pm 1
Bathydraconidae	<i>Bathyraco antarcticus</i>	no	Bathydemersal	5	16 - 18	73 \pm 2
Bathylagidae	<i>Bathylagus tenuis</i>	no	Mesopelagic	11	8 - 17	75 \pm 5
Carapidae	<i>Echiodon cryomargarites</i>	no	Bathydemersal	10	28 - 39	79 \pm 1
Channichthyidae	<i>Champscephalus gunnari</i>	yes ^{a-d}	Benthopelagic	10	19 - 28	79 \pm 3
	<i>Channichthys rhinocerotus</i>	no	Demersal	10	14 - 24	76 \pm 1
Gempylidae	<i>Paradiplospinus gracilis</i>	yes ^{b, c, e}	Benthopelagic	10	29 - 35	70 \pm 3
Macrouridae	<i>Macrourus carinatus</i>	no	Bathydemersal	10	17 - 29	74 \pm 3
Melamphaidae	<i>Poromitra crassiceps</i>	no	Mesopelagic	1	12	71
Microstomatidae	<i>Nansenia antarctica</i>	yes ^{c, e}	Mesopelagic	5	20 - 22	70 \pm 3
Muraenolepididae	<i>Muraenolepis</i> sp	yes ^c	Benthopelagic	10	18 - 30	76 \pm 3

Table 3.1: (continued)

Family	Species	Identified as Antarctic fur seal prey	Preferential habitat	n	Standard length (mm) (min -max)	Moisture % (mean \pm SD)
Myctophidae	<i>Electrona antarctica</i>	yes ^{a-f}	Mesopelagic	10	6 – 7	67 \pm 2
	<i>Electrona carlsbergi</i>	yes ^{a, c-e}	Mesopelagic	10	8 – 10	69 \pm 3
	<i>Electrona subaspera</i>	yes ^{a-f}	Mesopelagic	10	6 – 12	72 \pm 2
	<i>Gymnoscopelus bolini</i>	yes ^{a-e}	Mesopelagic	10	13 – 22	66 \pm 1
	<i>Gymnoscopelus braueri</i>	yes ^{a-d}	Mesopelagic	12	9 – 12	64 \pm 1
	<i>Gymnoscopelus fraseri</i>	yes ^{b-f}	Mesopelagic	12	7 – 8	71 \pm 2
	<i>Gymnoscopelus nicholsi</i>	yes ^{a-f}	Mesopelagic/epibenthic	10	12 – 13	68 \pm 2
	<i>Gymnoscopelus piabilis</i>	yes ^{b-f}	Mesopelagic/epibenthic	10	12 – 15	68 \pm 2
	<i>Krefftichthys anderssoni</i>	yes ^{a-f}	Mesopelagic	4	5 – 5	69 \pm 1
	<i>Protomyctophum andria-shevi</i>	yes ^{c-d}	Mesopelagic	4	4 – 5	75 \pm 1
	<i>Protomyctophum bolini</i>	yes ^{a-f}	Mesopelagic	10	4 – 5	72 \pm 4
	<i>Protomyctophum chori-odon</i>	yes ^{b-f}	Mesopelagic	8	6 – 6	73 \pm 1
	<i>Protomyctophum tenisoni</i>	yes ^{b-f}	Mesopelagic	10	4 – 5	71 \pm 2

Table 3.1: (continued)

Family	Species	Identified as Antarctic fur seal prey	Preferential habitat	n	Standard length (mm) (min -max)	Moisture % (mean \pm SD)
Notosudidae	<i>Luciosudis normani</i>	no	Mesopelagic	1	23	74
Nototheniidae	<i>Dissostichus eleginoides</i>	yes ^a	Demersal	2	26	75 \pm 3
	<i>Gobionotothen acuta</i>	yes ^{b, c, e}	Demersal	8	16 – 21	75 \pm 2
	<i>Lepidonotothen squamifrons</i>	no	Benthopelagic	10	9 – 20	73 \pm 2
	<i>Lindbergichthys mizops</i>	no	Benthopelagic	7	5 – 15	73 \pm 4
Paralepididae	<i>Arctozenus risso</i>	no	Mesopelagic	3	22 – 24	74 \pm 1
	<i>Notolepis coatsi</i>	no	Mesopelagic	10	6 – 9	73 \pm 5
Stomiidae	<i>Iliacanthus atlanticus</i>	no	Mesopelagic	1	40	67
	<i>Stomias</i> sp	no	Mesopelagic	10	15 – 23	74 \pm 5
Zoarcidae	<i>Melanostigma gelatinosum</i>	yes ^c	Mesopelagic	10	18 - 26	83 \pm 2

^aGreen and Williams (1986); ^bCherel et al. (1997); ^cGuinet et al. (2001); ^dLea et al. (2002a); ^eLea et al. (2008); ^fJeanniard-du Dot et al. (2017b)

Fecal samples were also individually thawed, cleaned of large plant debris, weighted and stored at -20°C before being freeze-dried for a minimum of 72 hours and ground to fine powder until analysis. The time between the last meal and the deposition of scats is likely to vary. During the breeding season, female Antarctic fur seals come ashore for 2-4 days while mature males fast to defend their harems (Jeanniard-du Dot 2015), and less is known about the behaviour of immatures. However, scat composition may vary depending on the stage of digestion of the animal and after a period of fasting. We reported the absence or presence of hard parts (*i.e.* fish bones and otoliths, cephalopod beaks, lenses or crustacean remains) in fecal samples as a possible indicator of the last meal proximity, by using a boolean "hard part index" (HPI). On the 58 samples, 10 had a HPI of 0 (*i.e.* no hard parts) and 40 a HPI of 1 (*i.e.* some hard parts).

3.2.3 Multi-nutrient composition analysis

Total concentrations of major constitutive chemical elements in biological tissues (P, Ca, K, Na, Mg) were determined by inductively coupled plasma atomic emission spectrometry (ICP-OES, Vista-Pro Varian). Aliquots of samples (~250 mg dry mass of homogenised powder) were digested using a 6:2 (v/v) mixture with nitric acid (HNO₃ 69%, Trace Metal Grade®, FisherScientific) and hydrochloric acid (HCl, 34%, Trace Metal Grade®, FisherScientific). Acidic digestion of the samples was performed over-night at room temperature and then in a microwave oven (START-D, Milestone). Finally, the digestats were diluted to 50 mL with ultrapure water before analyses with ICP-OES. Total concentrations of essential trace nutrients (As, Co, Cu, Fe, Mn, Ni, Se, Zn) were determined by inductively coupled plasma mass spectrometry (ICP-MS, ICAP-Qc ThermoFisher). Aliquots of samples (~200 mg dry mass of homogenised powder) were placed in Teflon bombs and mineralized with a mixture of ultrapure HNO₃ acid (PlasmaPure Plus grade, SCP Science®) and ultrapure water using a micro-wave (ETHOS-UP, Milestone). The digests were then diluted to 50 mL with ultrapure water before analyses with ICP-MS. The quality assurance of all metal analyses relied on blank and internal standard controls, and on the accuracy and reproducibility of data relative to the certified reference materials (CRMs) used in each analytical run. Blank values were systematically below the detection limits and CRM values concurred with certified concentrations.

3.2.4 Nutritional variability and multi-nutrient typology of forage fish and Antarctic fur seals scats

We first estimated the variability in nutrient concentrations of fish species and fur seal scats separately with a nutrient-by-nutrient approach, using basic descriptive statistics and boxplots. We also assessed co-variation between nutrients using correlation matrices. We used Mann-Whitney-Wilcoxon (MWW) non-parametric tests to compare (i) concentrations of forage fish previously identified as part of the Antarctic fur seal diet around the Kerguelen Islands vs never identified as part of it, (ii) concentrations in fecal samples collected on the two colonies, and (iii) concentrations in fecal samples with different HPI.

Second, we used hierarchical clustering (HC) on forage fish samples and fur seal scats separately to (i) identify relative similarity between samples and groups of samples in terms of concentrations in multiple nutrients, and (ii) identify nutrients that are the most discriminating between these groups. Clustering with high dimension can cause problems in differentiating similar and dissimilar objects, and this "curse of dimensionality" can occur with as few as ten dimensions (Assent 2012). Consequently, we performed a principal component analysis (PCA) to reduce the number of dimensions of the datasets (originally, 13 nutrients thus dimensions). We then used coordinates of samples on the first principal components of the PCA as an input for the HC analysis, selecting the first principal components that together explained at least 90% of the datasets' variance (5 for forage fish and 2 for Antarctic fur seal scats).

Classical statistical methods (such as PCA and HC) can be deemed unsuitable to analyse composition data, because they rely on Euclidean geometry (Filzmoser et al. 2018). Thus, we used algorithms designed for composition datasets using `Robcomposition` R package (Filzmoser and Hron 2009, Filzmoser et al. 2018, Templ and Templ 2021). Correlation coefficients between composition parts were based on symmetric pivot coordinates, and data was transformed to be expressed in isometric log-ratio coordinates before performing a robust PCA (Filzmoser and Hron 2009, Filzmoser et al. 2009, Templ and Templ 2021). By using PCA to reduce the number of dimensions of the datasets, the input for the hierarchical clustering was no longer compositional in nature, so we used a classical algorithm with Ward's minimum variance method (Ward 1963). We estimated the optimal number of clusters using dendrograms and standard validating measures (e.g. average and median distance between clusters, minimum cluster size). We also assessed nutrient-by-nutrient differences between clusters using MWW tests. Some forage fish species or families were over represented in the dataset (e.g. myctophids with $n = 119$;

Table 3.1), so we used nutrient concentrations averaged by species for the statistical analysis (PCA and HC) to supply similar statistical weight for each species. We detected 5 outliers in fish samples with extreme high values for one nutrient. These values were replaced with values of the 97.5% percentile (calculated with all forage species samples) to keep the samples while limiting their influence in the statistical analysis.

3.2.5 Comparison of forage fish and Antarctic fur seals scats multi-nutrient compositions

We first compared absolute nutrient concentrations in forage fish and Antarctic fur seal scats using boxplots, basic descriptive statistics and MWW tests, as well as the shapes of nutrient-by-nutrient concentration distributions.

To assess whether the ratios between nutrients in forage fish and fur seal scats were similar despite possible differences in their absolute concentration ranges, we compared relative compositions of samples using nutrient fractions. To do so, we calculated the total mass of nutrients in one kilogram of matter by summing nutrient concentrations (in mg.kg^{-1} dry weight), and divided each nutrient concentration by this total. We thus obtained the nutrient fraction of each nutrient within the mix of nutrients quantified. These nutrient fractions were first compared nutrient-by-nutrient. We then compared them in multiple dimensions by compiling them in a single dataset for forage fish and fur seal scats, on which we applied the same statistical analysis applied to each independent dataset, *i.e.* HC based on sample coordinates of PCA principal components. The first four principal components explained more than 90% of the variance of this compiled dataset, and were thus selected for the HC. We examined results for 2 clusters only to test if the separation between forage fish and fur seal scats was clear based on their multi-nutrient relative composition.

3.3 Results

3.3.1 Nutrient concentrations in forage fish species

Concentrations of major nutrients in forage fish species varied from $1,220 \pm 118 \text{ mg.kg}^{-1}$ dry weight (dw) (*G. braueri*, $n = 12$) to $4,185 \pm 400 \text{ mg.kg}^{-1}$ dw (*N. coatsi*, $n = 10$) for Mg, and from $7,445 \pm 3,947 \text{ mg.kg}^{-1}$ dw (*N. antarctica*, $n = 5$) to $35,956 \pm 408 \text{ mg.kg}^{-1}$ dw (*M. mancopsetta*, $n = 2$) for Ca (Table 3.2). Lowest concentrations in trace nutrients

were found for Co with 0.04 (*I. atlanticus*, n = 1) to 0.22 ± 0.08 mg.kg⁻¹ dw (*N. coatsi*, n = 10), while highest concentrations varied from 11.4 ± 4.5 (*C. gunnari*, n = 10) to 204.7 ± 69.6 mg.kg⁻¹ dw (*A. risso*, n = 3) for Fe.

The distribution of species within the concentration ranges in the forage fish community varied by nutrient (Fig. 3.1). For example, most species had low concentrations of the nutrients Fe and As and were below the median and mean values, while only a few were above. In contrast, there were an equal number of species with P and Zn concentrations above and below the mean and median. In addition, fish species were not consistent in their concentrations to specific nutrient compared to other species (Fig. 3.1). For example, *C. gunnari* showed the lowest Fe concentration, but was part of the eight most-concentrated species in P, Zn and As. In contrast, *A. risso* was the richest in Fe, but the second poorest in As, the 10th richest species in Zn and had an average P concentration. *N. coatsi* was part of the richest for all nutrients but As and Se (Fig. 3.1; Table 3.2), while some species that were consistently amongst the poorest for all nutrients (e.g. *G. braueri*).

Concentrations in forage fish species previously identified as prey of Antarctic fur seals were significantly poorer in the major nutrients Na and Mg (mean \pm standard deviation sd $9,345 \pm 4,331$ and $1,858 \pm 568$ mg.kg⁻¹ dw, respectively) and in the trace nutrients Fe, Cu and Mn (40.0 ± 36.3 , 4.83 ± 2.37 and 2.36 ± 2.33 mg.kg⁻¹ dw, respectively) than species never identified as prey of Antarctic fur seals (Na $15,371 \pm 5,537$, Mg $2,476 \pm 961$, Fe 91.2 ± 107.6 , Cu 7.31 ± 3.63 and Mn 3.31 ± 1.64 mg.kg⁻¹ dw and MWW p -values 3.1×10^{-3} , 3.7×10^{-2} , 3.7×10^{-2} , 1.7×10^{-2} and 1.5×10^{-2} , respectively; Fig. 3.2).

Table 3.2: **Nutrient concentrations (in mg.kg⁻¹ dry weight) for 34 forage fish species from waters around the Kerguelen Islands (mean \pm standard deviation).** Biochemical analysis was conducted on whole organisms, n indicating the number of individuals analysed per species. Only genus first latter is indicated for latin species name except when species not identified (*i.e.* "sp."), see [Table 3.1](#) for full names

Family	Species	n	Ca	P	Na	K	Mg	Fe	Zn	Cu	Mn	Se	As	Ni	Co
Achiro- psettidae	<i>M. man- copsetta</i>	2	35,956 \pm 408	24,590 \pm 196	14,209 \pm 845	10,623 \pm 621	2,194 \pm 162	43.8 \pm 8.3	44.3 \pm 2.1	5.67 \pm 0.04	3.82 \pm 1.31	2.61 \pm 0.39	2.66 \pm 0.31	1.27 \pm 0.00	0.11 \pm 0.00
Bathydra- conidae	<i>B. antarcti- cus</i>	5	33,387 \pm 13,714	22,954 \pm 7,270	9,917 \pm 1,192	11,734 \pm 590	1,874 \pm 235	64.0 \pm 28.2	65.6 \pm 9.9	6.32 \pm 1.53	4.07 \pm 1.21	2.66 \pm 0.57	9.74 \pm 4.24	1.15 \pm 0.26	0.12 \pm 0.03
Bathylagi- dae	<i>B. tenuis</i>	11	9,723 \pm 5,943	10,088 \pm 3,579	11,767 \pm 3,409	8,927 \pm 1,429	1,894 \pm 815	35.7 \pm 24.7	48.1 \pm 24.3	5.82 \pm 2.99	1.70 \pm 1.01	2.01 \pm 0.39	3.91 \pm 1.24	0.65 \pm 0.40	0.05 \pm 0.03
Carapidae	<i>E. cryomar- garites</i>	10	18,953 \pm 3,522	17,085 \pm 1,891	21,855 \pm 1,651	11,176 \pm 883	2,018 \pm 197	39.6 \pm 51.3	53.8 \pm 6.4	9.58 \pm 1.05	2.66 \pm 0.57	1.86 \pm 0.31	1.50 \pm 0.14	0.74 \pm 0.10	0.06 \pm 0.01
Channi- chthyidae	<i>C. gun- nari</i>	10	19,859 \pm 8,854	19,382 \pm 4,587	11,214 \pm 1,584	17,128 \pm 1,304	2,811 \pm 267	11.4 \pm 4.5	75.2 \pm 13.0	3.90 \pm 0.66	0.81 \pm 0.27	3.83 \pm 0.73	9.48 \pm 2.39	0.81 \pm 0.29	0.08 \pm 0.03
	<i>C. rhinocer- atus</i>	10	24,320 \pm 3,780	18,848 \pm 1,347	12,493 \pm 1,581	13,702 \pm 1,003	1,937 \pm 267	23.5 \pm 13.9	72.7 \pm 10.0	4.01 \pm 1.01	1.42 \pm 0.45	3.48 \pm 0.59	12.34 \pm 5.73	0.96 \pm 0.12	0.08 \pm 0.01
Gempyl- idae	<i>P. gracilis</i>	10	15,165 \pm 3,467	13,391 \pm 2,387	7,333 \pm 1,867	9,686 \pm 961	1,548 \pm 351	65.6 \pm 94.7	34.8 \pm 7.4	3.76 \pm 0.79	1.77 \pm 1.40	2.56 \pm 0.41	1.85 \pm 0.20	0.83 \pm 0.16	0.07 \pm 0.02

Table 3.2: (continued)

Family	Species	n	Ca	P	Na	K	Mg	Fe	Zn	Cu	Mn	Se	As	Ni	Co
Macrouri- dae	<i>M. cari- natus</i>	10	21,559	17,808	10,848	11,099	1,853 ±	63.7 ±	68.4 ±	5.28 ±	2.51 ±	2.77 ±	7.96 ±	0.92 ±	0.11±
			± 4,411	± 2,345	± 2,110	± 1,331	338	21.0	6.5	1.23	0.60	0.75	4.79	0.42	0.09
Melam- phaidae	<i>P. crassi- ceps</i>	1	12,626	9,89	9,726	5,958	1,354	27.9	30.6	3.63	1.98	3.19	3.00	0.62	0.05
Microsto- matidae	<i>N. antarc- tica</i>	5	7,475±	8,423 ±	7,719 ±	7,424 ±	1,356 ±	27.1 ±	35.1 ±	3.23 ±	1.82 ±	1.62 ±	2.90 ±	0.62 ±	0.05±
			3,947	1,724	1,315	2,144	191	7.7	17.3	0.74	0.52	0.23	1.00	0.20	0.01
Muraeno- lepididae	<i>Muraeno- lepis sp</i>	10	20,431	18,241	9,158 ±	15,143	2,001 ±	60.4 ±	53.6 ±	6.46 ±	1.38 ±	2.66 ±	4.86 ±	1.19 ±	0.11±
			± 9,526	± 5,453	1,515	± 1,226	451	23.1	8.0	2.10	0.43	0.55	2.19	0.41	0.05
Myctophi- dae	<i>E. antarc- tica</i>	10	13,285	10,886	8,090 ±	5,802 ±	1,624 ±	27.1 ±	29.6 ±	3.34 ±	1.40 ±	2.01 ±	1.49 ±	1.33 ±	0.08±
			± 1,048	± 501	1,494	426	197	5.5	3.6	0.58	0.22	0.52	0.19	0.18	0.01
	<i>E. carls- bergi</i>	10	18,477	13,932	7,537 ±	7,616 ±	1,793 ±	40.2 ±	39.7 ±	3.70 ±	2.21 ±	4.03 ±	2.53 ±	1.32 ±	0.11±
			± 3,428	± 2,145	1,617	699	326	18.7	8.0	0.69	0.45	0.63	0.26	0.30	0.02
	<i>E. sub- aspera</i>	10	19,616	15,730	7,014 ±	9,915 ±	1,729 ±	27.9 ±	40.3 ±	4.80 ±	2.22 ±	3.78 ±	3.01 ±	1.16 ±	0.09±
			± 3,510	± 2,394	1,441	1,307	344	8.0	7.0	0.90	0.43	0.57	0.61	0.10	0.01
	<i>G. bolini</i>	10	16,329	12,716	4,161 ±	8,369 ±	1,203 ±	24.0 ±	21.2 ±	2.54 ±	1.71 ±	2.39 ±	3.57 ±	1.09 ±	0.08±
			± 6,162	± 3,084	569	430	126	14.2	3.6	0.34	0.54	0.36	0.48	0.27	0.03

Table 3.2: (continued)

Family	Species	n	Ca	P	Na	K	Mg	Fe	Zn	Cu	Mn	Se	As	Ni	Co
	<i>G. braueri</i>	12	12,924 ± 1,699	10,116 ± 945	5,094 ± 561	6,647 ± 229	1,220 ± 118	18.0 ± 7.9	31.2 ± 4.9	2.71 ± 0.27	1.34 ± 0.28	1.95 ± 0.17	2.00 ± 0.20	0.96 ± 0.13	0.07± 0.01
	<i>G. fraseri</i>	12	19,601 ± 3,200	14,590 ± 1,663	8,142 ± 1,204	8,025 ± 556	1,994 ± 268	30.8 ± 8.2	50.9 ± 35.6	5.31 ± 1.61	2.65 ± 0.60	3.65 ± 0.61	2.73 ± 0.43	1.42 ± 0.15	0.10± 0.01
	<i>G. nicholsi</i>	10	13,620 ± 4,264	11,243 ± 2,657	6,242 ± 1,039	8,065 ± 728	1,486 ± 281	24.9 ± 11.1	24.2 ± 3.4	4.43 ± 0.47	1.37 ± 0.37	2.94 ± 0.59	3.18 ± 0.41	1.11 ± 0.25	0.08± 0.01
	<i>G. piabilis</i>	10	16,044 ± 1,748	12,972 ± 767	5,455 ± 962	8,405 ± 630	1,486 ± 203	24.3 ± 5.5	27.5 ± 4.8	3.74 ± 0.54	1.55 ± 0.21	2.85 ± 0.65	2.40 ± 0.26	1.09 ± 0.10	0.09± 0.01
	<i>K. anderssoni</i>	4	11,623 ± 1,619	11,787 ± 1,590	9,649 ± 1,409	6,833 ± 526	1,847 ± 163	63.7 ± 6.3	45.6 ± 10.8	5.73 ± 1.13	2.69 ± 0.60	3.10 ± 0.28	4.66 ± 0.26	0.87 ± 0.13	0.07± 0.01
	<i>P. andriashevi</i>	4	30,374 ± 7,698	21,764 ± 4,379	15,311 ± 2,059	8,886 ± 1,571	3,214 ± 609	84.2 ± 50.3	51.7 ± 17.6	6.06 ± 0.85	3.24 ± 0.99	3.39 ± 0.14	2.11 ± 0.23	1.99 ± 0.25	0.11± 0.01
	<i>P. bolini</i>	10	26,261 ± 4,970	17,957 ± 2,396	13,353 ± 2,951	6,284 ± 1,533	2,879 ± 572	99.0 ± 59.7	57.5 ± 10.6	6.29 ± 1.16	3.61 ± 0.95	2.79 ± 0.73	2.30 ± 0.56	1.68 ± 0.22	0.12± 0.01
	<i>P. chori-odon</i>	8	22,256 ± 2,533	17,573 ± 1,561	12,194 ± 1,198	8,524 ± 1,091	2,483 ± 274	70.2 ± 37.8	53.4 ± 6.2	6.35 ± 1.24	3.03 ± 0.42	2.62 ± 0.43	2.17 ± 0.45	1.32 ± 0.27	0.10± 0.01
	<i>P. tenisoni</i>	10	26,471 ± 3,736	19,493 ± 1,744	12,141 ± 1,367	7,991 ± 1,321	2,707 ± 213	73.9 ± 18.6	71.1 ± 26.3	8.22 ± 2.46	3.55 ± 0.76	3.34 ± 0.70	2.09 ± 0.37	1.85 ± 0.36	0.13± 0.02

Table 3.2: (continued)

Family	Species	n	Ca	P	Na	K	Mg	Fe	Zn	Cu	Mn	Se	As	Ni	Co
Notosudi- dae	<i>L. normani</i>	1	12,117	13,495	8,143	12,402	1,686	38.2	72.9	6.49	2.59	2.93	3.20	0.61	0.06
Notothe- niidae	<i>D. elegi- noides</i>	2	22,532 ± 1,260	20,935 ± 756	8,302 ± 805	16,603 ± 321	1,645 ± 95	32.6 ± 4.7	53.0 ± 0.3	3.99 ± 0.25	2.42 ± 0.15	3.57 ± 0.37	7.55 ± 0.21	1.09 ± 0.02	0.09± 0.01
	<i>G. acuta</i>	8	31,488 ± 14,137	23,221 ± 6,655	9,063 ± 1,624	12,993 ± 1,754	1,613 ± 353	43.0 ± 12.5	72.2 ± 9.9	3.47 ± 0.62	11.12 ± 5.81	3.92 ± 0.77	17.51 ± 8.82	1.24 ± 0.45	0.11± 0.03
	<i>L. squam- ifrons</i>	10	24,467 ± 6,100	18,474 ± 2,817	7,898 ± 504	12,716 ± 501	1,617 ± 150	32.6 ± 9.2	48.6 ± 7.2	3.29 ± 0.90	2.18 ± 0.33	2.31 ± 0.26	10.65 ± 2.19	1.18 ± 0.32	0.09± 0.02
	<i>L. mizops</i>	7	35,207 ± 6,034	24,524 ± 3,806	10,090 ± 1,717	13,460 ± 950	2,263 ± 388	44.9 ± 23.1	75.3 ± 26.1	7.29 ± 1.21	4.25 ± 0.94	3.33 ± 1.40	6.60 ± 1.77	1.51 ± 0.27	0.13± 0.03
Paralepidi- dae	<i>A. risso</i>	3	19,909 ± 519	17,977 ± 467	18,584 ± 122	13,053 ± 281	3,263 ± 151	204.7 ± 69.6	67.3 ± 2.5	10.50 ± 0.32	3.63 ± 0.42	3.71 ± 0.09	1.27 ± 0.02	0.82 ± 0.05	0.08± 0.00
	<i>N. coatsi</i>	10	21,455 ± 2,344	18,625 ± 1,509	21,796 ± 1,734	9,881 ± 686	4,185 ± 400	201.0 ± 116.9	107.7 ± 23.9	12.92 ± 4.43	5.88 ± 1.31	2.01 ± 0.40	0.80 ± 0.13	3.95 ± 1.39	0.22± 0.08
Stomiidae	<i>I. atlanti- cus</i>	1	7,771	8,642	20,069	7,073	2,726	39.2	42.9	5.78	2.08	2.23	1.48	0.37	0.04

Table 3.2: (continued)

Family	Species	n	Ca	P	Na	K	Mg	Fe	Zn	Cu	Mn	Se	As	Ni	Co
	<i>Stomias</i> sp	10	17,538 ± 7,301	14,184 ± 4,643	17,782 ± 4,365	8,671 ± 1,965	3,003 ± 783	171.6 ± 188.1	60.0 ± 16.9	3.88 ± 0.62	3.12 ± 1.58	1.49 ± 0.14	1.74 ± 0.34	1.03 ± 0.28	0.08± 0.02
Zoarcidae	<i>M.</i> <i>gelati-</i> <i>nosum</i>	10	17,731 ± 6,413	14,505 ± 3,684	22,335 ± 3,478	7,881 ± 1,108	2,384 ± 494	22.1 ± 2.2	90.7 ± 24.3	11.26 ± 2.19	1.01 ± 0.27	2.25 ± 0.16	4.17 ± 0.68	0.75 ± 0.19	0.07± 0.02

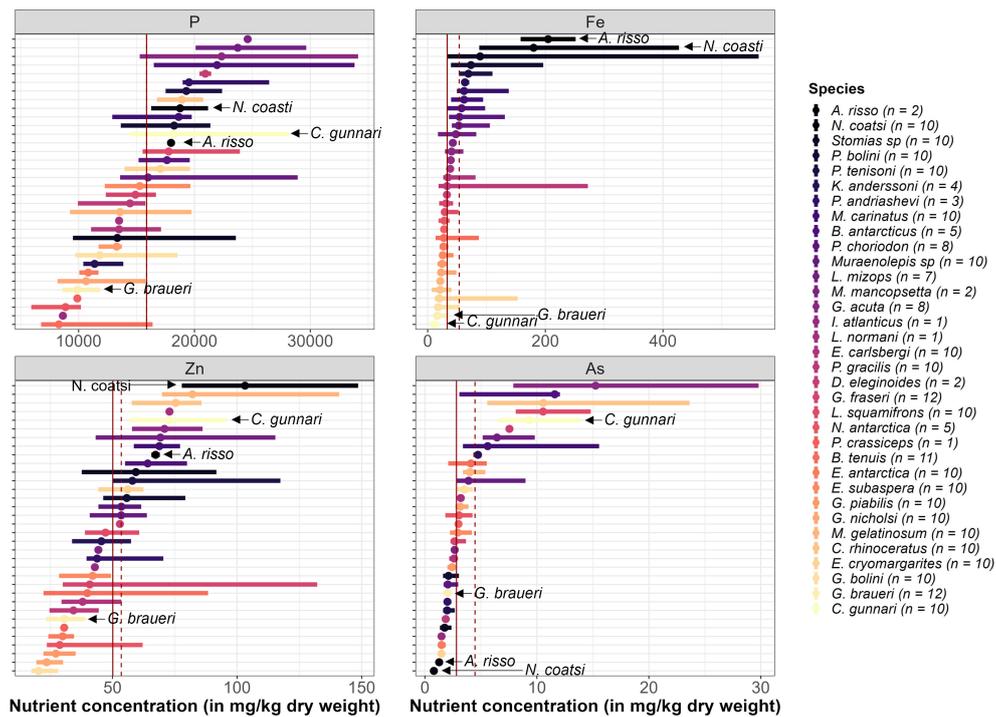


Figure 3.1: **Concentrations (in $\text{mg}\cdot\text{kg}^{-1}$ dry weight) in phosphorous P, iron Fe, zinc Zn and arsenic As in whole organisms for a range of forage fish species sampled around the Kerguelen Islands.** For each species, the central point is the median, and the line extend to the 2.5th and 97.5th percentiles respectively, with each being coloured by species. The colour gradient was set to match the species concentration order for Fe, and kept for other nutrients. Black arrows and associated species names point out to species called in the text. Red solid and dashed lines are median and mean values of all samples, respectively

3.3.2 Nutrient concentrations in Antarctic fur seal scats

The nutrient concentrations in Antarctic fur seal scats were highly variable and over several orders of magnitudes for a given nutrient (Fig. 3.3). For major nutrients, concentrations ranged from 712 to 8,100 $\text{mg}\cdot\text{kg}^{-1}$ dw for K ($2,291 \pm 1,108$) and from 1,196 to 235,647 $\text{mg}\cdot\text{kg}^{-1}$ dw for Ca ($79,043 \pm 76,164$). For trace nutrients, concentrations in scats ranged from 0.06 to 13.14 $\text{mg}\cdot\text{kg}^{-1}$ dw for Co (2.90 ± 3.35) and from 25.9 to 16,909 $\text{mg}\cdot\text{kg}^{-1}$ dw for Fe ($3,617 \pm 4,433$).

Concentrations were significantly higher in scats collected on the Cap Noir colony than on the Pointe Suzanne colony for Cu, Se and Zn (Fig. 3.3a; MWW p -values = 2.2e^{-4} , 2.3e^{-2} and 2.5e^{-2} , respectively). Concentrations of other nutrients were similar between the 2 locations, despite a few high values for As, K, Mn, Na and Ni in Pointe Suzanne and a few high values for Co and Fe in Cap Noir.

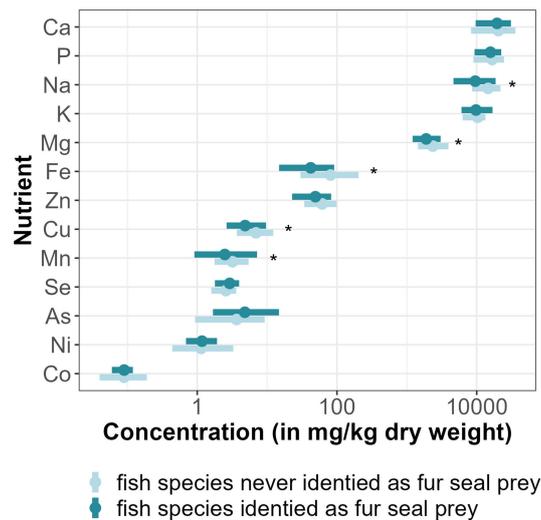


Figure 3.2: Concentrations (in $\text{mg}\cdot\text{kg}^{-1}$ dry weight) in calcium Ca, phosphorous P, sodium Na, potassium K, magnesium Mg, iron Fe, zinc Zn, copper Cu, manganese Mn, selenium Se, arsenic As, nickel Ni and cobalt Co in whole organisms for a range of forage fish species sampled around the Kerguelen Islands, with species never identified as part of Antarctic fur seal (*Arctocephalus gazella*) diet in light blue and species previously identified as part of Antarctic fur seal in steel blue. Black stars indicate nutrients for which the difference between two groups is significant as indicated by Mann-Whitney-Wilcoxon tests, each central point is the median and the line extends to the 2.5th and 97.5th percentiles, respectively

Scats that contained hard parts were significantly richer in Ca, P and Mg (MWW p -values = 2.9e^{-5} , 5.4e^{-5} and 1.6e^{-2} , respectively) and poorer in Se (MWW p -value = 5.2e^{-3}) than scats that contained no hard parts (Fig. 3.3b).

3.3.3 Co-variation between nutrient concentrations in forage fish and Antarctic fur seal scats

Nutrients did not vary independently in either forage fish or Antarctic fur seal scats, but co-variations were different between the two biological matrices (Fig. 3.4). In forage fish, highest correlation coefficients were between the trace nutrients Co and Ni and between the major nutrients Ca and P. There were also some strong co-variations between major and minor nutrients, such as K and As, P and As, Mg and As, Mg and Fe or Na and Zn. Co-variations were stronger in average in Antarctic fur seal scats than in forage fish, except for As (Fig. 3.4). In addition to the Ca-P couple (strongest correlation), they were some strong co-variations between concentrations of trace nutrients such as Fe and Co, Fe and Mn, Fe and Ni. In Antarctic fur seals, correlation coefficients between major and

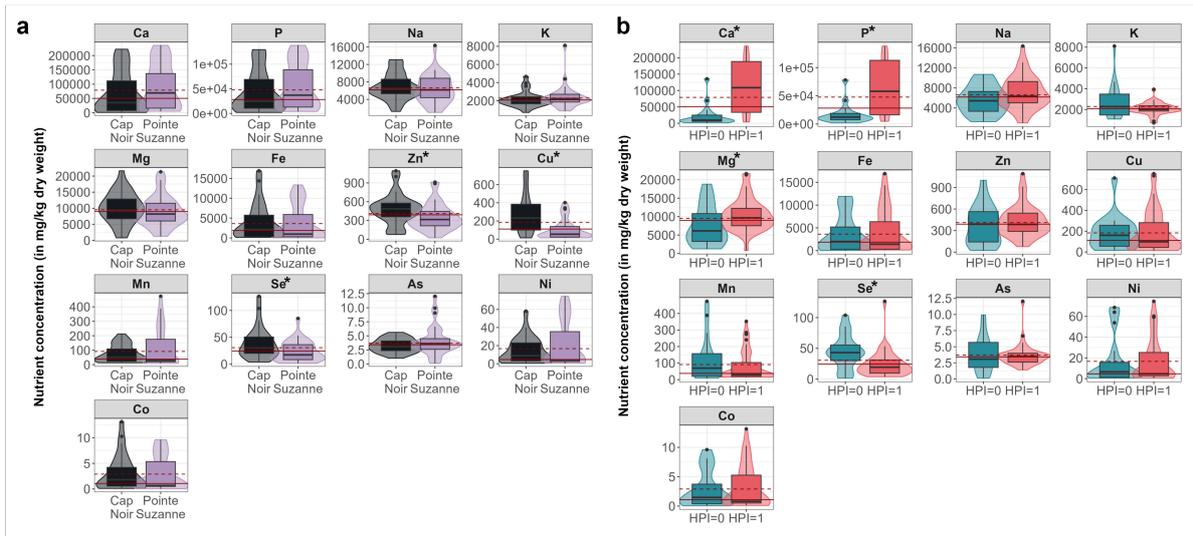


Figure 3.3: Concentrations (in $\text{mg}\cdot\text{kg}^{-1}$ dry weight) in calcium Ca, phosphorous P, sodium Na, potassium K, magnesium Mg, iron Fe, zinc Zn, copper Cu, manganese Mn, selenium Se, arsenic As, nickel Ni and cobalt Co in scats of Antarctic fur seals (*Arctocephalus gazella*) collected on two colonies (Cap Noir and Pointe Suzanne) of the Kerguelen Islands. (a) shows concentrations for samples separated per colony and (b) concentrations for samples containing no hard parts (hard-part index HPI = 0), and containing hard parts (HPI = 1). Black stars indicate nutrients for which the difference between two groups is significant as indicated by Mann-Whitney-Wilcoxon tests. Boxplots display the median with solid black line in each box, lower and upper hinges corresponding 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 individual points. Boxplots were combined to violin plots to highlight the distribution around the median. Median and mean for all samples are indicated with the red solid and dashed lines, respectively

trace nutrients were negative, except with Zn, Se and As.

3.3.4 Nutritional typology of forage fish species

Hierarchical clustering (HC) resulted in four clusters of forage fish species with shared nutrient composition characteristics (Fig. 3.5; Table 3.3). Cluster 1 contained 11 species (including eight myctophids species) and had the lowest average concentrations in Na and Zn. Cluster 2 contained eight demersal, bathydemersal or benthopelagic species, characterised by the highest concentrations in K and As and high concentrations in Ca, P, Zn and Se. Cluster 3 contained eight deepsea species, with a majority of mesopelagic species and one bathydemersal species (*E. cryomargarites*). They were characterised by low Ca and P concentrations, and by the lowest concentrations in Ni and Co. Cluster 4 contained seven mesopelagic species that had the highest concentration in Fe and Mg,

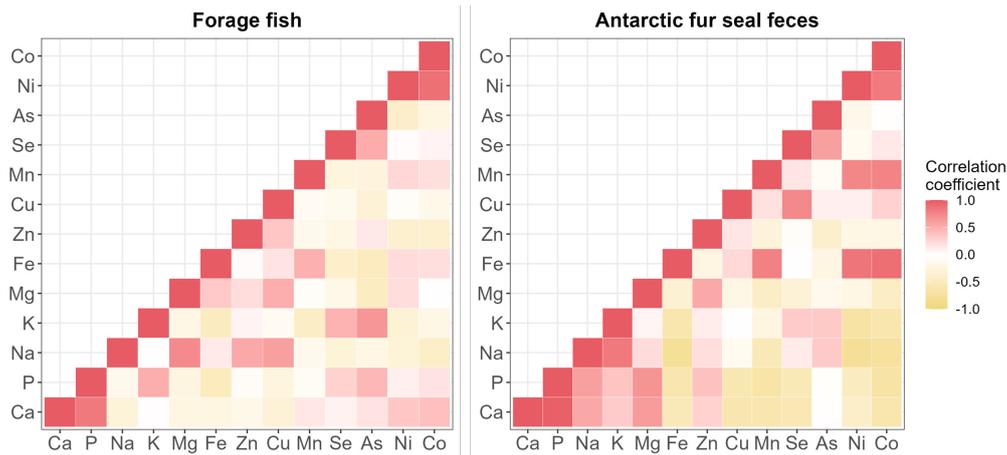


Figure 3.4: **Coefficient of correlation between different nutrient concentrations in forage fish (left) and Antarctic fur seal (*Arctocephalus gazella*) scats (right)**. Samples were collected around (fish) and on (scats) the Kerguelen Islands

and relatively high concentrations of Ca, Na, P, Zn and Cu. The four clusters contained species both identified and not identified as prey of Antarctic fur seals around Kerguelen (Table 3.1). The difference between Mn concentrations in clusters 3 and 4 was the only between-cluster difference that was statistically significant (MWW p -value = 2.1×10^{-2}).

3.3.5 Nutritional typology of Antarctic fur seal scats

Two clusters of Antarctic fur seal scats were identified using HC (Fig. 3.6a), with seven samples from Cap Noir and 16 from Pointe Suzanne in cluster 1 and 20 samples from Cap Noir and 15 from Pointe Suzanne in cluster 2. The 23 samples in cluster 1 were characterised by significantly higher concentrations in major nutrients Ca, P, and Na (MWW p -values = 4.3×10^{-15} , 8.5×10^{-14} and 5.4×10^{-4} , respectively) Fig. 3.6b. The 35 samples in cluster 2 were characterised by higher concentrations in trace nutrients Fe, Cu, Mn, Se, As, Ni and Co (MWW p -values = 1.2×10^{-4} , 3.3×10^{-8} , 4.0×10^{-5} , 8.0×10^{-13} , 1.3×10^{-4} , 9.6×10^{-4} and 8.0×10^{-6} , respectively). Concentrations in K, Mg and Zn did not significantly differ between the two clusters (MWW p -values = 8.5×10^{-1} , 5.7×10^{-1} and 9.2×10^{-2} , respectively). Most cluster 1 samples contained hard parts (21/23), and cluster 2 samples contained a mix of scat with (19/35) and without (8/35) hard parts.

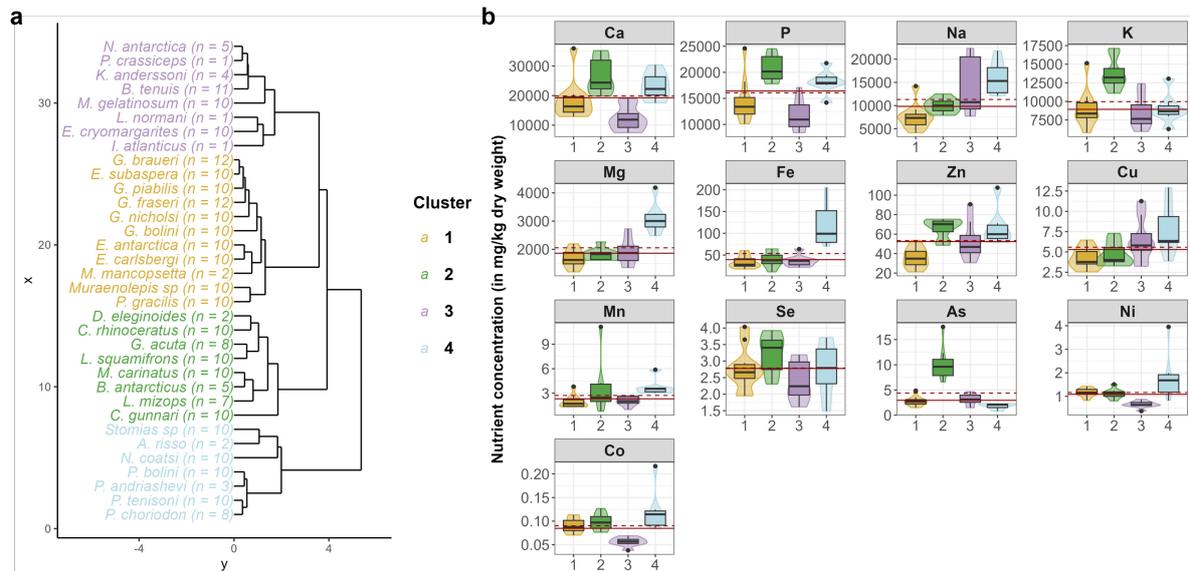


Figure 3.5: **Hierarchical clustering analysis from Ward's minimum variance method distinguished four clusters in the 34 forage fish species sampled around the Kerguelen Islands, based on their concentrations in calcium Ca, phosphorous P, sodium Na, potassium K, magnesium Mg, iron Fe, zinc Zn, copper Cu, manganese Mn, selenium Se, arsenic As, nickel Ni and cobalt Co.** Species of the four clusters are shown on a dendrogram (a) and their nutrient concentrations are shown with boxplots (b). Only the difference between Mn concentrations in clusters 3 and 4 was shown to be statistically significant using Mann-Whitney-Wilcoxon tests. 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 individual points. Boxplots were combined to violin plots to highlight the distribution around the median. Median and mean for all samples are indicated with the red solid and dashed lines, respectively

Table 3.3: **Nutrient concentrations (mean \pm standard deviation, in mg.kg⁻¹ dry weight) for clusters resulting from a hierarchical clustering of forage fish from around the Kerguelen Islands.** hierarchical clustering (HC) was based on Ward's minimum variance method, using sample coordinates on the first principal components of a principal component analysis (PCA) conducted on the compositional datasets prior to HC, with the selected principal components explaining 90% minimum of the variance of the original dataset

Cluster	Ca	P	Na	K	Mg	Fe	Zn	Cu	Mn	Se	As	Ni	Co
Cluster 1 (11 species)	18,313 \pm 6,438	14,400 \pm 4,089	7,494 \pm 2,674	8,936 \pm 2,488	1,662 \pm 318	34.0 \pm 13.6	35.7 \pm 10.1	4.22 \pm 1.24	1.95 \pm 0.75	2.77 \pm 0.62	2.75 \pm 0.92	1.16 \pm 0.17	0.09 \pm 0.02
Cluster 2 (8 species)	26,602 \pm 5,870	20,768 \pm 2,523	19,978 \pm 1,540	13,679 \pm 2,149	1,827 \pm 216	39.4 \pm 18.4	66.4 \pm 10.2	4.69 \pm 1.45	3.60 \pm 3.26	3.23 \pm 0.59	10.23 \pm 3.46	1.12 \pm 0.21	0.10 \pm 0.02
Cluster 3 (8 species)	12,253 \pm 4,222	11,739 \pm 3,072	13,908 \pm 6,368	8,467 \pm 2,250	1,908 \pm 474	36.7 \pm 12.7	52.5 \pm 20.1	6.44 \pm 2.74	2.06 \pm 0.58	2.40 \pm 0.60	3.10 \pm 1.16	0.65 \pm 0.15	0.06 \pm 0.01
Cluster 4 (7 species)	23,323 \pm 4,580	18,225 \pm 2,280	15,880 \pm 3,656	9,041 \pm 2,079	3,105 \pm 549	119.4 \pm 52.6	66.9 \pm 19.3	7.75 \pm 3.07	3.72 \pm 0.98	2.76 \pm 0.80	1.78 \pm 0.55	1.81 \pm 1.04	0.12 \pm 0.05
Total (34 species)	19,869 \pm 7,474	16,060 \pm 4,602	11,314 \pm 5,005	9,963 \pm 3,023	2,056 \pm 668	53.5 \pm 42.8	53.3 \pm 20.1	5.58 \pm 2.49	2.73 \pm 1.84	2.79 \pm 0.68	4.39 \pm 3.76	1.16 \pm 0.61	0.09 \pm 0.03

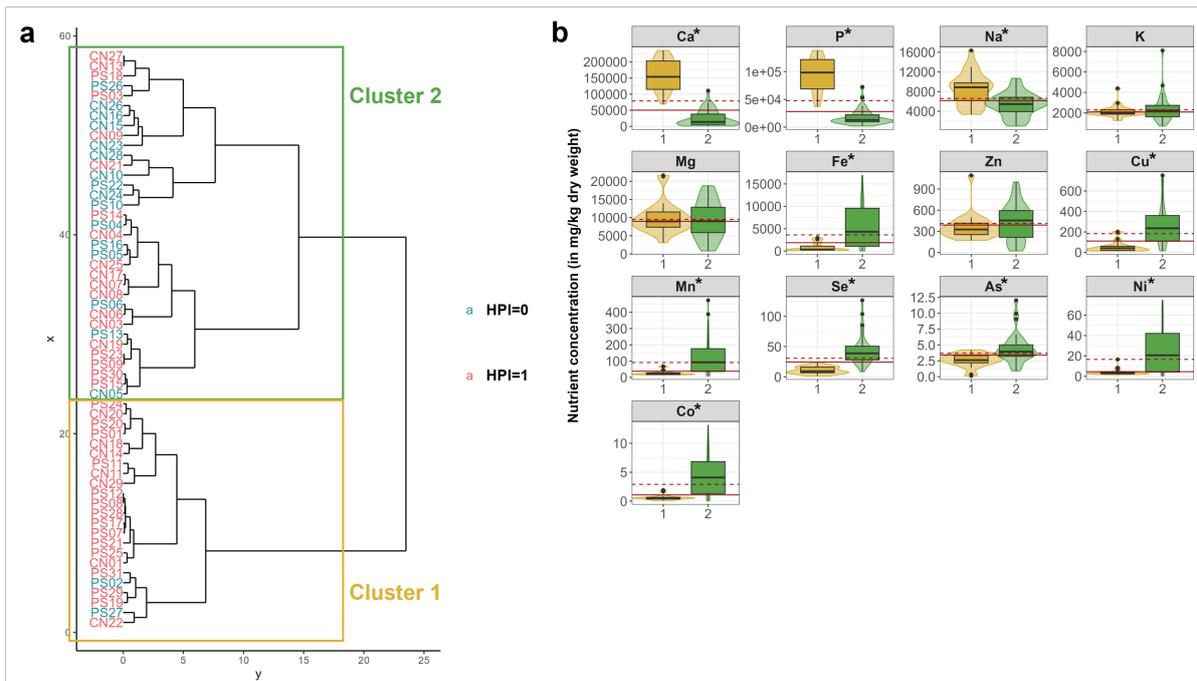


Figure 3.6: **Hierarchical clustering analysis from Ward's minimum variance method distinguished two clusters of Antarctic fur seal (*Arctocephalus gazella*) scats collected on the Kerguelen Islands based on their concentrations in calcium Ca, phosphorous P, sodium Na, potassium K, magnesium Mg, iron Fe, zinc Zn, copper Cu, manganese Mn, selenium Se, arsenic As, nickel Ni and cobalt Co.** (a) dendrogram of samples (samples with codes starting with "CN" are from Cap Noir colony and that starting with "PS" from Pointe Suzanne colony) and (b) boxplots of nutrient concentrations (in $\text{mg}\cdot\text{kg}^{-1}$ dry weight) for the two clusters. Black stars indicate nutrients for which the difference between the two clusters is significant as indicated by Mann-Whitney-Wilcoxon tests. 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 individual points. Boxplots were combined to violin plots to highlight the distribution around the median. Median and mean for all samples are indicated with the red solid and dashed lines, respectively

3.3.6 Comparison between nutrient compositions of forage fish and Antarctic fur seal scats

Concentrations in major nutrients Na and K were significantly greater in forage fish than in Antarctic fur seal scats ($\times 2$ and $\times 4$ respectively, MWW p -value = 2.2e^{-6} and 3.4e^{-15} ; Fig. 3.7a), while Antarctic fur seal scats were more concentrated in major nutrients Ca, P and Mg ($\times 4$, $\times 3$ and $\times 4$ respectively, MWW p -values = 1.1e^{-2} , 1.8e^{-2} and 1.5e^{-12}). Variability between samples was greater for trace nutrients than for major nutrients, and

concentrations were more variable in Antarctic fur seal scats than in forage fish. Antarctic fur seal scats also contained Zn concentrations of trace nutrients eight times greater than those of forage fish (MWW p -value = 1.9×10^{-14}), and up to 33 and 68 times greater for Mn and Fe, respectively (MWW p -values = 1.7×10^{-15} and 1.7×10^{-14}). There was no significant difference between forage fish and fur seal scats for As (MWW p -value = 6.0×10^{-1}).

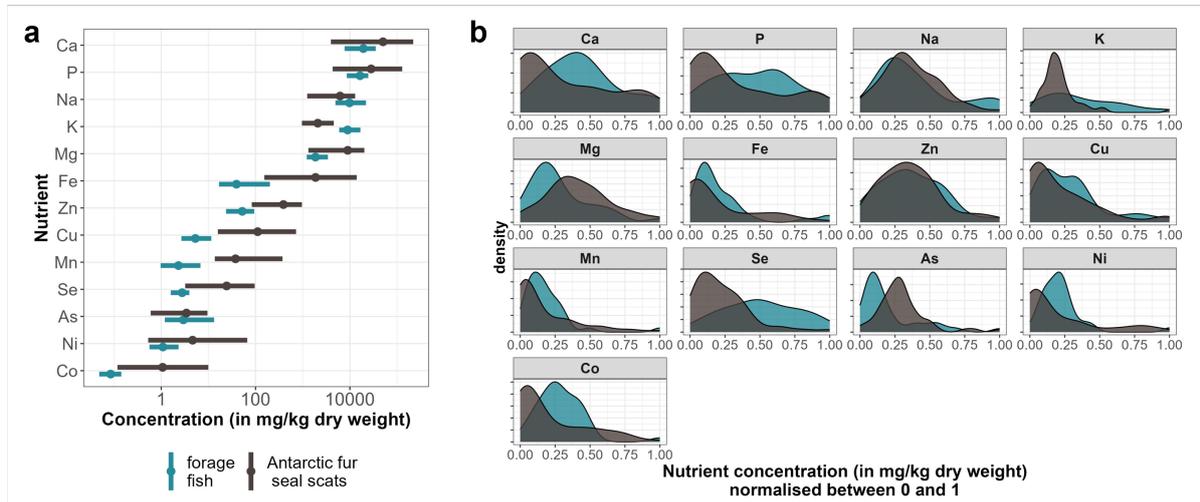


Figure 3.7: **Differential nutrient concentrations and variability in forage fish and Antarctic fur seal (*Arctocephalus gazella*) scats for concentrations in calcium Ca, phosphorous P, sodium Na, potassium K, magnesium Mg, iron Fe, zinc Zn, copper Cu, manganese Mn, selenium Se, arsenic As, nickel Ni and cobalt Co (in mg.kg-1dry weight).** (a) Line-range plots of nutrient concentrations where central point is the median and the line extend to the 2.5th and 97.5th percentiles and (b) density plots of nutrient concentrations where concentrations were normalised between 0 and 1. On (a), all differences between concentrations in forage fish and fur seal scats were shown to be statistically different using Mann-Whitney-Wilcoxon tests, but that of As. Samples were collected around (fish) and on (scats) the Kerguelen Islands

In both forage fish and Antarctic fur seal scats, nutrient concentration distributions tended to be right-skewed, *i.e.* contained a majority of lower values close to the mean and a few highly concentrated fish species or fur seal scats, except for Ca, P, Se and K for fish, and Ca and P for scats (Fig. 3.7b). Forage fish Ca and P distributions were unimodal with large interquartile range, while they were bimodal with two modes at the extremes for scats. Fish K and Se distributions show flat patterns compared to the narrow unimodal and right-skewed distributions in scats.

Relative Na and K nutrient ratios were greater in fish than in scats (MWW p -values = 4.2×10^{-9} and 1.3×10^{-14} , respectively) but lower for Ca and Mg (MWW p -values = 1.0×10^{-2} and 3.0×10^{-9} , respectively). The relative P nutrient ratio did not significantly differ in the two matrices (MWW p -value = 8.3×10^{-2}). In total, the ratio between all trace nutrients and

major nutrients in Antarctic fur seal scats was 15 times greater than that of forage fish (median \pm sd 0.028 ± 0.13 vs 0.0019 ± 0.0008 , respectively; Fig. 3.8a). Within their trace nutrients mix only, forage fish had significantly greater ratios of Zn, Se, As, Ni and Co than fur seal scats (MWW p -values = 1.2×10^{-6} , 1.7×10^{-6} , 1.5×10^{-14} , 4.3×10^{-12} and 1.7×10^{-2} , respectively; Fig. 3.8b). In contrast, in fur seal scats the Fe fraction within the trace nutrient mix was significantly greater than that of forage fish (MWW p -value = 6.8×10^{-5}). Differences were not significant for Cu and Mn (MWW p -values = 5.1×10^{-1} and 7.0×10^{-1}).

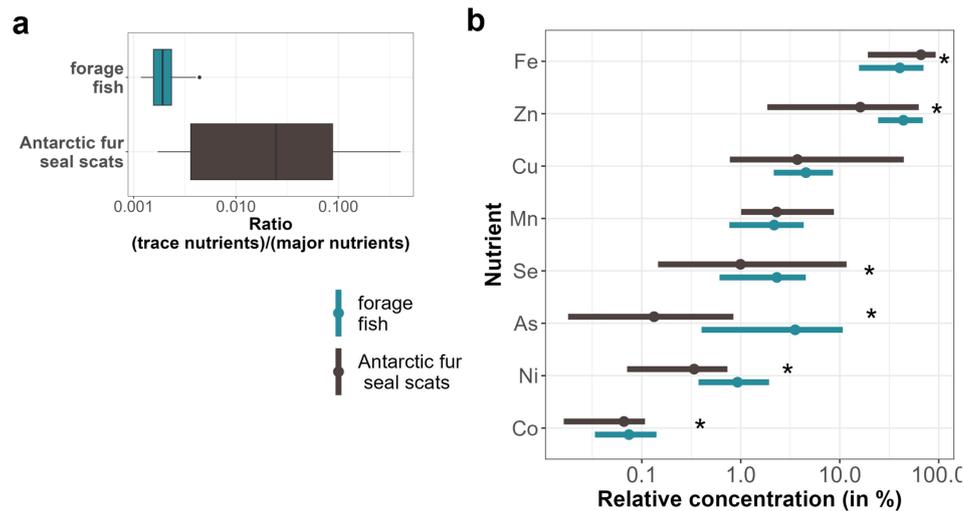


Figure 3.8: **Differential relative nutrient composition in forage fish and Antarctic fur seal (*Arctocephalus gazella*) scats.** (a) Ratio of the total concentration in trace nutrients (iron Fe, zinc Zn, copper Cu, manganese Mn, selenium Se, arsenic As, nickel Ni and cobalt Co) compared to the total concentration in major nutrients (calcium Ca, phosphorous P, sodium Na, potassium K, magnesium Mg); and (b) line-range plots of relative nutrient concentrations for trace nutrients only in both biological matrices, where central point is the median and the line extends to the 2.5th and 97.5th percentiles. Black stars indicate significantly different relative concentrations as shown by Mann-Whitney-Wilcoxon tests. Samples were collected around (fish) and on (scats) the Kerguelen Islands

When forage fish and fecal samples relative nutrient concentrations were compiled in a unique dataset for all the nutrients, they were separated in two distinct clusters through the HC.

3.4 Discussion

The results presented here provide evidence for differential nutrient concentrations in potential prey species compared to the waste products of a marine amphibious predator,

with the case of forage fish and Antarctic fur seals around the Kerguelen Islands. We show that nutrients do not flow homogeneously at these levels of ecosystems depending on the ecology, physiological needs and homeostasis of both prey and predator, and that the multi-nutrient typology of both forage fish and Antarctic fur seal scats can provide information on their respective contributions to nutrient cycling ecosystem dynamics.

3.4.1 Multi-nutrient typology of forage fish

Our results showed four clusters of forage fish species around the Kerguelen Islands based on their composition in multiple nutrients. This classification is likely associated to aspects of ecology and/or physiology of the sampled fish, to some extent. For example, bottom-associated species classified in cluster 2 showed higher P and Ca compared to other clusters, likely due to heavier bones than pelagic species, and the two ice fish species *C. gunnari* and *C. rhinoceratus* (also in cluster 2), which have no haemoglobin (Galbraith et al. 2019), showed the lowest and the 4th lowest Fe concentrations (Fig. 1). In addition, species from cluster 2 had high As concentrations, similar to what was found in benthopelagic bony fish species in the Northeast Atlantic (Chouvelon et al. 2022c). Cluster 4 on the other hand, included species enriched in Fe and Na, but interestingly, the two species we collected in the Southern Ocean (SO) also present in Chouvelon et al. (2022c) (*Stomias* sp and *A. risso*) were not as Fe-enriched ($119.4 \pm 52.6 \text{ mg.kg}^{-1} \text{ dw}$) as in the Northeast Atlantic ($269.7 \text{ mg.kg}^{-1} \text{ dw}$). In the context of the SO, where Fe paucity limits the growth of primary producers, these lower Fe concentrations are consistent with the hypothesis that Fe limitation may extend to trophic levels above primary producers (Galbraith et al. 2019). Interestingly, Fe enrichment in Northeast Atlantic fish, where Fe is not the primary limiting nutrient (Moore et al. 2013), was associated with the lowest average Cu concentrations ($1.99 \text{ mg.kg}^{-1} \text{ dw}$) (Chouvelon et al. 2022c), whereas fish in our cluster 4 were characterised by high Cu concentrations ($7.75 \pm 3.07 \text{ mg.kg}^{-1} \text{ dw}$). Diatoms have higher Cu requirements in Fe-limited oceanic environments than in coastal and comparatively nutrient-enriched waters (Peers and Price 2006). Differences in Fe and Cu co-variations in fish from ecosystems with different nutrient regimes suggest physiological adaptations to Fe limitation may also extend to higher trophic levels, the absence of haemoglobin being an extreme example of such adaptation (Galbraith et al. 2019).

This typology differs from traditional nutritional classification, mostly based on content in energy and macromolecules (e.g. lipids, proteins), but provides a complementary

functional view of prey field in marine ecosystems. For example, most of the species of myctophids analysed here, which are identified as energy-rich prey, are separated into two clusters (1 and 4). However, species of the same genus are found in the same cluster (*Electrona*, *Gymnoscopelus* and *Protomyctophum*), so there may be taxonomic patterns of nutrient composition beyond macronutrient and energy content. It is also noteworthy that *Protomyctophum* species belong to the cluster enriched in trace nutrients despite having a lower average trophic level than *Gymnoscopelus* and *Electrona* species (Cherel et al. 2010), which may indicate that nutrient concentration patterns in fish are not necessarily proportionate to their trophic levels.

3.4.2 Multi-nutrient typology of Antarctic fur seal scats

Antarctic fur seal scats were divided into 2 clusters based on their trace nutrient or Ca, P and Na content. These clusters did not reflect prey digestion stage or colony location (Cap Noir vs. Pointe Suzanne). Scat nutrient composition partially reflect Antarctic fur seal diet, their digestion and nutrient requirements (reflected in their intestinal absorption and release rates). Thus, although they were not separated in the two clusters, the nutrient differences between scats with and without hard parts and between scats from Cap Noir and Pointe Suzanne may still indicate physiological or ecological patterns, as for fish. Ca, P and Mg are major constituents of bone and otoliths (Blaine et al. 2015), so the higher concentrations found for these nutrients in scats with hard parts compared to scats without hard parts could be a marker of (partial) digestion of prey bony parts. We also found that Cu, Se and Zn concentrations in scats differed between Cap Noir and Pointe Suzanne. Antarctic fur seals from different colonies around Kerguelen do not forage in the same areas (Jeanniard-du Dot et al. 2017b, Lea et al. 2002b), so this may translate into different prey preferences. Interestingly, benthic to benthopelagic cephalopod and crustacean species were shown to contain higher Cu, Se, and Zn concentrations in the Northeast Atlantic Ocean (Chouvelon et al. 2022b). Cephalopods and crustaceans were not available for our study, but are part of Antarctic fur seals' diet (Jeanniard-du Dot et al. 2017b, Lea et al. 2002a). Although historical dietary data based on scat hard parts inventory for Cap Noir and Pointe Suzanne colonies did not suggest a site difference in their prevalence in fur seal's diet (between 1 and 17%), this greater Cu, Se and Zn concentrations in Cap Noir scats could indicate a greater proportion of cephalopods for fur seals from this colony. Indeed, the methods used to quantify prey items in Cap Noir and Pointe Suzanne scats differ between the 2 sites (reconstituted biomass vs split

sampling frequency of occurrence; Jeanniard-du Dot et al. 2017b, Lea et al. 2002a), and cephalopod consumption may also be underestimated if a large proportion of squid beaks are regurgitated (Gudmundson et al. 2006, Lea et al. 2008). A site-specific difference could therefore have been masked by uncertainties inherent to these diet reconstructions specific to cephalopods. Alternatively, given that the most recent dietary studies date from 2012 at Pointe Suzanne and from 2000 at Cap Noir, fur seal diets may have evolved toward a greater proportion of cephalopods in Cap Noir vs Pointe Suzanne. Finally, it is also possible that similar prey species from different areas may have different nutrient compositions (e.g. Ratnarajah et al. 2016b).

For both clusters, Fe concentrations in Antarctic fur seal scats were the highest when compared to other SO pinniped species, such as Hooker's sea lion *Phocarcos hookeri* and Weddell seals *Leptonychotes weddellii* (Table 3.4; Wing et al. 2021, 2017). The same was observed for Cu, except for New Zealand fur seals *Arctocephalus forsteri* that had scats nearly three times more concentrated in Cu than Antarctic fur seals' (cluster 2). For Mn, Ni and Co, concentrations in scats of other SO pinniped species were close to concentrations in samples enriched in major nutrients but with the lowest trace nutrient concentrations (cluster 1). While the higher Cu concentrations in New Zealand fur seal scats may be due to the high proportion of cephalopods in their diet (Fea et al. 1999, Harcourt et al. 2002), it is difficult to hypothesise about the highest average Fe, Cu, Mn, Ni and Co concentrations in Antarctic fur seal scats compared to other SO pinnipeds without more information about the prey mix of our fecal samples. As for comparison with other marine mammals, for both clusters Fe concentrations in Antarctic fur seal scats were also above that measured in feces of SO baleen whales (Table 3.4) (Nicol et al. 2010, Ratnarajah et al. 2014). Baleen whales feces P concentrations were close to that of the Antarctic fur seal cluster 1 scats, except for highest concentrations in fin whale *Balaenoptera physalus* feces, and lower concentrations closer to that of cluster 2 fur seal scats for humpback whale *Megaptera novaeangliae* feces (Ratnarajah et al. 2014). Zinc concentrations were equivalent in SO blue *Balaenoptera musculus* and fin whale and Antarctic fur seal scats, but humpback and pygmy blue *Balaenoptera musculus breviceuda* whale feces were more concentrated. Southern ocean baleen whale feces concentrations were closest to that of Antarctic fur seal scats impoverished in trace nutrients (cluster 2) for Mn and Co but closest to the cluster enriched in trace nutrients for Cu (except for humpback whale feces) (Ratnarajah et al. 2014). All of these baleen whale species prey mainly on krill in the SO, but some species such as humpback and fin whales may include

some small fish in their diet (Shirihai 2008), which may explain the specific differences observed between whale species and between whales and fur seals. It should also be noted that whale fecal samples were collected after they had been deposited in the water (Nicol et al. 2010, Ratnarajah et al. 2014), so it is possible that some of the nutrients they originally contained were already dissolved in the water and therefore not quantified. In comparison, feces collected in the intestinal track of hunted North Atlantic minke whales, which include a larger proportion of fish in their diets (Windsland et al. 2007) had Cu, Mn and Co concentrations close to that of the trace nutrient-poor Antarctic fur seal scats, lower Fe, Se and Ni concentrations than both clusters and higher As concentrations (Freitas et al. 2023). Southern Ocean sperm whale *Physeter macrocephalus* feces, based on a unique sample, had relatively high concentration in P, equivalent concentration in Mn and lower Fe concentration than Antarctic fur seal scats (Ratnarajah et al. 2014) (Table 3.4). However, it was richer in Cu and Zn than the richest fur seal scats by one order of magnitude. These differences may be due to their nearly exclusive deep-sea squid diet (Shirihai 2008). Whales (baleen and sperm) and fur seals are also likely to have different metabolic and nutrient requirements, which could further result in the differential concentration of nutrients in their feces. Finally, Fe, Cu, Zn, Ni, Mn and Co concentrations in trace nutrient-poor fur seal scats were close to concentrations in the guano of SO penguins and Antarctic terns *Sterna vittata* (Sparaventi et al. 2021, Wing et al. 2021, 2017), whereas those of trace nutrient-rich scats were close to concentrations in the guano of predatory or scavenging seabirds (e.g. brown skua *Stercorarius antarcticus* or southern giant petrel *Macronectes giganteus*; Table 3.4; Wing et al. 2021, 2017), with the differences between the two seabird groups largely correlating with differences in their trophic levels (Wing et al. 2017). For major nutrients, comparison with other marine predators are limited to minke whales (*Balaenoptera acutorostrata*) from the North Atlantic (Freitas et al. 2023). On average, Antarctic fur seal scats had lower concentrations of Ca, Na, K and Mg than minke whale feces, except for Ca concentrations in the major nutrient-rich scats (Table 3.4).

Table 3.4: **Nutrient concentrations (mean \pm standard deviation, in mg.kg⁻¹ dry weight) for egesta (i.e. guano or feces) of several pinniped, baleen whale and seabird species as documented in the literature (Ref.) and in the present study (in bold).** For data of the present study, the number of samples n is associated to the two clusters ('cl') of samples as differentiated using a hierarchical clustering (HC) based on Ward's minimum variance method and using sample coordinates on the first principal components of a principal component analysis (PCA) conducted on the compositional datasets prior to HC, with the selected principal components explaining 90% minimum of the variance of the original dataset. All samples were collected in Antarctic or sub-Antarctic areas, except that of Freitas et al. (2023), collected in the North Atlantic

Taxa	Species	n	Ca	P	Na	K	Mg	Fe	Zn	Cu	Mn	Se	As	Ni	Co	Ref.
Pinnipeds	Antarctic fur seal (all)	58	79,043 \pm 76,164	47,675 \pm 43,714	6,611 \pm 3,158	2,291 \pm 1,108	9,210 \pm 5,092	3,617 \pm 4,433	412 \pm 233	183 \pm 187	91 \pm 106	24.4 \pm 25.2	3.70 \pm 2.11	16.6 \pm 20.7	2.90 \pm 3.35	^a
	Antarctic fur seal (cl 1)	23	161,220 \pm 48,092	93,141 \pm 32,234	8,513 \pm 3,289	2,161 \pm 611	9,998 \pm 4,362	818 \pm 914	360 \pm 187	56.5 \pm 53.7	26.3 \pm 14.7	10.9 \pm 5.88	2.61 \pm 1.03	3.99 \pm 3.18	0.60 \pm 0.42	^a
	Antarctic fur seal (cl 2)	35	25,041 \pm 25,660	17,797 \pm 14,626	5,362 \pm 2,381	2,377 \pm 1,341	9,210 \pm 5,092	5,456 \pm 4,861	446 \pm 257	266 \pm 197	134 \pm 119	43.7 \pm 24.6	4.4 \pm 2.33	25.0 \pm 23.1	4.41 \pm 3.58	^a
	New Zealand fur seal	-	-	-	-	-	-	279 \pm 58	495 \pm 74	696 \pm 229	18.7 \pm 4.4	-	5.29 \pm 0.97	3.61 \pm 1.09	1.92 \pm 0.55	^b
	Hooker's sea lion ¹	-	-	-	-	-	-	334 \pm 38	319 \pm 23	38.1 \pm 9.4	24.0 \pm 1.9	-	1.76 \pm 0.10	0.47 \pm 0.05	0.24 \pm 0.06	^b

Table 3.4: (continued)

Taxa	Species	n	Ca	P	Na	K	Mg	Fe	Zn	Cu	Mn	Se	As	Ni	Co	Ref.
	Hooker's sea lion ²		-	-	-	-	-	1,014 ± 572	228 ± 69	5.96 ± 0.63	16.7 ± 40.4	-	0.91 ± 0.13	1.83 ± 1.33	0.39 ± 0.39	^b
	Weddell seal	116	-	-	-	-	-	950.8 ± 148.9	270.7 ± 15.7	17.2 ± 2.8	28.7 ± 2.3	-	-	3.56 ± 0.4	0.73 ± 0.06	^c
Cetaceans	Blue whale	15	-	-	-	-	-	172.4 ± 114.1	-	-	-	-	-	-	-	^d
	Blue whale	2	-	98,000 ± 19,000	-	-	-	161.8 ± 106.5	460.8 ± 187.2	239.5 ± 68.6	33.4 ± 10.6	-	-	-	1 ± 0.8	^e
	Pygmy blue whale	7	-	-	-	-	-	63.4 ± 17.7	-	-	-	-	-	-	-	^d
	Pygmy blue whale	2	-	87,000 ± 25,000	-	-	-	63.4 ± 17	607.2 ± 66.0	312.2 ± 98.6	16.2 ± 9.0	-	-	-	0.5 ± 0.2	^f
	Hump-back whale	2	-	-	-	-	-	118.6	-	-	-	-	-	-	-	^d

Table 3.4: (continued)

Taxa	Species	n	Ca	P	Na	K	Mg	Fe	Zn	Cu	Mn	Se	As	Ni	Co	Ref.
	Hump-back whale	2	-	29,000 ± 21,000	-	-	-	118.6 ± 30.1	1,099 ± 553	74.1 ± 5.2	18.2 ± 10.7	-	-	-	0.9 ± 0.8	^e
	Fin whale	2	-	-	-	-	-	237.4	-	-	-	-	-	-	-	^d
	Fin whale	2	-	121,000 ± 4,000	-	-	-	237.4 ± 45.3	407.1 ± 52.8	290.7 ± 11.4	30.5 ± 6.9	-	-	-	2.1 ± 1.3	^e
	Sperm whale	1	-	69,000	-	-	-	756.7	2,664	1,635	96	-	-	-	2.2	^e
	Minke whale	31	97,929 ± 19,698	-	14,507 ± 4,323	6,723 ± 2,306	19,755 ± 5,024	489 ± 119	558 ± 104	34.3 ± 24.6	34.0 ± 10.3	6.1 ± 0.7	8.7 ± 1.8	1.0 ± 0.4	0.3 ± 0.1	^f
Sea birds	Adélie penguin	110	-	-	-	-	-	804.1 ± 153.9	281.9 ± 15.9	69.1 ± 2.9	21.8 ± 2.4	-	6.50 ± 0.38	3.1 ± 0.3	0.38 ± 0.06	^c
	Adélie, Gentoo & Chin-strap penguin	-	-	-	-	-	-	409.5 ± 288.7	210 ± 90.3	204.1 ± 141.7	30.2 ± 33.8	-	2.1 ± 2.4	4.1 ± 5.5	0.40 ± 0.35	^g

Table 3.4: (continued)

Taxa	Species	n	Ca	P	Na	K	Mg	Fe	Zn	Cu	Mn	Se	As	Ni	Co	Ref.
	Emperor penguin	18	-	-	-	-	-	832.6 ± 356.5	266.8 ± 37.8	31.5 ± 6.9	22.7 ± 5.5	-	3.87 ± 0.75	1.76 ± 0.9	0.30 ± 0.15	^c
	Snares crested penguin	-	-	-	-	-	-	193.7 ± 32.6	327.0 ± 63.3	43.6 ± 6.1	10.97 ± 0.84	-	5.83 ± 0.38	0.25 ± 0.11	0.07 ± 0.03	^b
	Yellow-eyed penguin	-	-	-	-	-	-	139.9 ± 27.6	182.5 ± 20.9	50.6 ± 26.3	18.75 ± 1.63	-	6.35 ± 2.77	0.38 ± 0.17	0.00 ± 0.00	^b
	Antarctic tern	-	-	-	-	-	-	222.2 ± 26.7	187.6 ± 20.7	61.7 ± 15.6	8.12 ± 0.45	-	6.95 ± 0.91	1.76 ± 0.16	0.21 ± 0.03	^b
	Brown skua ¹	-	-	-	-	-	-	882.0 ± 195.0	200.0 ± 26.0	20.0 ± 2.9	6.52 ± 0.84	-	2.40 ± 0.23	0.03 ± 0.02	0.00 ± 0.01	^b
	Brown skua ²	-	-	-	-	-	-	6,577 ± 1,309	413.2 ± 94.5	17.9 ± 4.9	53.14 ± 7.34	-	1.79 ± 0.27	32.23 ± 6.12	3.55 ± 0.63	^b
	Buller's albatross	-	-	-	-	-	-	173.5 ± 42.1	86.7 ± 26.7	15.4 ± 4.0	5.31 ± 2.30	-	3.79 ± 0.69	0.23 ± 0.07	0.05 ± 0.03	^b

Table 3.4: (continued)

Taxa	Species	n	Ca	P	Na	K	Mg	Fe	Zn	Cu	Mn	Se	As	Ni	Co	Ref.
	Southern royal albatross	-	-	-	-	-	-	158.0 ± 42.3	217.5 ± 28.4	19.3 ± 6.6	24.78 ± 7.15	-	1.01 ± 0.47	0.00 ± 0.00	0.00 ± 0.00	^b
	Wandering albatross	-	-	-	-	-	-	442.1 ± 114.2	404.6 ± 145.1	26.2 ± 8.9	13.67 ± 4.18	-	11.04 ± 2.50	1.16 ± 0.60	0.31 ± 0.24	^b
	Auckland Island shag	-	-	-	-	-	-	2,254 ± 1301	233.7 ± 158.2	38.3 ± 28.1	20.99 ± 10.93	-	6.50 ± 0.38	3.14 ± 1.10	0.73 ± 0.29	^b
	Southern giant petrel	-	-	-	-	-	-	2,343 ± 502	171.1 ± 38.6	181.9 ± 111.1	25.66 ± 5.44	-	3.87 ± 0.75	8.45 ± 3.15	1.11 ± 0.38	^b
	South polar skua	4	-	-	-	-	-	3,928 ± 782	111.7 ± 82.8	32.2 ± 15.1	43.1 ± 12.1	-	1.79 ± 0.27	4.98 ± 1.8	1.43 ± 0.33	^c

Table 3.4: (continued)

Taxa	Species	n	Ca	P	Na	K	Mg	Fe	Zn	Cu	Mn	Se	As	Ni	Co	Ref.
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Only vernacular names were indicated in the table for brevity: Antarctic fur seal *Arctocephalus gazella*, New Zealand fur seal *Arctocephalus forsteri*, Hooker's sea lion *Phocarctos hookeri*, Weddell seal *Leptonychotes weddellii*, blue whale *Balaenoptera musculus*, pygmy blue whale *Balaenoptera musculus breviceuda*, humpback whale *Megaptera novaeangliae*, fin whale, *Balaenoptera physalus*, minke whale *Balaenoptera acutorostrata*, Sperm whale *Physeter macrocephalus*, Adélie penguin *Pygoscelis adeliae*, gentoo penguin *Pygoscelis papua*, chinstrap penguin *Pygoscelis antarcticus*, emperor penguin *Aptenodytes forsteri*, snares crested penguin *Eudyptes robustus*, yellow-eyed penguin *Megadyptes antipodes*, Antarctic tern *Sterna vittata*, brown skua *Stercorarius antarcticus*, Buller's albatross *Thalassarche bulleri*, Southern royal albatross *Diomedea epomophora*, Wandering albatross *Diomedea exulans*, Auckland Island shag *Leucocarbo colensoi*, Southern giant petrel *Macronectes giganteus*, South polar skua *Stercorarius maccormicki*

^aThis study; ^bWing et al. (2017); ^cWing et al. (2021); ^dNicol et al. (2010); ^eRatnarajah et al. (2014); ^fFreitas et al. (2023); ^gSparaventi et al. (2021)

¹Snares Islands; ²Auckland Islands

3.4.3 Differential nutrient concentrations in potential fish prey versus potential predator feces

Differences in major and trace nutrient concentrations between potential fish prey and Antarctic fur seal scats likely reflect absorption rates and physiological needs of prey vs predator, and attest to the different nature of the two biological matrices. Forage fish are whole organisms and their composition reflects their physiological needs and homeostasis, whereas predator feces are waste, so their composition reflects the partial digestion of a prey mixture, some of which has been absorbed in the digestive process to meet the predator's body homeostasis. Absolute concentrations in major nutrients were of the same order of magnitude in both forage fish and Antarctic fur seal scats. Some were significantly higher in fish (Na, K) or in scats (Ca, P, Mg). These major nutrients are found in large concentrations in most living vertebrates, but are associated to different physiological functions (Banci et al. 2013). While Na^+ and K^+ cations are largely involved in cellular exchanges (Clausen and Poulsen 2013), including nutrient absorption in the gut (Hynd 2019), Ca, P and Mg are mostly found in intracellular compartments such as bones (Blaine et al. 2015). They may be associated to different availability in prey, given the higher concentrations in Ca, P and Mg associated to the presence and thus digestion of prey hard parts in Antarctic fur seal scats, or, alternatively, to different gut absorption rates. On the other hand, most trace nutrients were more concentrated in scats than in fish samples by at least one order of magnitude. This bio-concentration of trace nutrients is typical of predator egesta, and reflects the seals' low requirement and therefore active egestion of these nutrients compared to major nutrients (Ratnarajah et al. 2014). This was not the case for all trace nutrients however, as As was found in similar concentrations in both matrices. The different behaviour of As was also observed in seabird and pinniped egesta compared to As concentration in biological samples from lower trophic levels (algae, zooplankton or fish) (Sparaventi et al. 2021, Wing et al. 2017). This may indicate that predators have a higher absorption rate for this trace nutrient compared to others, although As metabolism is still unclear (Sattar et al. 2016, Ventura-Lima et al. 2011). With the exception of As, even Antarctic fur seal scats with high concentrations of major nutrients and low concentrations of trace nutrients were above those of the most concentrated forage fish species (Tables 3.3 and 3.4).

It is important to note that the mixture of ingested prey associated with each scat sample and cluster is unknown and may differ significantly from average diet descriptions, particularly given the temporal mismatch between the sampling used for these descriptions

and for the present study. In addition, forage fish samples in this study did not include all known Antarctic fur seal prey, such as cephalopods and crustaceans, or fish prey such as *Lichthys australis* (Lea et al. 2008). There is also a temporal mismatch between the fish and scat sampling campaigns, so we cannot exclude a temporal difference in nutrient concentrations in these fish over time not reflected in the more recent scats. This limits our ability to more accurately correlate nutrient concentration patterns in whole fish prey and fur seal scats, and to assess differential nutrient absorption rates. For example, we found that the fish species analysed here and previously identified as Antarctic fur seal prey were on average less concentrated in Fe, Cu and Mn than fish species never identified as fur seal prey. While this contrasts with Fe and Mn being the most bio-accumulated trace nutrients in fur seal scat, any specific comparison between the two biological matrices must take into account the relative contribution of each prey species. If only one species in the diet was enriched in these nutrients within the range of prey species (and thus contributed little to their average concentrations), but made up the bulk of the ingested biomass, then the consumption of this specific species could explain their high concentration in the scat. In the extreme case where the seal has fed on only one species before returning to its colony, the scat may reflect only the composition of that species and the seal's metabolism. Alternatively, if the ingested biomass consisted mainly of species with low concentrations of these nutrients, better described by the average values, then lower absorption rates for these nutrients compared to others could explain their high concentrations in the scats.

3.4.4 Implications for nutrient cycling

Nutrients contained in forage fish prey or in released inert Antarctic fur seal scats have different biological availability, so the patterns of differential concentration we found have different implications for nutrient biological recycling even without inferring a direct link between particular fish species and fecal samples. Due to the digestive process, nutrients in scats are more likely to be in a form that facilitates their re-introduction into lower levels of the food web. Once released, they can leach into the environment and may be up-taken by primary producers, either directly, after complexation with free bacterial ligands (Ratnarajah et al. 2017) or remineralisation by the microbial community (which can occur both on land and in the oceans). Alternatively, they can also be ingested directly by lower trophic levels (e.g. zooplankton; Roman and McCarthy 2010, or coprophagous terrestrial microfauna), and in the oceans they can sink to deeper water ecosystems.

In contrast, nutrients in fish are fixed in living biomass and are not available to lower trophic levels. Through predation however, an undigested fraction can be returned to lower trophic levels through the feces of its predator, with the remainder being transferred to higher trophic levels in the food web. Our results thus highlight the role of specific fish species in nutrient cycling when they are potential prey, and the potential for Antarctic fur seal scat to be a natural fertiliser at sea or in terrestrial and coastal ecosystems during the breeding season.

Our clustering of pelagic fish prey showed that some fish species were enriched in specific nutrients, for example *Champsocephalus gunnari* in Ca and P (cluster 2) or *Protomyctophum tenisoni* in Mg, Fe and Mn (cluster 4). If predators consume these prey, their egesta may be even more enriched in these nutrients - if they are not preferentially absorbed during digestion - and fertilise the environment where they defecate. In the SO, Fe and Mn can both be limiting to the growth of primary producers (Hassler et al. 2012a, Hawco et al. 2022). Thus, the consumption of species from cluster 4, enriched in Mg, Fe and Mn, may facilitate their return to euphotic waters and their recycling in light-based food webs, making them 'super-contributors' to the biological recycling of these nutrients. As said above, we cannot attribute the specific enrichment of fur seal scats in these nutrients to the consumption of super-contributors given the uncertainties associated to the mix of prey in the fecal samples and the temporal mismatch between fish and scat collection. However, it remains noteworthy that, of these potential super-contributors, *Protomyctophum* species have been previously identified in the diet of Antarctic fur seals around the Kerguelen Islands. Depending on the colony, year of assessment and method, they were found to make up from less than 1% to up to 18% of the average diet by weight (Cherel et al. 1997, Jeanniard-du Dot et al. 2017b, Lea et al. 2002a). They were also found to constitute up to ~ 20% (in reconstituted biomass) of the diet of King penguins *Aptenodytes patagonicus* around Kerguelen (Bost et al. 2002, Raclot et al. 1998), and could be included in the diet of other major air-breathing predators, such as Southern elephant seals *Mirounga leonina* (Cherel et al. 2010). They may thus represent important intermediary nutrient vectors in the waters around Kerguelen.

On the other hand, the specific enrichment of Antarctic fur seal scat in Fe and Mn is notable in the nutrient context of the Kerguelen Islands, and suggest they may be significant vectors for these nutrients when the animals are at sea. The surface waters of the Kerguelen Plateau are enriched in these two nutrients in the global SO context, but the sources and supply processes of natural fertilisation of these waters are not yet fully

understood (Bucciarelli et al. 2001, van Der Merwe et al. 2015). Marine predators are unlikely to fertilise waters on such a large scale, and their quantitative contribution to the biological cycling of nutrients is thought to be small compared to processes mediated by the microbial community or zooplankton (Maldonado et al. 2016), and more so to abiotic processes such as upwelling or atmospheric dust (Bowie et al. 2015). Nevertheless, Antarctic fur seals may induce patchy and transient enrichment events at local scales. If primary producers and microbiota respond to these events, similarly to what is observed with whale and seabird fecal material (Shatova et al. 2017, Smith et al. 2013), Antarctic fur seals could locally participate in shaping patterns of heterogeneity in the ecosystem nutrient background and productivity (McInturf et al. 2019). As they are present in high numbers during the productive season, along with other top marine predators, these local 'perturbations' to nutrient dynamics may add up in space and time to form a notable component of ecosystem dynamics in the area.

Furthermore, different species of primary producers (either terrestrial or marine) have specific nutrient needs so that communities of primary producers may respond differently when fertilised with a given nutrient recipe (Coale 1991, Shatova et al. 2017). Inputs from scats of different relative compositions could thus help maintain the heterogeneity in assemblages of species at lower trophic levels, if nutrients are reintegrated into organic production where they are deposited. The differences in Cu, Se and Zn concentrations between scats from the two colonies of Antarctic fur seals thus show how nutrients flow can vary at fine spatial and temporal scales, both at sea and on land. At sea, these differences are likely driven by characteristics of foraging habitats, *i.e.* prey availability, prey type and nutrient content, etc. Thus, spatial variation in the composition of predator scat may reflect the heterogeneity in their foraging environment, and the deposition of scat with different relative nutrient compositions at sea may further perpetuate this heterogeneity (McInturf et al. 2019). In addition, like most marine and amphibious predators Antarctic fur seals are highly mobile. For example, lactating females do not stay in one area for extended periods of time during their foraging trip (Jeanniard-du Dot et al. 2017b). They may therefore participate in nutrient transfers between areas with different ecological and biochemical contexts within their digestive time.

Fur seals also defecate on land when they come ashore during the breeding season. In this case, the coastal ecosystem benefit from allopatric marine-derived nutrients, with specific fertilisation pathways. On land, productivity is mainly limited by availability - or lack thereof - of major nutrients such as nitrogen (N) or P (Bokhorst et al. 2007,

Smith 2008), and nutrient inputs mediated by marine predators was shown to influence several sub-antarctic coastal ecosystems (Bokhorst et al. 2019a,b, Souza-Kasprzyk et al. 2022, Zmudczyńska-Skarbek et al. 2023). Interestingly, we have shown that a proportion of fish was specifically in major nutrients P and Ca (cluster 2). If their consumption translates into higher concentration for these nutrients in the feces of their amphibious predators, they may be potential super-contributors to their biological transfer to terrestrial ecosystems. From this cluster, *C. gunnari* and *G. acuta* were previously identified in the diet of Antarctic fur seal (Cherel et al. 1997, Lea et al. 2002a), and several species were also found in the diet of Gentoo penguins *Pygoscelis papua*, another amphibious predator inhabiting the Kerguelen area (Lescroël et al. 2004). In this context, it is interesting that we found a proportion of Antarctic fur seal scats enriched in the major nutrients P and Ca, whereas it is generally assumed that predator feces primarily bioaccumulate trace nutrients (Ratnarajah et al. 2014). This highlights the importance of multi-dimensional approaches to nutrient cycling in the context of nutrient transfers between different ecosystems.

Although we did not quantify N concentrations in either forage fish or Antarctic fur seal scats, most of the N ingested by pinnipeds is excreted in urine (Keiver et al. 1984, Ronald et al. 1984), which can be an additional fertiliser produced by predators both at sea and on land. In contrast to seabirds, the nutrient content of scats from amphibious predators with different pathways for egestion and excretion, such as pinnipeds, provides a partial picture of the biological cycling of nutrients they mediate. However, urine produced by Antarctic fur seals (and other pinnipeds) is more likely to stimulate primary productivity on land, where these major nutrients are limiting, than at sea in the High Nutrient Low Chlorophyll (HNLC) waters around the Kerguelen Archipelago.

While trace nutrient concentrations in soils may not be the primary limiting factor shaping patterns of terrestrial primary productivity, they are also essential for soil bacteria, terrestrial plants and fauna (He et al. 2005). Thus, the deposition of marine nutrients on land could affect ecosystems beyond the supply of major limiting nutrients. The differences in nutrient blends deposited by marine predators on land around their colonies, which are likely to result from the heterogeneity of nutrient fluxes at sea, could also promote heterogeneity in coastal ecosystems, either on land as nutrients are taken up into terrestrial food webs (Bokhorst et al. 2019a), or in coastal marine food webs as nutrients are leached out in front of colonies (Shatova et al. 2016). Our results therefore highlight the multiple facets of the role of Antarctic fur seals as active nutrient vectors in their ecosystems. At sea, the complexity of the processes involved makes it impossible to quantify *in situ* how

nutrients released by fur seals may be reintroduced to lower trophic levels of light-based food webs and affect ecosystem functioning. On land, however, conditions are more amenable to measurements and analyses that may reveal how these predators actively participate in the functioning of their ecosystem.

Data and code availability

Data generated and used for this study will be deposited on the securised public repository InDoRes (<https://www.indores.fr/>). Data and code to generate results presented in the present study are available in the public Github repository https://github.com/Lola-san/Ker_Arctgazella-prey-poop.

Essential nutrient release by two colonies of Antarctic fur seals on and around the Kerguelen Islands

The Kerguelen Plateau is characterised by unique nutrient and productivity dynamics compared to the surrounding Southern Ocean. It supports large populations of seabirds and marine mammals, some of which breed on the Kerguelen Islands. These species are involved in the recycling of essential nutrients at sea and the transfer of nutrients from sea to land on their land-based colonies, making them unique nutrient vectors in their ecosystems. However, their contribution to local nutrient dynamics is unknown. Here, we investigate the contribution of Antarctic fur seals (*Arctocephalus gazella*) to the biological cycling of seven nutrients on and around the Kerguelen Islands during their breeding season. Total nutrient concentrations were measured in 56 fur seal scats from two colony sites and used to determine nutrient output from lactating females on these sites using a bioenergetic model. We showed that they collectively deposit 635 kg (95% CI [553 - 717]) of phosphorus, 46.9 [40.2 - 54.0] kg of iron, 1.1 [1.0 - 1.3] kg of manganese and 38 [33 - 44] g of cobalt, the least released nutrient. About 75% of these nutrients are deposited at sea, in an area that likely includes waters on the Plateau and an offshore plume under its influence. At sea, fur seal defecation may trigger locally significant enrichment, even in the naturally fertilised waters of the Kerguelen Plateau. On land, fur seal nutrient deposition is more spatially concentrated and phosphorus deposition intensity is in the range of global crop fertiliser use. In addition, we identified commonalities and differences in multi-nutrient scat compositions between colonies, and highlighted the influence of variations in individual scat composition on nutrient release patterns at the scale of the colony. Assuming that observed differences reflect differences in diets, we explored the potential consequences of dietary shifts on nutrient deposition patterns in Antarctic fur seals on their role as nutrient vectors both on land and at sea. We argue that the role of marine predators, such as Antarctic fur seals, in the local nutrient dynamics of the Kerguelen area should not be overlooked and requires further investigation.

This chapter is a manuscript in preparation

4.1 Introduction

The Southern Ocean (SO) is the largest High Nutrient Low Chlorophyll (HNLC) region in the world's oceans (Blain et al. 2001). Its mixed layer is overall replete with major nutrients such as nitrogen (N) or phosphorus (P), but the growth and productivity of primary producers are limited by low concentrations of essential trace nutrients, mainly iron (Fe), so that any addition of this nutrient can stimulate the productivity throughout the food web if conditions are favorable (Blain et al. 2007, Boyd et al. 2000, Hassler et al. 2012a). The waters surrounding the Kerguelen Islands, a remote sub-Antarctic archipelago in the SO located on the northern part of the largest SO volcanic plateau (Kerguelen Plateau), benefit from natural Fe fertilisation by a combination of physical processes such as upwelling and atmospheric dust (Blain et al. 2001, van Der Merwe et al. 2015). The islands are also surrounded by the subtropical, sub-Antarctic and polar fronts, three circumpolar oceanographic currents that determine the SO nutrient background and fluxes (Bestley et al. 2020a). As their natural flows are influenced by the physical barrier created by the Plateau, these fronts participate in creating the unique nutrient and productivity dynamics of the Kerguelen region (Chapman et al. 2020, Lefèvre et al. 2008).

The increased productivity of Kerguelen waters makes the area an oasis for marine predators. Being also the only lands in thousands of kilometers around, the Kerguelen Islands support large colonies of amphibious species, such as Antarctic fur seals (*Arctocephalus gazella*), southern elephant seals (*Mirounga leonina*) and king penguins (*Aptenodytes patagonicus*), which rely on the coastal land for breeding, resting and moulting. Some of these species were severely depleted in the SO by direct human exploitation (fur seals and to a lesser extent elephant seals) in the 19th century (Hofman 2017, Miller 1991), but their populations have partially or fully recovered on Kerguelen (Guinet et al. 1996, Laborie et al. 2023).

These air-breathing predators consume large quantities of diverse prey (Guinet et al. 2001) and subsequently produce feces and urine enriched in essential major and trace nutrients (Belyaev et al. 2023, Wing et al. 2014, 2017). The processes of prey ingestion, digestion and predator metabolism facilitate the return of nutrients trapped in live prey to a form that can be re-mobilised by primary producers in their environment, either directly or after remineralisation by the microbial community (Subalusky and Post 2019). These highly mobile predators are thus potential nutrient vectors involved in the recycling

of nutrients in their environment, whether at sea or on their terrestrial colonies (Wing et al. 2014, 2021, 2017). On the latter, the deposition of marine nutrients by seabirds and pinnipeds has a structuring effect on soil enrichment and development (Ball et al. 2015, Benkwitt et al. 2021, Bokhorst et al. 2007). This nutrient enrichment can trigger bottom-up processes and positively influence the abundance and diversity of plant and soil communities (Bokhorst et al. 2019a). However, while the nutrient background and dynamics of the Kerguelen region have been extensively studied and modelled (e.g. Blain et al. 2008, D'Ovidio et al. 2015, van Der Merwe et al. 2015), the contribution of marine predators to the biological cycling of nutrients both at sea and on the islands' shores has been largely overlooked.

Amongst these top predators, Antarctic fur seals spend the eight winter months at sea, and the four austral summer months on land to breed and moult. During this period, they alternate between foraging trips at sea and land-based bouts. When at sea, they can transport nutrients from their predation point at depth to the surface where they defecate when they come to breathe, rest and travel, as well as to a different location given the time needed for digestion, possibly against physical forces such as wind, currents and gravity (McInturf et al. 2019, Roman and McCarthy 2010, Wing et al. 2021, 2017). As predators' feces can stimulate phytoplankton growth and influence their community structure (Shatova et al. 2017, Smith et al. 2013) and Antarctic fur seal scats are highly concentrated in Fe, manganese (Mn) or cobalt (Co) (Chapter 3), the local fur seal-mediated nutrient enrichment could locally enhance productivity and influence trophic dynamics. As they alternate between foraging at sea and feeding their young on land, lactating females also release some of their waste into terrestrial and coastal ecosystems, mediating cross-ecosystem nutrient transfers from sea to land (Smith 2008), and as such could help shaping the heterogeneity of coastal sub-Antarctic and Antarctic lands (Bokhorst et al. 2019a,b, Erskine et al. 1998, Smith 2008).

This study examines the role of Antarctic fur seals in the cycling and transfer of nutrients in the waters of the Kerguelen Plateau and in the coastal ecosystem of the Kerguelen Islands. We hypothesise that the contribution of such an amphibious top predator should not be neglected, although it operates at different spatio-temporal scales than the physical processes involved in shaping the unique context of the Kerguelen region. We have therefore quantified the nutrients released by lactating Antarctic fur seal females from two Kerguelen colonies during the Austral summer, when they forage at sea and on their land-based colony sites. Given the relative importance of different types

of nutrients at sea and on land, we determined the major (P) and trace (iron Fe, zinc Zn, copper Cu, manganese Mn, selenium Se and cobalt Co) essential nutrient inputs of fur seals. Ultimately, this study aims to provide a better functional understanding of the quantitative, qualitative, spatial and temporal contribution of fur seals to the biological cycling of nutrients in their ecosystems at different scales (individual, colony).

4.2 Material & Methods

4.2.1 Field data collection

Antarctic fur seal pups were counted on Cap Noir (Kerguelen Islands, Courbet Peninsula, 49°07' S 70°45' E) and Pointe Suzanne (Kerguelen Islands, Courbet Peninsula, 49°44' S 70°44' E) Antarctic fur seal colonies by two to three operators independently as an index of number of breeding females (one female per pup), between late December 2022 and mid-January 2023 (austral summer). Pups were counted separately along the land side of the colony, and on the beach. Counts started at dawn at both sites, when a majority of animals were resting on land. At Pointe Suzanne, several counts were carried out within 15 days. Pup counts served as an input in our bioenergetic model (detailed below).

4.2.2 Antarctic fur seal scat nutrient composition data

We used a scat nutrient composition dataset including dry weight concentrations of 58 fecal samples for phosphorous P, calcium Ca, potassium K, sodium Na, magnesium Mg, iron Fe, zinc Zn, copper Cu, manganese Mn, selenium Se, cobalt Co, arsenic As, nickel Ni, cadmium Cd, chromium Cr, molybdenum Mo, lead Pb, strontium Sr, vanadium V and silver Ag ([Chapter 3](#), dataset to be published in InDoRes repository). Methodological details of collection and analysis are described in [Chapter 3](#). Briefly, samples were collected on Cap Noir (27 samples) and Pointe Suzanne (31 samples), in 2021-2022 Austral Summer, and analysed by inductively coupled plasma mass spectrometry (ICP-MS, ICAP-Qc ThermoFisher) (for trace nutrients) and inductively coupled plasma atomic emission spectrometry (ICP-OES, Vista-Pro Varian) (for major nutrients).

In this study, we focused on scat concentrations for P, Fe, Zn, Cu, Mn, Se and Co. Two samples were identified as possible technical and statistical outliers and removed from the dataset. Concentration statistics (mean and standard deviation) are provided

in Table 4.1. Single scat relative compositions were described using the fraction of each nutrient in the total mix of nutrients included for the study.

Table 4.1: **Nutrient concentrations (median \pm standard deviation in mg.kg^{-1} dry weight) in Antarctic fur seal scat samples from two colonies (Cap Noir and Pointe Suzanne) on Kerguelen Islands (Southern Ocean).** Bold values indicate significant differences between the two sites (Mann-Whitney-Wilcoxon non parametric tests)

Colony site	n	P	Fe	Zn	Cu	Mn	Se	Co
Cap Noir	27	42,044 \pm 41,462	3,818 \pm 4,572	479 \pm 244	274 \pm 215	73.3 \pm 59.7	38.8 \pm 29.3	3.26 \pm 1.20
Pointe Suzanne	29	52,941 \pm 46,552	3,455 \pm 4,517	356 \pm 213	109 \pm 112	95.5 \pm 119.0	24.6 \pm 18.9	2.81 \pm 3.39
Cap Noir + Pointe Suzanne	56	47,687 \pm 44,114	3,630 \pm 4,506	415 \pm 235	189 \pm 188	84.8 \pm 95.0	31.4 \pm 25.3	2.95 \pm 3.39

4.2.3 Scat samples hierarchical clustering

We determined different classes of scats based on their nutrient composition using a hierarchical clustering (HC) for each colony.

We used an algorithm designed for compositional datasets, as their relative nature makes classical statistical methods such as HC unsuited for their analysis because these methods rely on Euclidean geometry (Filzmoser et al. 2018). We used `Robcomposition` R package (Filzmoser et al. 2018, Templ and Templ 2021), for which data is expressed in orthonormal coordinates through a specific transformation (isometric logratio) before conducting the clustering analysis based on Ward's minimum variance method. We selected the optimal number of clusters for each colony based on mean and median distances between clusters and minimum cluster size, and by visual assessment of the dendrogram. Nutrient concentrations in samples from the resulting clusters were described nutrient-by-nutrient using basic descriptive statistics (e.g. mean, median, standard deviation) and boxplots. We also computed Mann-Whitney-Wilcoxon (MWW) non-parametric tests to assess the statistical significance of nutrient-by-nutrient differences between clusters.

4.2.4 Nutrient release at individual and colony levels

The population structure of the fur seal colonies in the Kerguelen Islands was never assessed, so the proportion of mature males, breeding females and immature individuals is unknown in Cap Noir and Pointe Suzanne. The strong sexual dimorphism of this species (Shirihai 2008) would require to set specific metabolic parameters for each sex and life stage (body mass, energy requirements). In addition, mature and immature males and females likely have different foraging strategies and ecologies and therefore different time allocated to being at sea or staying on land (Green et al. 1989, Jones et al. 2021, March et al. 2021, Staniland and Robinson 2008). For example, lactating females divide their time between sea and land to balance the constraints of pup care given their limited fasting capacity, whereas mature males fast while maintaining harem territories (Goldsworthy 2008). Lactating females are the most numerous part of the population feeding at sea on breeding colonies (Page et al. 2003). Thus, as a first index we quantified nutrient release only for lactating females on the two breeding colonies of Cap Noir and Pointe Suzanne.

We used a bioenergetic model to estimate individual fur seal daily needs and food consumption, and extended it to estimate the production of dry fecal matter. Average Daily Metabolic Rate ($ADMR$, in $kJ.day^{-1}$) was estimated based on the Basal metabolic rate (BMR , in $kJ.day^{-1}$) using Kleiber (1975) formula (previously applied to marine mammal populations, e.g Barlow et al. 2008, 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. 2018, 2012). For an individual i :

$$ADMR_i = \beta_i \times BMR_i = \beta_i \times 293.1 \times BM_i^{3/4} \quad (4.1)$$

where BM stands for body mass (in kg). Costs of daily activities are different on land or at sea (Jeanniard-du Dot et al. 2017a), as fur seals feed at sea and fast on land when nursing their pup. We thus used β_{land} and β_{sea} to compute $ADMR_{land}$ and $ADMR_{sea}$ from Eq. (4.1). We also accounted for the percentage of time fur seal females spent on land (t_{land}) versus at sea ($1 - t_{land}$) during the breeding season to estimate the ration R (in $kg.day^{-1}$) needed for each individual to meet its $ADMR$, considering the mean energy content of its diet (E , in $kJ.kg^{-1}$ fresh weight) and the digestive assimilation efficiency (AE):

$$R_i = \frac{ADMR_{land} \times t_{land} + ADMR_{sea} \times (1 - t_{land})}{AE \times E_i} \quad (4.2)$$

This ration R_i represents the average daily ration if a seal i were to feed everyday throughout the breeding and moulting season in the model, but it is actually consumed

only during foraging bouts at sea. Similarly, we estimated individual fecal dry matter production for one daily ration F_{dm} (in kg) based on the dry matter content of this daily ration DM_R and on the individual dry matter release rate r_{dm} :

$$F_{dm,i} = R_i \times DM_{R,i} \times r_{dm,i} \quad (4.3)$$

We used Monte-Carlo simulations to simulate individual variability for each model parameter. Individual BM , β_{sea} , β_{land} , E and AE were defined using truncated normal distributions, with average, lower and upper limits set based on the literature (Table 4.2). Body mass for lactating females was set with a mean of 27 kg and a standard deviation of 20%, and with 20 and 38 as lower and upper limits, respectively (Jeanniard-du Dot and Guinet 2021). β_{land} was set with a mean of 3.3 and a standard deviation of 0.1 and β_{sea} with a mean of 4.7 and a standard deviation of 0.3, with minima and maxima set according to measured values (Arnould et al. 1996, Boyd 2002, Costa et al. 1989, Jeanniard-du Dot et al. 2017a). Average energy content of the diet and associated standard deviation were taken from Jeanniard-du Dot et al. (2017b), and lower and upper limits were set based on minimum and maximum energy density of identified prey species (Jeanniard-du Dot et al. 2017b; Table 4.2). Assimilation efficiency AE was defined as 0.85 ± 0.05 , based on experimental studies on captive pinniped (Booth et al. 2023). Fish water content approximate 80% (Chouvelon et al. 2022b, Nordøy et al. 1993), so we defined the dry matter content of the diet DM_R as following a uniform distribution between 15 and 25%. Similarly, individual dry matter release r_{dm} was defined as following a uniform distribution between 10 and 20% (Ronald et al. 1984).

4.2.4.1 Spatial and temporal parameters

We limited our estimate to the breeding and moulting period t , which lasts from December to March on the Kerguelen Islands (≈ 4 months). Each estimate of fecal dry matter production was multiplied by a duration of stay on land or at sea (d in days) to obtain the individual total production over the period t :

$$F_{dm,i,t} = F_{dm,i} \times d_i \quad (4.4)$$

Similarly to BM , β_{land} , β_{sea} , E , AE , DM_R and r_{dm} , d was set to vary individually following a uniform with 100 and 140 days as lower and upper limits (Shirihai 2008), respectively (Table 4.2).

Even though the duration of foraging and pup attendance bouts vary throughout the season (Goldsworthy 1995, Luque et al. 2007), lactating females alternate between 7-8 d

Table 4.2: Bioenergetic model parameters settings for Monte-Carlo simulations (n = 5000) with references used (Ref.)

Model parameter	Monte-Carlo simulation setting	Ref.
BM (kg)	$\sim \mathcal{N}(27, 5.4, 20, 38)$	a
β_{land}	$\sim \mathcal{N}(3.3, 0.1, 2, 4.5)$	b
β_{sea}	$\sim \mathcal{N}(4.7, 0.3, 3.5, 6.5)$	c
AE	$\sim \mathcal{N}(0.85, 0.05, 0.8, 0.9)$	d
E (KJ.kg ⁻¹ wet weight)	$\sim \mathcal{N}(7.75, 2.47, 4.0, 13.0)$	e
DM _R	$\sim \mathcal{U}(0.15, 0.25)$	f
r _{DM}	$\sim \mathcal{U}(0.1, 0.2)$	g
d	$\sim \mathcal{U}(100, 140)$	h
t _{land}	$\sim \mathcal{U}(0.15, 0.35)$	i
A (No.)	$\sim \mathcal{U}(\text{min pup count}, \text{max pup count} + 0.2 \times \text{max pup count})$	

BM is individual body mass, β_{land} the metabolic multiplier when on land, β_{sea} the metabolic multiplier when at sea, AE the assimilation efficiency, E the average energy content of ration R, DM_R the diet dry matter content the ration R, r_{DM} the dry matter release rate, d the number of days present on site, t_{land} the % of time spent on land and A the abundance of lactating females on the colony.

Truncated normal parameters are indicated as

follows: $\sim \mathcal{N}(\text{mean}, \text{standard deviation}, [\text{lower limit}, \text{upper limit}])$

^aJeanniard-du Dot and Guinet (2021)

^bJeanniard-du Dot et al. (2017a)

^cArnould et al. (1996), Boyd (2002), Costa et al. (1989), Jeanniard-du Dot et al. (2017a)

^dBooth et al. (2023)

^eJeanniard-du Dot et al. (2017b)

^eChouvelon et al. (2022b)

^eRonald et al. (1984)

^eShirihai (2008)

^eBoyd (1999), Boyd et al. (1991), Doidge and Croxall (1989), Goldsworthy (1999)

foraging trips at sea and 2-4d nursing on land on average (Boyd 1999, Boyd et al. 1991, Doidge and Croxall 1989, Goldsworthy 1999, Guinet et al. 2001, Jeanniard-du Dot et al. 2017b, Lea et al. 2008, 2002b). We thus used an average proportion of time spent on land t_{land} for each individual over the breeding period, following a uniform distribution between 15 and 35%. We obtained, for each individual i, the proportion of fecal matter deposited on land F_{dm,i,t,land} and at sea F_{dm,i,t,sea}:

$$F_{dm,i,t,land} = F_{dm,i,t} \times t_{land} \quad (4.5)$$

$$F_{dm,i,t,sea} = F_{dm,i,t} \times (1 - t_{land}) \quad (4.6)$$

Food passage rate ranges from a 5 to over 80-h in fur seals (Staniland 2002), so defecation is likely to cease after a 2-3-d of fasting on land. Similarly, when at sea, females are unlikely to defecate at the start of their foraging trip, i.e. before the first meal and

before first meal passage through the gastrointestinal tract. The time between departure from colony and the first foraging activity is $\approx 4-9$ -h (Bonadonna et al. 2000). Thus, both sea- and land-based bouts show a possible 12-48h period without defecation. We consequently considered these periods without defecation on land and at sea to balance each other out.

4.2.4.2 Individual nutrient releases

We then estimated nutrients released by each individual over the breeding period using dry matter nutrient concentrations of collected scats as follow:

$$N_{n,i,t} = F_{dm,i,t} \times x_{n,i} \quad (4.7)$$

where $N_{n,i,t}$ (in kg) is the total amount of nutrient n released in the feces of individual i over its breeding and moulting period t , and $x_{n,i}$ is the concentration of nutrient n in this individual's feces (in $mg.kg^{-1}$ dry weight, hereafter dw). We bootstrapped scat samples with resampling, and each individual in the colony was randomly assigned a scat sample with its specific nutrient concentrations.

4.2.4.3 Nutrient release at the colony level

Nutrient deposition at the colony level were then estimated based on colony lactating female abundance A :

$$N_{n,t} = \sum_{i=1}^A N_{n,i,t} \quad (4.8)$$

With visual pup counts, the abundance is unlikely to be positively biased because pups are more likely missed than counted twice. We therefore considered that lactating female population abundance A followed a uniform distribution with minimum set as the minimum pup count (Section 4.2.1) and maximum as the maximum pup count + 20% for each colony (Table 4.2). We performed 5000 simulations to account for the uncertainty in the abundance of animals at each colony. Then, we used the obtained colony abundance estimate as the number of simulations for Monte-Carlo simulations of individual parameters. That is to say that a population abundance of x individuals was defined by x individual random samplings of BM , β_{land} , β_{sea} , E , AE , DM_R , r_{dm} , t , t_{land} , and a simulated scat composition dataset with x samples obtained from a bootstrap procedure with resampling from our collected scat samples.

4.2.5 Different scat composition datasets to estimate total nutrient release

We estimated the total amount of nutrients released by lactating females in the two colonies using different versions of the simulated scat composition dataset to mitigate the small scat sample size by colony and increase their potential representativity at the colony level. This approach also allows to assess impacts of individual variation in the relative composition of waste produced at larger scales (within and between colonies).

4.2.5.1 At the colony scale

We estimated nutrient release in Cap Noir and Pointe Suzanne colonies using two different versions of the scat composition dataset. First, we used scat samples from each colony to generate two independent scat composition datasets using a balance bootstrap procedure, *i.e.* individuals simulated to estimate nutrient release at Cap Noir were assigned scats collected at Cap Noir only, and individuals at Pointe Suzanne scat samples collected at Pointe Suzanne only. Second, scat samples collected at both colony sites were combined into a single dataset, and the bootstrap procedure for assigning a scat nutrient composition to each individual in the colony was set so that scats from Cap Noir and Pointe Suzanne were resampled with equal probability. Individuals at Cap Noir could thus be matched to scat samples collected at Pointe Suzanne, and *vice versa*. In other words, we compared estimates that could be obtained using an average scat composition - in which case the differences observed between colonies would reflect differences in the number of animals at each site - to estimates obtained by adding the effect of possible spatial variation in the scat composition of animals from different colonies.

4.2.5.2 Within each colony

We used the estimates of nutrient release from the colony-specific scat composition as baseline estimates. We then tested if total nutrient release at each colony were significantly different when ratios of different scat types (*i.e.* from different clusters, [Section 4.2.3](#)) varied. We created bootstrap simulation scenarios giving different weights to each scat type cluster. For example, we first generated a dataset where only samples from cluster x were resampled in the bootstrap procedure, then a dataset where there was a 90% chance of samples from cluster x being resampled compared to samples from other clusters (which were all given an equal chance of being resampled), then 80%, 70%, *etc.* down

to a dataset where only samples from other clusters were resampled in the bootstrap procedure. We simulated 11 sets of scat composition data for each scat cluster, which we then used to estimate nutrient release at the colony level. We evaluated how the proportions of different scat types affected the total release of Fe, Zn, Cu, Mn, Se and Co by comparing the results of each scenario with baseline estimates.

4.2.5.3 Statistical assessment of differences

Given the aforementioned Monte-Carlo simulations and bootstrap procedures, our bioenergetic model outputs provide high-dimension results ($N = 5000$) which prevents the use of standard comparison statistical test (*e.g.* comparisons between colonies, or between colony estimates obtained with different scat composition datasets). Instead, we assessed unilateral binary relationships by calculating the percentage of values from one set of estimates that were superior to the compared set of estimates. We considered the difference to be significant when this percentage p was either $\geq 95\%$ or $\leq 5\%$ and we expressed p -values as $|0 - p|$ as in classic statistical tests (*i.e.* difference significant for $p \leq 0.05$). It should be noted that with this method, and unlike with classic statistical tests, our p can be equal to 0 or 1.

4.3 Results

4.3.1 Antarctic fur seal scat relative nutrient composition

The relative proportion of each nutrient within their total mix showed high inter-sample variations at both colonies (Fig. 4.1), even if P represented the greatest proportion in most. Fe followed by Zn were amongst the trace nutrients with the highest relative proportion in the total mix. Cu was seen as the most concentrated trace nutrient in few samples from Cap Noir only. On both colonies, proportion of Mn and Se were generally similar, while Co fraction remained below 1.0×10^{-3} .

4.3.2 Hierarchical clustering of scat samples in each colony

We identified the optimal number of 3 clusters for scats of both Cap Noir and Pointe Suzanne based on standard validity measures and sample dendrograms.

On Cap Noir, cluster 1 ($n = 7$) was characterized by the highest P concentrations (median \pm sd: $113,673 \pm 27,059 \text{ mg.kg}^{-1} \text{ dw}$; Fig. 4.2a, Table 4.3), intermediate Mn

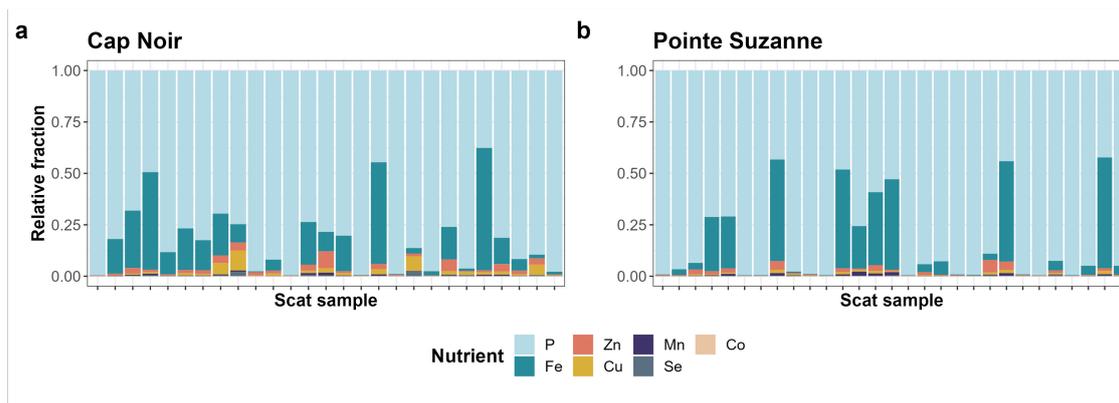


Figure 4.1: **Relative proportion of phosphorous P, iron Fe, zinc Zn, copper Cu, selenium Se and cobalt Co within the total nutrient mix in each Antarctic fur seal scat from (a) Cap Noir colony and (b) Pointe Suzanne colony (Kerguelen Islands, Southern Ocean).** Each bar represents one sample

concentrations ($22.5 \pm 9.4 \text{ mg.kg}^{-1} \text{ dw}$) and the lowest Cu ($76.3 \pm 78.0 \text{ mg.kg}^{-1} \text{ dw}$) and Se ($11.6 \pm 6.4 \text{ mg.kg}^{-1} \text{ dw}$) concentrations. Scats in cluster 2 ($n = 17$) had the highest concentrations in Fe ($4,316 \pm 4,805 \text{ mg.kg}^{-1} \text{ dw}$), Mn ($90.5 \pm 56.2 \text{ mg.kg}^{-1} \text{ dw}$) and Co ($4.09 \pm 3.44 \text{ mg.kg}^{-1} \text{ dw}$). Finally, scats in cluster 3 ($n = 3$) were characterized by the highest Se concentrations ($103.8 \pm 29.4 \text{ mg.kg}^{-1} \text{ dw}$) and the lowest Mn concentrations ($15.6 \pm 2.8 \text{ mg.kg}^{-1} \text{ dw}$). Results of between-clusters comparison MWW tests are provided in [Table 4.3](#).

Table 4.3: **p-values of Mann-Whitney-Wilcoxon non parametric tests comparing nutrient concentrations in Antarctic fur seal scats from different clusters**, as identified through a hierarchical clustering analysis using Ward's minimum variance method. Samples were collected on two colonies (Cap Noir and Pointe Suzanne) on the Kerguelen Islands (Southern Ocean), and the clustering was conducted on scats separated per colony. Bold values indicate a significant difference between clusters

Colony site	Clusters compared	P	Fe	Zn	Cu	Mn	Se	Co
Cap Noir	1 & 2	2.3×10^{-5}	7.6×10^{-4}	2.3×10^{-1}	2.5×10^{-3}	3.8×10^{-4}	4.0×10^{-5}	5.8×10^{-6}
	1 & 3	1.7×10^{-2}	1.8×10^{-1}	1.8×10^{-1}	1.7×10^{-2}	3.3×10^{-2}	1.7×10^{-2}	5.2×10^{-1}
	2 & 3	4.8×10^{-1}	3.5×10^{-3}	4.0×10^{-2}	2.2×10^{-1}	3.5×10^{-3}	3.5×10^{-3}	1.8×10^{-3}
Pointe Suzanne	1 & 2	1.0×10^{-6}	1.0×10^{-4}	6.3×10^{-1}	1.9×10^{-5}	2.0×10^{-6}	3.7×10^{-4}	1.1×10^{-6}
	1 & 3	6.7×10^{-4}	3.7×10^{-1}	7.7×10^{-1}	8.0×10^{-3}	5.9×10^{-1}	8.0×10^{-3}	6.8×10^{-1}
	2 & 3	1.9×10^{-1}	1.7×10^{-4}	3.0×10^{-1}	1.1×10^{-1}	1.7×10^{-4}	5.6×10^{-1}	1.7×10^{-4}

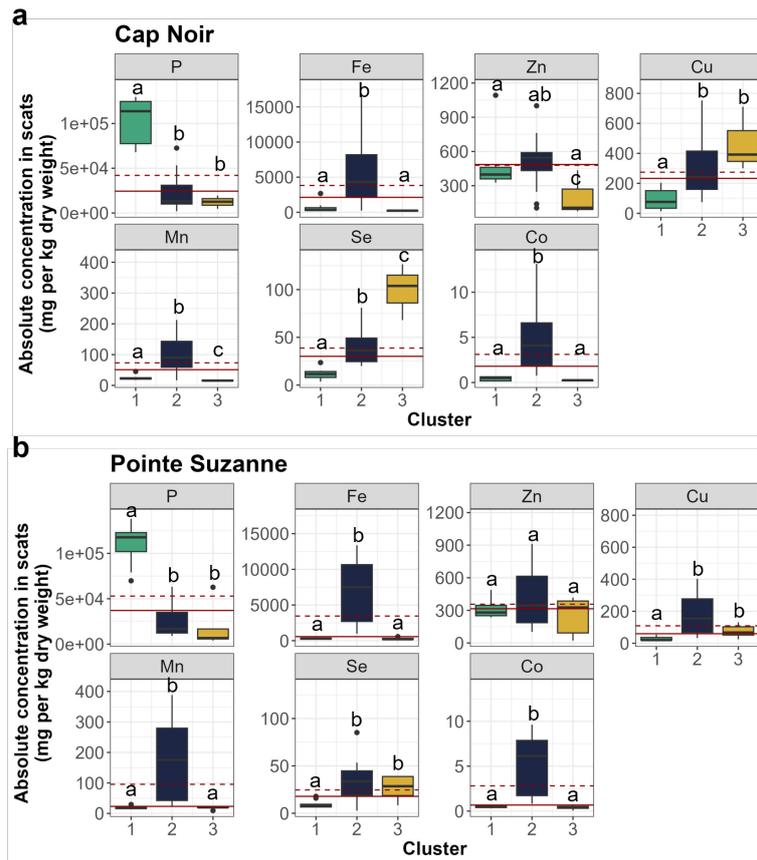


Figure 4.2: **Nutrient concentrations (in mg.kg^{-1} dry weight) in the 3 clusters (hierarchical clustering analysis based on Ward's minimum variance) of Antarctic fur seal scats from (a) Cap Noir and (b) Pointe Suzanne colonies (Kerguelen Islands, Southern Ocean).** Boxplots display the median and mean with solid dashed black lines in each box, lower and upper hinges correspond to the 25th and 75th percentiles, 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 individual points. Median and mean for all samples are indicated with the red solid and dashed lines, respectively. Letters above boxplots indicate significant difference between clusters (Mann-Whitney-Wilcoxon tests)

On Pointe Suzanne, scats in cluster 1 ($n = 10$) showed the highest P concentrations ($117,710 \pm 21,627 \text{ mg.kg}^{-1} \text{ dw}$; Fig. 4.2b; Table 4.3) and by the lowest concentrations in Cu ($19.8 \pm 13.8 \text{ mg.kg}^{-1} \text{ dw}$) and Se ($7.6 \pm 4.2 \text{ mg.kg}^{-1} \text{ dw}$). Scats in cluster 2 ($n = 14$) showed the highest concentrations in Fe ($7,496 \pm 4,476 \text{ mg.kg}^{-1} \text{ dw}$), Mn ($175.6 \pm 128.0 \text{ mg.kg}^{-1} \text{ dw}$) and Co ($6.15 \pm 3.38 \text{ mg.kg}^{-1} \text{ dw}$). Finally, scats in cluster 3 ($n = 5$) had the highest Cu ($67.2 \pm 41.9 \text{ mg.kg}^{-1} \text{ dw}$) and Se ($28.5 \pm 13.2 \text{ mg.kg}^{-1} \text{ dw}$) concentrations, although they were not significantly different from concentrations of samples from cluster 2 (19.8 ± 13.8 and $7.6 \pm 4.2 \text{ mg.kg}^{-1} \text{ dw}$ respectively; Table 4.3).

4.3.3 Colony counts and model outputs

The lowest pup counts were 500 in Cap Noir and 942 in Pointe Suzanne, and the highest 698 and 969, respectively. The average daily metabolic rates (*ADMR*) of lactating Antarctic fur seal females was 16,569 kJ.day⁻¹ (95% confidence interval [12,840 - 20,925]) when at sea and 11,633 [9,306 - 14,314] kJ.day⁻¹ when on land. The estimated average daily ration needed for lactating female fur seals was 2.4 kg.d⁻¹ [1.4 - 4.3], which represents 9% [5 - 15] of their body mass. We estimated colony abundance *A* at 728 lactating females [662 - 794] at Cap Noir and 1008 [913 - 1091] at Pointe Suzanne. For both colonies, the duration of the breeding and moulting season was 120 [101 - 139] days, and during this period 75% [65 - 85] of nutrient release was estimated to occur at sea and 25% [15 - 35] on land.

4.3.4 Colony nutrient release estimates using balanced scat composition datasets

When scats collected on both colonies were equally represented in the nutrient composition dataset, lactating Antarctic fur seal females released 263 kg [232 - 295] of P at Cap Noir and 364 kg [322 - 406] at Pointe Suzanne over their breeding period (Table 4.4; Fig. 4.3a). This translates into 198 kg [174 - 221] of P deposited at sea vs 65 kg [174; 221] deposited on land at Cap Noir, and 273 kg [242 - 305] at sea vs 90 kg [80 - 101] on land at Pointe Suzanne. For trace nutrients, quantities deposited in scats ranged from 20.1 kg [17.3 - 22.8] and 27.8 kg [24.2 - 31.4] for Fe in Cap Noir and Pointe Suzanne respectively to 17 g [14; 19] and 23 g [20; 25] for Co. With this nutrient composition dataset, all nutrients were released in greater quantities at Pointe Suzanne than at Cap Noir ($p \leq 5.0 \times 10^{-2}$, *p* referring to our calculated *p*-value as detailed in Section 4.2.5.3), in the same proportion of their relative population abundance ($\approx \times 1.6$).

Table 4.4: **Estimates of total nutrient released in scats by lactating Antarctic fur seal females (*Arctocephalus gazella*) at two colonies (Cap Noir and Pointe Suzanne) on the Kerguelen Islands (Southern Ocean).** Estimates were derived from a bioenergetic model including measures of nutrient concentrations in scats collected at the two colony sites (mean and 95% confidence interval in brackets), and took into account nutrients released at sea during their foraging trip or on land during their nursing bouts. "All scats combined" indicates that scat samples from both colonies were pooled together indistinctively in the simulated scat composition dataset used in the models and "Scats separated by colony site" that we used scat samples from both colonies independently (see [Section 4.2.5.1](#) for methodology details)

Simulated scat composition dataset	Colony site	Location		P	Fe	Zn	Cu	Mn	Se	Co
All scats combined	Cap Noir	Total	263 [232-295]	20.1 [17.3-22.8]	2.29 [2.05-2.54]	1.04 [0.92-1.17]	0.47 [0.41-0.53]	0.17 [0.15-0.19]		0.017 [0.014-0.019]
	Cap Noir	At sea	198 [174-221]	15.1 [13.0-17.1]	1.72 [1.54-1.91]	0.78 [0.69-0.88]	0.35 [0.31-0.40]	0.13 [0.12-0.15]		0.012 [0.011-0.014]
	Cap Noir	On land	65 [56-74]	5.0 [4.3-5.7]	0.57 [0.51-0.63]	0.26 [0.23-0.29]	0.12 [0.10-0.13]	0.04 [0.04-0.05]		0.004 [0.004-0.005]
	Pointe Suzanne	Total	364 [322-406]	27.8 [24.2-31.4]	3.2 [2.9-3.5]	1.4 [1.3-1.6]	0.65 [0.57-0.73]	0.24 [0.21-0.27]		0.023 [0.020-0.025]
	Pointe Suzanne	At sea	273 [242-305]	20.8 [18.1-23.5]	2.38 [2.13-2.63]	1.08 [0.95-1.21]	0.48 [0.43-0.55]	0.18 [0.16-0.2]		0.017 [0.015-0.019]

Table 4.4: (continued)

Simulated scat composition dataset	Colony site	Location	P	Fe	Zn	Cu	Mn	Se	Co
	Pointe Suzanne	On land	90 [80-101]	6.9 [6.0-7.8]	0.79 [0.70-0.87]	0.36 [0.31-0.40]	0.16 [0.14-0.18]	0.06 [0.05-0.07]	0.006 [0.005-0.006]
Scats separated by colony site	Cap Noir	Total	232 [203-261]	21.0 [18.3-24.0]	2.3 [2.4-2.9]	1.5 [1.3-1.7]	0.40 [0.35-0.45]	0.21 [0.19-0.24]	0.017 [0.015-0.020]
	Cap Noir	At sea	174 [152-197]	15.8 [13.7-18.1]	1.99 [1.78-2.20]	1.14 [1.0-1.27]	0.30 [0.27-0.34]	0.16 [0.14-0.18]	0.013 [0.011-0.015]
	Cap Noir	On land	58 [50-65]	5.2 [4.5-6.0]	0.66 [0.59-0.73]	0.37 [0.33-0.42]	0.10 [0.09-0.11]	0.05 [0.05-0.06]	0.004 [0.004-0.005]
	Pointe Suzanne	Total	405 [359-451]	26.4 [23.0-29.9]	2.7 [2.5-3.0]	0.8 [0.7-0.9]	0.73 [0.64-0.82]	0.19 [0.17-0.21]	0.021 [0.019-0.024]
	Pointe Suzanne	At sea	303 [269-338]	19.8 [17.2-22.4]	2.05 [1.83-2.25]	0.62 [0.55-0.70]	0.55 [0.48-0.62]	0.14 [0.13-0.16]	0.016 [0.014-0.018]
	Pointe Suzanne	On land	100 [89-112]	6.6 [5.7-7.5]	0.68 [0.61-0.75]	0.21 [0.18-0.23]	0.18 [0.16-0.21]	0.05 [0.04-0.05]	0.005 [0.005-0.006]

When scats were separated by their respective colony to generate the nutrient composition dataset, P and Mn releases were twice greater at Pointe Suzanne (405 kg [359 - 451] and 26.4 kg [23.0 - 29.9]) than at Cap Noir (405 kg [359 - 451] and 26.4 kg [23.0 - 29.9]); $p = 1$ for both nutrients; Table 4.4, Fig. 4.3b). Fe and Co releases were also significantly greater at Pointe Suzanne (728 g [635 - 822] and 21 g [19 - 24]) than at Cap Noir (404 g [358 - 452] and 17 g [15 - 20]), with $p = 1.0 \times 10^{-2}$ for both nutrients). However, Zn and Se releases were now similar between the two colonies ($p = 3.8 \times 10^{-1}$ and 6.3×10^{-1} , respectively), while Cu release was 1.6 times greater at Cap Noir (1.5 kg [1.3; 1.7]) than at Pointe Suzanne (0.8 kg [0.7; 0.9]); $p = 4.0 \times 10^{-4}$).

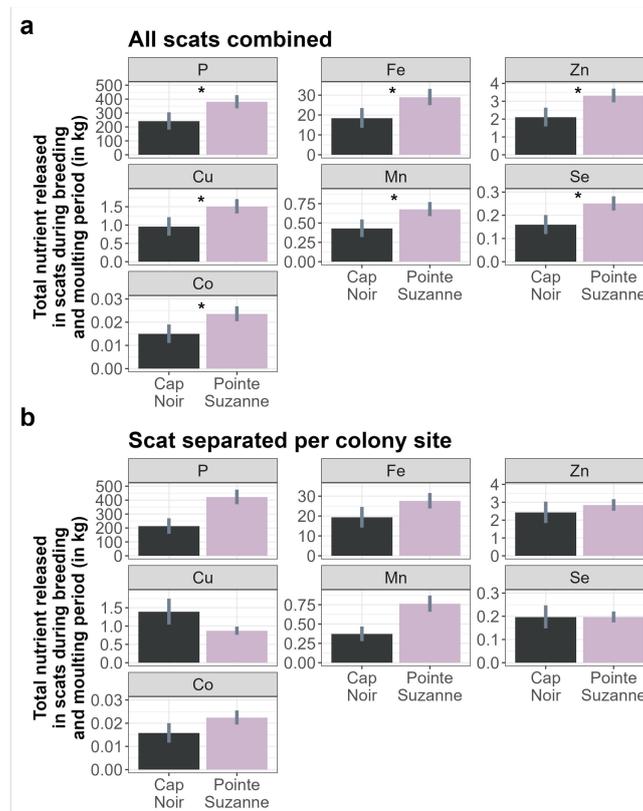


Figure 4.3: **Total nutrient released by lactating Antarctic fur seal females at Cap Noir (black) and Pointe Suzanne (purple) colonies (Kerguelen Islands, Southern Ocean) over a breeding season.** Estimates result from a bioenergetic model combined with a scat composition dataset where scat samples were either combined **(a)** or separated by colony site **(b)**. Bar height is the mean estimate (in kg), with the vertical line showing the 2.5 and 97.5 percentiles. Stars above bar plots indicate a significant difference between the two colonies (see Section 4.2.5.3)

4.3.5 Colony nutrient release estimates using cluster-varying scat composition datasets

Cap Noir

When all scats from Cap Noir were bootstrapped with equal chances of being resampled (*i.e.* baseline estimates, [Table 4.4](#)), the simulated scat composition dataset was composed of 26% of samples from cluster 1, 63% from cluster 2 and 11% from cluster 3. Variation in proportion of cluster 1 in the scat simulated dataset affected P total release the most, *i.e.* 65% [-50; +144] where 65% represents the mean absolute change compared to the baseline estimate and [-50; +144] the changes given a scenario where cluster 1 is not represented in the final dataset or represents 100% of the final dataset ([Fig. 4.4a](#), [Table 4.5](#)). Fe release levels were most affected by changes in the % of cluster 2 in the dataset (37% [-85; +51]), with the increase getting significant compared to the baseline values when there was $\geq 70\%$ of samples from this cluster in the scat composition dataset. Increasing the % of other clusters negatively affected total Fe release levels. The same patterns were observed for Mn (30% [-69; +42]) and Co (38% [-89; +53]). Zn release levels were most affected by changing importance of cluster 3 in the simulation dataset (18% [+8; -57]), with the decrease becoming significant only when % of cluster 3 in the dataset was $\geq 90\%$. Cu and Se release levels decreased when the % of cluster 1 increased in the simulation dataset, and increased with increasing % of cluster 3, even if rates of changes were different between the two nutrients. Cu release levels changed the most (decrease) when increasing the % of cluster 1 (29% [+23; -65]), whereas Se increased the most when the % of cluster 3 increased (50% [-19; +157]). Cu and Se releases remained stable when the % of cluster 2 varied.

Pointe Suzanne

When all scats from Pointe Suzanne were bootstrapped with equal chances of being resampled (*i.e.* baseline estimates, [Table 4.4](#)), it was composed of 35% of samples from cluster 1, 48% of samples from cluster 2 and 17% of samples from cluster 3. P release levels were the most affected - positively - by changes in the % of samples from cluster 1 in the scat composition dataset (56% [-57; +110]; [Fig. 4.4b](#), [Table 4.5](#)). Fe, Mn and Co release levels were similarly affected by changes in the % of the three clusters of scat samples, with a positive response when the % of samples from cluster 2 was increased, even though the change rate was higher for Fe (60% [-91; +100]) than for Mn (53%

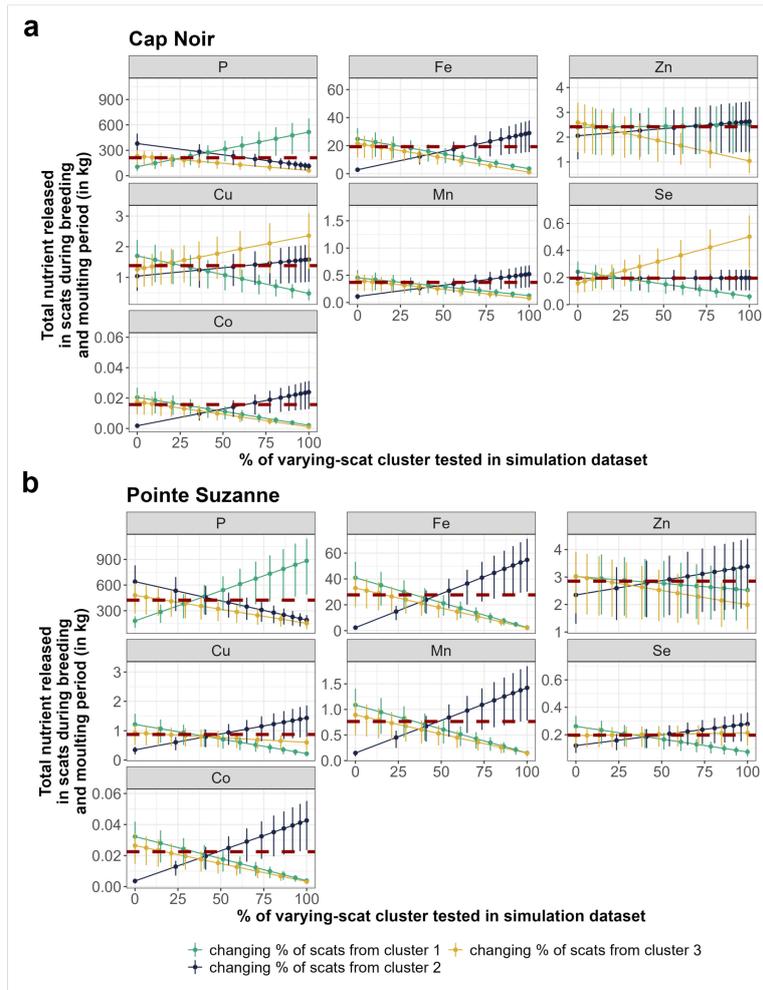


Figure 4.4: **Nutrient release estimates for lactating Antarctic fur seal females at Cap Noir (a) and Pointe Suzanne (b) colonies (Kerguelen Islands, Southern Ocean) given a proportion of specific scat cluster within the simulated scat composition dataset.** Estimates result from a bioenergetic model combined with a scat composition dataset obtained from several bootstrapping scenarios where the proportion of scat samples from different clusters varied from 0 to 100% (see [Section 4.2.5.2](#) for methodology details). Scats were clustered in 3 groups at each colony site (cluster 1 in green, cluster 2 in deep blue and cluster 3 in yellow). For each cluster-varying scenario, the circles and vertical lines indicate the estimate mean and 10 and 80 percentiles, respectively. Red dashed horizontal lines indicate the mean of baseline estimates obtained with a balanced bootstrap procedure including all colony scat samples

[-80; +88]) and Co (55% [-84; +92]). Fe, Mn and Co release levels decreased to the same extent when the % of samples from cluster 1 increased (46 [+49; -91], 41 [+44; -80] and 42% [+45; -83], respectively) and 3 (35 [+20; -92], 31 [+18; -81] and 33% [+19; -86]). Zn release levels remained constant, while Cu and Se release levels significantly decreased when the % of samples from cluster 1 were $\geq 80\%$ for Cu (38 [+41; -75]) and

Table 4.5: **Comparison between estimates of total nutrient released by lactating Antarctic fur seal females from two colonies on the Kerguelen Islands (Southern Ocean) derived from a bioenergetic model with varying simulated scat composition datasets.** Scats collected on Cap Noir and Pointe Suzanne were separated into 3 most similar clusters (using a hierarchical clustering). Proportion of these clusters were allowed to vary from 0 to 100%, with scats from other clusters being sampled with equal chances (see Section 4.2.5.2 for methodology details) in the final simulate scat composition dataset used in the bioenergetic model. We compared results from these different generated scat nutrient datasets with baseline values obtained with all scats from the colony being resampled with equal chances (Table 4.4 "Scats separated by colony site"). We reported the changes as follows: $[-NoValue-]-NoValue-[\Delta_{0\%}; \Delta_{100\%}]$ where $[-NoValue-]-NoValue-$ is the mean absolute % of change compare to the baseline value, and $\Delta_{0\%}$ and $\Delta_{100\%}$ the % of change when the % of scats from the cluster tested was set to 0 and 100, respectively. Bold values indicate cases where $[-NoValue-]-NoValue- \geq 50\%$

Colony site	Clusters compared	P	Fe	Zn	Cu	Mn	Se	Co
Cap Noir	1	65 [-50;	36 [+29;	2 [-1;	29 [+23;	29 [+24;	31 [+25;	39 [+31;
		+144]	-81]	+4]	-65]	-66]	-69]	-87]
	2	34 [+79;	37 [-85;	7 [-14;	11 [-24;	30 [-69;	1 [-1;	38 [-89;
	-46]	+51]	+9]	+15]	+42]	+1]	+53]	
	3	23 [+9; -	30 [+13;	18 [+8; -	23 [-9;	25 [+11;	50 [-19;	30 [+12;
		71]	-95]	57]	+71]	-79]	+157]	-93]
Pointe Suzanne	1	56 [-57;	46 [+49;	5 [+7; -	38 [+41;	41 [+44;	32 [+34;	42 [+45;
		+110]	-91]	11]	-75]	-80]	-82]	-83]
	2	33 [+52;	60 [-91;	12 [-17;	40 [-60;	53 [-80;	25 [-38;	55 [-84;
	-55]	+100]	+20]	+66]	+88]	+43]	+92]	
	3	24 [+14;	35 [+20;	11 [+7; -	11 [+7;	31 [+18;	4 [-1;	33 [+19;
		-64]	-92]	29]	+30]	-81]	+9]	-86]

$\geq 90\%$ for Se (42 [+45; -83]).

Results of statistical tests (*i.e.* our calculated p -value p , Section 4.2.5.3) between baselines estimates and simulated scenarios estimates are provided in Chapter 4 - Supplementary Table 1 for both colonies.

4.4 Discussion

This study provides quantitative estimates of the contribution of Antarctic fur seal females from two Kerguelen Islands colonies to the biological cycling of seven essential nutrients through defecation during their breeding season. We show how fine-scale variations in the nutrient composition of individual scats can affect nutrient release at the colony level.

These results provide insights into seal-mediated nutrient release patterns, their spatio-temporal variability on and around the Kerguelen Islands, and their potential contribution to ecosystem dynamics.

4.4.1 Inter- and intra-colony differences in total nutrient release and individual scat compositions

Scat-mediated multi-nutrient releases in Cap Noir and Pointe Suzanne not only reflected differences in population abundance, but also the differences in individual scat compositions. Indeed, female fur seals were 1.6 times more numerous at Pointe Suzanne colony than at Cap Noir, and yet, females at Cap Noir released 1.6 times more Cu than lactating females at Pointe Suzanne, or similar levels of Zn. In addition, females at Pointe Suzanne released twice as much P and Mn than females at Cap Noir. These colony-specific nutrient depositions likely reflect differences in fur seal prey and diet between individuals from each colony. These inter-colony differences suggest that estimating large-scale predator nutrient release based on averages, whether of diet and prey compositions (e.g. [Chapter 1](#), [Lavery et al. 2010](#), [Roman and McCarthy 2010](#)) or of fecal nutrient contents (e.g. [Lavery et al. 2015](#), [2014](#)), likely overlooks important individual-based fine-scale variability within a given species. Population variability may not be important if the focus is on large-scale estimates only and not population relative contributions. However, our results suggest that small-scale variations in diets, prey or scat composition of different populations should be considered in any approach that focuses on fine-scale spatial patterns of nutrient deposition, whether quantitative (amounts released) or qualitative (relative composition of nutrient cocktails released), such as the present study.

Interestingly, scat composition clustering showed similarities between colonies. For both of them, the most abundant scat type was enriched in Fe, Mn and Co (cluster 2), the second was enriched in P and had low concentrations of trace nutrients except for Zn (cluster 1), and the least abundant was characterised by low concentrations of all nutrients but Cu and Se (cluster 3). These similarities could be due to (i) a similar population structure on the two colonies and/or (ii) a similar intra-colony variability in fur seals' foraging strategies and diets. Indeed, mature fasting males, lactating females or non-breeding juveniles have different physiological needs and diets ([Jones et al. 2021](#), [March et al. 2021](#), [Staniland and Robinson 2008](#)) - which might result in individual variability in scat composition, and population structure is likely similar at both colonies. Alternatively and maybe concomitantly, it may reflect the diversity of individual diets, as suggested

by the variability in foraging behaviour observed at the colony level (Jeanniard-du Dot et al. 2017a, Lea et al. 2002b) and the differences in the foraging areas targeted by the animals (Lea and Dubroca 2003). Scats enriched in Fe, Mn and Co may reflect the preferential consumption of prey species enriched in these nutrients (e.g. *Protomyctophum* myctophids fish) and be associated with a specific foraging behaviour and/or area, whereas scats enriched in P may reflect the preferential consumption of prey species enriched in this nutrient (e.g. ice-fish *Champsocephalus gunnari*) and be associated with a different foraging behaviour and/or area (Bost et al. 2002, Lea and Dubroca 2003, Lea et al. 2002b, Chapter 3). Benthic cephalopod and crustacean species can also have higher concentrations in Cu and Se (Chouvelon et al. 2022b), so scats in cluster 3 may reflect individuals with a greater proportion of these taxa in their diet. The proportion of seals with one or the other diet and strategy may be similar in both colonies, explaining the similar colony ratios between different scat composition type. In any case, these similarities indicates a common diet and prey base at both colonies amidst notable individual variability.

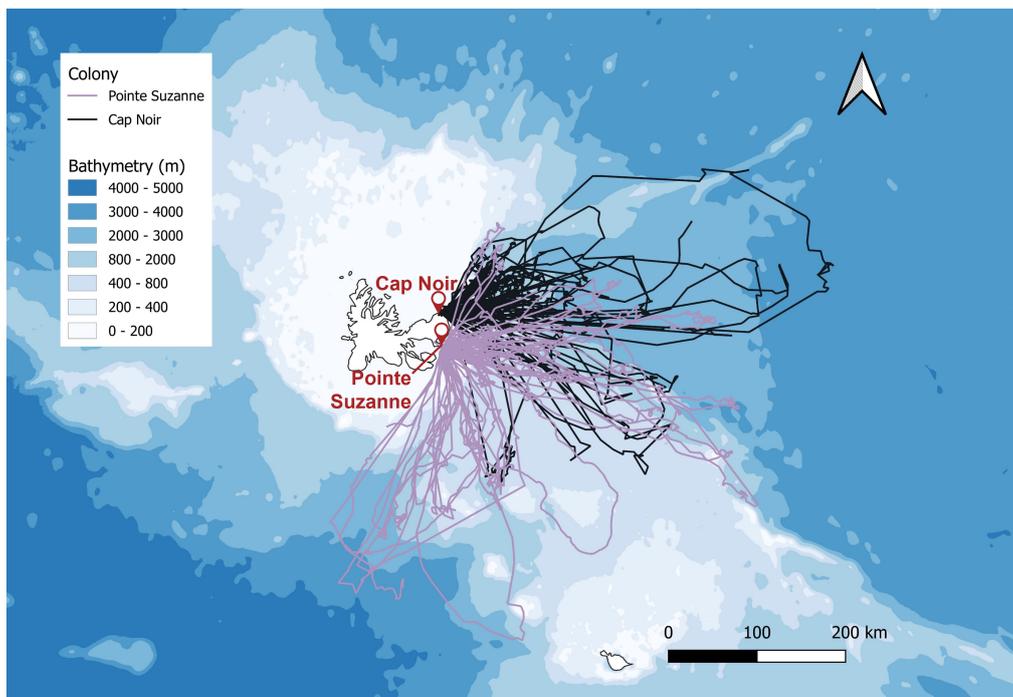


Figure 4.5: **At-sea tracks of lactating Antarctic fur seal females from two colonies on Kerguelen Islands (Southern Ocean) equipped at Cap Noir in 1998, 1999, 2000 (in black) or Pointe Suzanne in 2007, 2010, 2012, 2022 (in purple).** Data published in Guinet et al. 2001, Jeanniard-du Dot et al. 2017a, Lea et al. 2002a, Lea and Dubroca 2003, Lea et al. 2008 for years 1998, 1999, 200, 2007, 2012; 2010 data were not published and 2022 data are not yet published and were collected under permit #37480-2022052514544991-V7 in 2022-2023 Austral Summer. Blue gradient background indicates bathymetry

On the other hand, there were also clear differences in scat composition between the two colonies. For example, in cluster 2, P, Fe, Mn and Co concentrations were higher in Pointe Suzanne than in Cap Noir, while Zn, Cu and Se concentrations were higher in Cap Noir. In cluster 3, scats from Cap Noir were ≈ 6 and 4 times more concentrated in Cu and Se than scats from Pointe Suzanne, respectively. Here, assuming similar population structures between the two breeding colonies, these differences most likely reflect colony differences in diet that could be related to their different foraging areas (Fig. 4.5). Cap Noir fur seals forage in the eastern part of the Kerguelen Plateau and in deep waters off the shelf break (>500 m deep), while Pointe Suzanne fur seals forage mainly Southeast of the Kerguelen Islands on the plateau (<500 m) (Lea et al. 2008, Jeanniard-du Dot et al. 2017a; Fig. 4.5). The relative availability of prey species may differ between these areas (Duhamel et al. 2017), which could result in slight (cluster 1 and 2) or drastic (cluster 3) differences in proportion of prey species in the fur seal diet between colonies. Alternatively, the differences could also reflect differences in the nutrient content of the same species from different areas.

We cannot associate each scat type with specific diets or prey species without more information on the prey mix associated with each scat sample. However, scat nutrient concentrations and their variability within and between colonies already provide valuable information on Antarctic fur seal contributions to nutrient cycling on and around the Kerguelen Islands at individual, colony and population levels, and highlight how individual differences are a source of variation in these processes (McInturf et al. 2019).

4.4.2 Antarctic fur seal nutrient release at sea

Given the limited overlap between at-sea foraging areas of seals from Cap Noir and Pointe Suzanne (Fig. 4.5), nutrients biologically recycled by fur seals from these two colonies will likely not be released in the same areas around the Kerguelen Islands. Foraging areas of fur seals from the two colonies are both associated with meanders of the circumpolar polar front but they also correspond relatively well to two water masses with different nutrient and productivity dynamics (Bowie et al. 2015, Koubbi et al. 2016).

Waters on the plateau (where fur seals from Pointe Suzanne preferentially forage) show higher Fe and Mn nutrient concentrations and productivity regimes than waters off the eastern plateau (where fur seals from Cap Noir preferentially forage), which can be identified as an offshore plume, *i.e.* a re-circulation structure under the influence of the plateau but with comparatively lower nutrient concentrations and productivity

regimes (Bowie et al. 2015, van Der Merwe et al. 2015). Differences in dissolved nutrient concentrations between these two water masses are on average greater for Fe and Mn than for other trace nutrients such as Cu and Co (Bowie et al. 2015, Qu  rou   2014). Overall, fur seals thus appear to release more Fe and Mn in the most enriched waters. However, this is not the case for all nutrients. Fur seals from Cap Noir release twice as much Cu as fur seals from Pointe Suzanne, likely also in the offshore plume where they forage and where dissolved Cu concentrations are ≈ 4.4 lower than in waters on the Kerguelen plateau (Qu  rou   2014). However, while total colony levels of nutrient release provide information on large-scale deposition patterns, Antarctic fur seals do not swarm or hunt in groups when at sea. Nutrient concentrations in individual scats may therefore be more relevant to understand their potential impact on nutrient dynamics, taking into account the characteristics of the ecosystem in which they are released. The nutrient enrichment caused by fur seal defecation in the offshore plume may be relatively greater than the nutrient enrichment caused by fur seal defecation on the plateau, since the latter is naturally more nutrient rich. In addition, the different water masses are likely to be associated to differences in their low trophic levels communities (microbial community, phytoplankton, zooplankton) in terms of species assemblages and relative abundance. As different primary producer communities may respond differently to a perturbation in their biochemical environment (Moore et al. 2007), including different local enrichment from predators defecation, even apart from the differences observed in the multi-nutrient content of scats from the two colonies. The contribution of fur seals to the biological cycling of nutrients in their ecosystems may therefore differ not only spatially and quantitatively, but also qualitatively between colonies.

It is difficult to infer the ecosystem response to potential fertilisation by Antarctic fur seals around The Kerguelen Islands, given the mismatch between the large-scale biochemical characterisation of nutrient dynamics in this region and the very local scale of their individual contribution. It is even more so difficult when the biochemical forms of released nutrients (e.g. dissolved or particulate) as well as their dissolution and retention rates in surface waters are unknown. Yet, total nutrient concentrations in scats can be used as an indicator of relative enrichment when compared to the total nutrient concentrations in the upper mixed layer (dissolved + particulate), or to the biological growth of microbial and mesozooplanktonic communities. For example, one square meter of the mixed layer contains $\approx 934 \mu\text{mol}$ of Fe on the plateau (with a mixed layer of $\approx 144 \text{ m}$) and $63 \mu\text{mol}$ in the offshore plume (with a mixed layer of $\approx 45 \text{ m}$) (Bowie et al. 2015). In comparison,

fur seal scats contained $\approx 0.38 \mu\text{mol}$ of Fe (5.86 g of dry matter including 21.3 mg of Fe per scat). It could represent a significant enrichment depending on the relative dispersion and dilution of nutrients contained in scats in the mixed layer. If we assume an even distribution of Fe throughout the mixed layer, a m^3 of water would contain $\approx 6.5 \mu\text{mol}$ of iron on the plateau and $\approx 1.4 \mu\text{mol}$ in the offshore plume. At the immediate time of release, a scat would potentially increase the iron background by ≈ 6 and 27% in one m^3 of water on the plateau and in the offshore plume, respectively. These % are likely higher if defecation occur near the surface, as concentrations of both dissolved and particulate Fe typically increase with depth (Blain et al. 2008, van Der Merwe et al. 2015). On the other hand, if we assume that iron contained in scats disperse homogeneously throughout one square meter of the mixed layer, concentrations of fur seal fecal Fe once dispersed could reach $\approx 2.6 \times 10^{-3} \mu\text{mol} \cdot \text{m}^{-2}$ on the plateau and $\approx 8.4 \times 10^{-3} \mu\text{mol} \cdot \text{m}^{-2}$ in the offshore plume. In comparison, the microbial and mesozooplanktonic communities regenerated on average $45 \times 10^{-3} \mu\text{mol} \cdot \text{m}^{-2}$ on the plateau and $27 \times 10^{-3} \mu\text{mol} \cdot \text{m}^{-2}$ in the offshore plume (Bowie et al. 2015).

The above iron concentrations (scats and water masses) and biological regeneration rates (water masses) were measured and estimated during one campaign and on a couple of stations. However, they provide an indication of the order of magnitude at which these processes operate. These simplistic calculations suggest fur seal could be locally important contributors to the biological recycling of iron when they defecate at sea, despite the non-limiting conditions observed during the high productivity season. Incubation experiments with seabird guano fertilisation in waters of different nutrient regimes have shown productivity to be boosted by guano addition both in area depleted and repleted with micronutrients (Shatova et al. 2016). Moreover, the multi-nutrient patchy and transient scat-mediated enrichment may influence species assemblages of low trophic levels, by for example locally favouring a specific phyto- or zooplankton species or microbial strain depending on their affinity for specific nutrients (Shatova et al. 2017). Antarctic fur seals, together with the other marine predators present in these waters, thus likely contribute to the overall nutrient and trophic dynamics of these areas. It is however still difficult to integrate them as biological components of biogeochemical models given the patchiness and spatio-temporal variability of their release patterns. In any case, the local perturbations in nutrient distribution and availability caused by Antarctic fur seal defecation are likely to increase the heterogeneity in the nutrient background of their environment, thereby increasing fine-scale habitat complexity, with possible effects

on lower trophic level community responses (patchiness, productivity, diversity, species assemblages) (Kovalenko et al. 2012, McInturf et al. 2019, Mouillot et al. 2013, van der Plas 2019).

Finally, Antarctic fur seals are also highly mobile at sea, and are as such involved and spatial nutrients transfers. Lactating females can travel from 143 ± 113 to 635 ± 77 km on a single foraging trip and do not spend long periods in their foraging areas, but are constantly moving through them (Jeanniard-du Dot et al. 2017b, Lea et al. 2006, 2008). The foraging areas of an individual fur seal can be as large as $\approx 2,500$ km², reaching $\approx 40,000$ km² at the colony scale (Lea et al. 2008). Thus, individual fur seals are likely to mediate horizontal nutrient transport, possibly over several tens of kilometres within their digestion time, potentially against abiotic forces such as wind and currents. The nutrient characteristics of the area where the prey was uptaken and those of the area where nutrients are released through fur seal defecation may differ, which adds another level of complexity to the local ecosystem heterogeneity they may mediate (McInturf et al. 2019, Subalusky and Post 2019). Antarctic fur seal may also mediate vertical nutrient transfers within the water column. While their foraging dives are relatively shallow (≈ 20 -50 m) (Jeanniard-du Dot et al. 2017b, Lea et al. 2002b), they mostly feed on mesopelagic prey (Cherel et al. 1997, Jeanniard-du Dot et al. 2017a, Lea et al. 2002a) which migrate in the upper water column at night (Bost et al. 2002). The nutrients released in their scats may therefore be in part allochthonous *i.e.* originating from outside the surface water layer where they are released (Lavery et al. 2010).

4.4.3 Antarctic fur seal nutrient release on land

On land, fur seal-mediated nutrient deposition is concentrated on limited coastal surface areas where animals gather in dense colonies during a specific time period. In our case, fur seal's colonies occupy ≈ 53 km² at Cap Noir and ≈ 26 km² at Pointe Suzanne at mid breeding season. This is ≈ 100 times smaller than a potential colony influence area at sea as defined by their foraging range (Section 4.4.2). In addition and unlike at sea, nutrient dispersion remains limited on land even if abiotic conditions (wind, precipitation) can slightly increase scats spatial footprints. As such, this fur seal-mediated nutrient enrichment can accumulate during their breeding season on land and likely persists beyond the seals departure, as seen for mammal grazers fecal deposition (Abbas et al. 2012, Barthelemy et al. 2018, Tabeni et al. 2022). This intense pulse of allochthonous nutrient input can thus impact primary producers of the terrestrial trophic web.

Major nutrients such as nitrogen N and phosphorus P, potassium K, calcium Ca, magnesium Mg and sodium Na, are more limiting for terrestrial plant production than trace nutrients (Uchida, R. and Silva 2000). In this study, we only quantified fur-seal mediated P release levels which reached $\approx 58 - 65$ kg at Cap Noir and $\approx 90 - 100$ kg at Pointe Suzanne over their breeding season. Assuming an homogeneous release by seals over the colony areas (and no drain from rainwater), fur seals would deposit ≈ 0.9 to 1.4 g.P.m⁻² at Cap Noir and ≈ 3.1 to 4.3 g.P.m⁻² at Pointe Suzanne, which are in the range of phosphorus fertilizer used for agricultural production worldwide (0.1 to over 4 g.P.m⁻²; Lu and Tian 2017). This further suggests that Antarctic fur seals quantitatively shape patterns of productivity at their colony site. Beyond P, Antarctic fur seal scats also contain high Ca, Mg and Na concentrations (Chapter 3), and could as such provide a complete fertiliser formula for terrestrial ecosystems. In addition, pinnipeds mainly excrete N in urine (Keiver et al. 1984, Ronald et al. 1984), so scats provide only a partial picture of fur seal contribution to biological nutrient cycling in terrestrial ecosystems.

Trace nutrients are also essential for most terrestrial life form (Hu et al. 2021, Uchida, R. and Silva 2000), and low concentrations can provoke deficiencies and limit plant productivity (He et al. 2005, Hu et al. 2021, Uchida, R. and Silva 2000). On land, the capacity of the ecosystem to recycle nutrients from organic matter such as feces is mainly determined by decomposers, from bacteria to invertebrates, that subsequently make them available to primary producers. However, soil microorganisms and plant communities can respond to trace nutrients supplies by changes in their biomass, activity and community structure, whether positive or negative (if concentrations are too high) (He et al. 2005, Mooshammer et al. 2014, Thies and Grossman 2006). Because each species has specific nutrient requirements and metabolism, their response to a given enrichment may differ for the same supply of major nutrients if the concurrent supply of trace nutrients varies. In addition, the supply of multiple nutrients may promote complementary and more efficient use of resources at lower trophic levels, as each organism uses them according to its needs and capabilities (Monk and Schmitz 2022, Scherer-Lorenzen et al. 2022). Thus, the trace nutrient fraction of marine predator inputs should not be neglected when considering the effects of marine nutrient deposition by amphibious predators on land, and the effects of nutrient deposition by fur seals may extend beyond the productivity aspects of major nutrient inputs to potential community structuring by both major and trace nutrients.

Our results finally highlighted a difference in intensity and quality of nutrient deposition between Cap Noir and Pointe Suzanne, which could thus lead to different impacts

on terrestrial ecosystem primary productivity and community structure. However, the ecosystems at the two colonies may differ in their nutrient requirements and recycling capacities, as can be the case in marine ecosystems. As these characteristics are largely determined by abiotic factors such as exposure, slope, wind and rain regimes (Aiba et al. 2012, Kimberley et al. 2014, Kreft and Jetz 2007, Wang et al. 2023), these differences between Cap Noir and Pointe Suzanne alone may imply a different response of the ecosystem to similar type and quantity of fertilisers. We suggest that the influence of fur seal-mediated nutrient deposition on their colony sites should be further investigated separately to account for both the different abiotic characteristics of the sites and the differences in the nutrient cocktails released by fur seals on the two colonies.

4.4.4 Spatio-temporal variability in deposition patterns

Oceanographic conditions vary both spatially and temporally (seasonally and annually) (Bowie et al. 2015, D'Ovidio et al. 2015). As fur seals are opportunist feeders, they can switch prey depending on what is available and accessible in their environment at a given time (Lea et al. 2002a, Lea and Dubroca 2003). Thus, the diet of Antarctic fur seals is likely to change within and between seasons (Arthur et al. 2015, Guinet et al. 2001, Lea et al. 2002a). For example, Antarctic fur seal diets at Cap Noir varied in the relative proportions of *Chamsocephalus gunnari* and *Protomyctophum tenisoni* between years (Lea et al. 2002a). The former is enriched in P whereas the latter is enriched in Fe and Mn (Chapter 3), so this may translate into inter-annual shifts in fur seal nutrient deposition patterns. Temporal shifts in diet might reflect shifts in foraging areas at sea in response to different oceanographic conditions (Arthur et al. 2015, Bost et al. 2002, Dragon et al. 2010, Guinet et al. 2001, Lea and Dubroca 2003, Lea et al. 2006). For example, female fur seals from Pointe Suzanne foraged east of the colony in 2012, whereas in 2010 and 2022 they mostly foraged southward (Fig. 4.6). In contrast, female fur seals from Cap Noir consistently foraged east of their colony, even though travel distances might differ between years. Consequently, changes in diet in response to oceanographic conditions at given foraging locations and at a given time would alter the quantity and quality of nutrients released by fur seals by changing the nutrient content of their feces (Wing et al. 2021), as well as the spatial transfers they mediate in their environment. On land, fur seals are limited to their colony area, so nutrient deposition from scats will not greatly vary spatially. However, temporal changes in the composition of scats in a given area may occur. For example, a colony area could sequentially be enriched mostly in P and then in

Fe and Mn throughout a season if fur seal diet notably changed during the breeding period, or annually if conditions and diets shift year to year. In either case, it could influence the terrestrial ecosystem dynamics and structuring, albeit on different timescales.

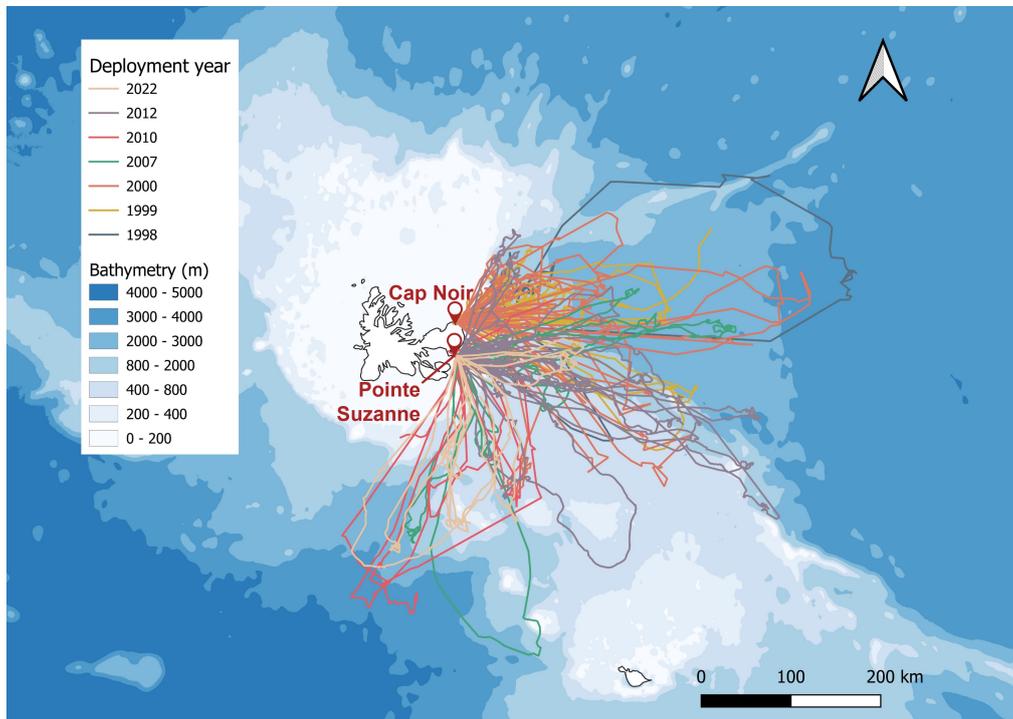


Figure 4.6: **Map showing at-sea tracks of lactating Antarctic fur seals females from two colonies on Kerguelen Islands (Southern Ocean), with coloration per year of tracking.** Data published in Guinet et al. 2001, Jeanniard-du Dot et al. 2017a, Lea et al. 2002a, Lea and Dubroca 2003, Lea et al. 2008 for years 1998, 1999, 2000, 2007, 2012; 2010 data were not published and 2022 data are not yet published and were collected under permit #37480-2022052514544991-V7 in 2022-2023 Austral Summer. Blue gradient background indicates bathymetry

To understand how these spatial and temporal shifts in diets might impact global nutrient deposition patterns and thus impacts on nutrient cycling in their environments, we simulated different scenarios of scat composition datasets with varying relative abundances of each scat type. Changes in the proportion of scats from cluster 1 was critical in determining the quantity of P deposited at both Cap Noir and Pointe Suzanne. If fur seal diet were to evolve towards a higher proportion of this scat composition type, the influence of fur seal nutrient deposition on their colony sites may evolve in response, given the importance of this nutrient to terrestrial ecosystems. Similarly, changes in the proportion of scats in cluster 2 may significantly alter the scat-mediated release of Fe and Mn and the role of fur seals in the cycling of these limiting nutrients at sea. That said, significant changes in nutrient release levels were mostly observed for extreme simulation

scenarios, especially in Pointe Suzanne ([Chapter 4 - Supplementary Table 1](#)). These most extreme scenarios are probably unlikely to occur, although our large inter-sample variability and low sample size in some cluster (especially for bootstrapping) might have hindered our statistical power to uncover more subtle significant differences. Nevertheless, our approach provided interesting insights into effects of variability of fur seal-mediated nutrient deposition patterns. Given the scale of climate changes in this region, and their impacts on abiotic parameters both at sea and on land and subsequently on the biota ([Lebouvier et al. 2011](#), [Smith 2002](#)), this potential spatio-temporal variability should not be overlooked. Our approach could be replicated with a larger numbers of samples and extended to multiple time scales. Additional scat samples collected in different years should also be informative to assess the consistency of the compositional patterns we observed and their variability.

4.4.5 Limits

Although we provide the first estimates of nutrient release by Antarctic fur seals on and around Kerguelen, they are likely underestimated. We only considered lactating females, whereas the nutrient supply mediated by mature males and immatures could also be significant, both at sea and on land. In addition, nutrients deposited by pup cohorts following milk consumption, which are secondary transferred from the marine environment via the mother, are deposited exclusively on colonies or in their adjacent coastal waters and should be included in future studies. Estimating population size from terrestrial counts is challenging for fur seals, as the proportion of animals seen on land is only partially representative of the total population. Population studies of Antarctic fur seals suggest that multiplying the number of pups by four can provide a good estimate of population size ([Lea et al. 2008](#), [Page et al. 2003](#)). Extending our estimates from lactating females to whole populations would require taking into account the population structure of each population, given the strong sexual dimorphism of the species, but it gives an idea of how far off our estimates might be from what is actually released. However, the spatial differences we found are still indicative of the true relative deposition patterns, assuming an equivalent population structure for the two colonies.

It should also be noted that we only estimated nutrient release for two extensively studied Antarctic fur seal colonies. Some less studied colonies are not included, and they are also other predator species present in the area. At Pointe Suzanne, the impact of Antarctic fur seals on the terrestrial ecosystem is combined with that of gentoo penguins

(*Pygoscelis papua*) and elephant seals. In terrestrial ecosystems, the additional supply of carcasses, fur and feathers, which can be intense during the breeding and moulting seasons, is another pathway for nutrient transfer (Smith 2008). All these species also release nutrients at sea, where the contribution of cetacean species adds up, whether they are resident or seasonal visitors to Kerguelen waters.

4.4.6 Conclusion

Our results shed light on the quantitative and functional contribution of female Antarctic fur seals from two colonies on and around the Kerguelen Islands to the biological cycling and transfer of nutrients. The variation in nutrient release patterns we observed in fur seals, both at the individual scat level and at the colony level, revealed the degree of variation in the contributions of predator communities. Each predator species found in the region also has different distribution, phenology, physiology, diet and behaviour (Koubbi et al. 2016, Thiebot et al. 2012, Thiers et al. 2017), which is likely to add another level of complexity to their contribution to local nutrient dynamics. This study thus provides a first insight into the role of marine predators in such processes in the unique area of the Kerguelen Plateau, and lays the groundwork for further assessment of their contribution at larger specific and population scales.

Data and code availability

No original data were used nor generated for this analysis which mobilised data from a soon-to-be published dataset (Section 3.4.4; the dataset will be made available on InDoRes public repository (<https://www.indores.fr/>), and data from the literature for the setting of most parameters in our bioenergetic model (references provided in Table 4.2). Data and code to generate results presented in the present study are available in the public Github repository <https://github.com/Lola-san/Agazella.modelling.Ker>.

Towards an assessment of the influence of marine-derived nutrient deposition by Antarctic fur seals on coastal ecosystem dynamics on the Kerguelen Islands

5.1 Context

Nutrient fluxes are a major dynamic component of ecosystem functioning. On land, the mineralisation of organic matter by decomposers releases essential nutrients in the ecosystem which become available to plants for new primary production (Coleman et al. 1983, Thies and Grossman 2006). The nature of the organic matter and the soil biological activity thus determine the quality and quantity of nutrients available to plants and, more generally, the food web structure (Dubeux et al. 2007, Thies and Grossman 2006).

Physical phenomena (wind, rainwater, *etc.*) largely determine the large-scale movement of nutrients and shape their availability in habitats. However, animals can also be an important source of production, transport and transfer of processed organic matter (McInturf et al. 2019, Subalusky and Post 2019), although they might operate on a smaller spatial scale. By digesting essential nutrients stored in an unavailable form (slowly decomposing living organic matter) and releasing them in a more available form through the production of feces and urine, animals facilitate the transfer of these nutrients to primary producers (Subalusky and Post 2019). Their role in biogeochemical fluxes are non-negligible, and sometimes structuring over large scales (Doughty et al. 2016, Wolf et al. 2013). For example, woolly monkeys transport nutrients between oligotrophic and eutrophic zones in the Amazon rainforest (Stevenson and Guzmán-Caro 2010). Animals also facilitate the transfer of nutrients between terrestrial and aquatic ecosystems. In British Columbia, large carnivores transfer nutrients of marine origin to forest environments through the consumption of salmon (Reimchen et al. 2003), while hippos and wildebeests bring nutrients of terrestrial origin to the Mara River in Kenya (Subalusky et al. 2018).

Marine vertebrates, such as seabirds and pinnipeds, spend their time between the marine environment where they feed, and the land where they rest, breed and moult. This life cycle specificity facilitates the transfer of nutrients from the open sea to land-based

colony sites and coastal ecosystems through the deposition of feces, urine, carcasses or food losses during the feeding of juveniles (Bokhorst et al. 2007, Lorrain et al. 2017, Smith 2008, Souza-Kasprzyk et al. 2022). These deposited marine nutrients can be integrated into the soil and through the food web (Bokhorst et al. 2019b, Fariña et al. 2003, Wang et al. 2020) and significantly affect the productivity and structure of the ecosystem around colonies (Bokhorst et al. 2019a). The influence of these sea-to-land nutrient transfers were highlighted when islands where seabird populations have been eradicated or severely impacted by rat invasions were compared to pristine islands (Benkwitt et al. 2022, 2021). The enrichment of terrestrial trophic chains may be all the more important in oligotrophic environments such as the extreme terrestrial ecosystems of Antarctic and sub-Antarctic islands, where seasonal returns of mammals and seabirds are major. The effects of this nutrient enrichment can be shaped by land-based biogeographic features (e.g. topography), especially when the species involved have limited mobility on land (e.g. elephant seals) (Fariña et al. 2003), but can also extend beyond colony boundaries as observed with nitrogen fractionation and volatilisation (Bokhorst et al. 2019b, Theobald et al. 2006). In addition, some nutrients deposited on colony sites may leach to the coastal marine ecosystems and be reintroduced into coastal marine food webs (Finne et al. 2022, Souza-Kasprzyk et al. 2022, Wang et al. 2020).

In sub-Antarctic and Antarctic terrestrial ecosystems, primary productivity is mainly limited by availability - or lack thereof - of major nutrients such as nitrogen (N) or P (Bokhorst et al. 2007, Smith 2008). In contrast, supplies of trace nutrients such as iron (Fe) or manganese (Mn) are less likely to affect plant productivity, but are still essential for soil bacteria, plants and fauna (He et al. 2005, Uchida, R. and Silva 2000). Species at these trophic levels have different affinities and tolerances for each trace nutrient (Thies and Grossman 2006, Uchida, R. and Silva 2000). Consequently, their supply may be important in shaping species assemblages, and thus the biological structure and dynamics of the ecosystem (Mooshammer et al. 2014, Pankhurst et al. 1996). These trace nutrients are often found in high concentrations in marine predator waste products (Nicol et al. 2010, Sparaventi et al. 2021, Wing et al. 2021; Chapter 3). Their transfer from marine to terrestrial environments may thus be influential where they are deposited, although these processes are still poorly understood (Souza-Kasprzyk et al. 2022).

The Kerguelen Islands are a remote sub-Antarctic archipelago located in the southern Indian Ocean. They support colonies of several amphibious predators species including pinnipeds, e.g. Antarctic fur seals (*Arctocephalus gazella*) and southern elephant seals

(*Mirounga leonina*), and seabirds, such as gentoo penguins (*Pygoscelis papua*) and king penguins (*Aptenodytes patagonicus*). Some of these species have gradually returned to these coasts after being virtually eradicated by direct human exploitation (e.g. fur seals) (Hofman 2017), and populations are now reaching high numbers (Guinet et al. 1996). During their breeding and moulting periods, fur seals and penguins alternate land-bouts where they feed their young and sea-bouts where they feed on krill, lipid-rich fish (myctophids) and cephalopods, depending on species (Bost et al. 2002, Jeanniard-du Dot et al. 2017b, Lea et al. 2002a, Lescroël et al. 2004). In contrast, elephant seals fast during these periods, but as their metabolism is still active, they still emit feces and urine on land. Marine predator colonies are very localised near beaches, where the input of marine nutrients is therefore spatially and temporally well-defined. However, the content and spatial and temporal extent of the effects of this marine input on terrestrial diversity are still largely unknown. The terrestrial flora and fauna in the Kerguelen Islands are characterized by a low diversity, and include endemic species with biological adaptations linked to their exceptional living environment (extreme climatic conditions and geographical isolation) (Badenhausser et al. 2020, Hooker 1879, Lebouvier et al. 2001). This specific ecological situation, in a context of low anthropisation and absence of tree and shrub cover, represents a rare opportunity to explore the transfer of nutrient-rich matter between marine and terrestrial ecosystems, and how this shapes terrestrial biodiversity (plants, insects).

In this context, the goal of this study is to (i) assess whether the seasonal presence of marine predators breeding on Kerguelen Island influences nutrient fluxes and the dynamics structuring coastal ecosystems in the vicinity of their colonies, and (ii) quantify these influences. To this end, we conducted a field data collection campaign during the Austral Summer 2022-2023 to collect samples from Antarctic fur seal, southern elephant seal and penguin feces (nutrient vector), soil, plants and invertebrates. We also aimed to integrate multiple aspects related to nutrient dynamics (stable isotopes and multidimensional nutrient concentrations) and ecosystem productivity and structure (soil microbial activity, biodiversity, species composition and vigour). We focused on two study sites with different abiotic and biotic characteristics and hosting marine predator colonies. While our primary focus was on the Antarctic fur seal, other species were included when they were present.

All data and samples have been collected and retrieved from the field, but biochemical and statistical analysis will be carried out at a later stage. Here, we will first present technical and methodological aspects of the data collection campaign and explain the

future analysis of the collected data in the context of our study objectives. Finally, we will discuss the expected results and the potential caveats in their interpretation.

5.2 Data collection

5.2.1 Study sites

Field data and samples were collected from late December 2022 to mid-January 2023 on the Courbet Peninsula of the Kerguelen Islands at two sites (Fig. 5.1).

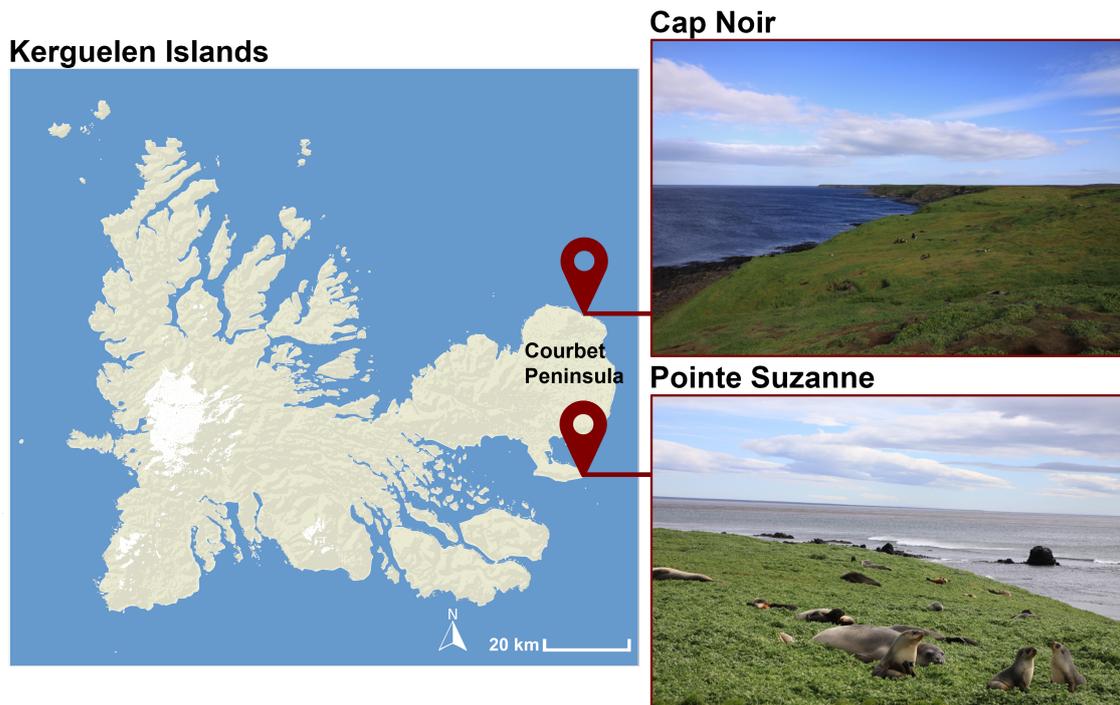


Figure 5.1: Location of study sites of Cap Noir and Pointe Suzanne on the Courbet Peninsula of the Kerguelen Islands (left panel), and photo of Antarctic fur seals (*Arctocephalus gazella*) on each colony (right panels). Original map from <http://cmap.comersis.com>, photo: Lola Gilbert

The site of Cap Noir (49°07' S 70°45' E) hosts a breeding colony of Antarctic fur seals and moulting elephant seals at this time of year. The colony is spread around a small cape, with the vegetation bordering the beach starting on a steep grassy slope, followed by a few flat terraces with gentler slopes in between, and a plateau (Fig. 5.1). Elephant seals are found only on the rocky shore, whereas fur seals occupy both the beach, the slope and terraces up to the beginning of the plateau. Fur seals are found on $\approx 53,000$ m². The site is frequently exposed to strong winds.

The site of Pointe Suzanne (49°44' S 70°44' E) hosts a colony of breeding Antarctic fur seals, moulting elephant seals, two breeding colonies of gentoo penguins *Pygoscelis papua* and occasional non-breeding king penguins *Aptenodytes patagonicus* visitors during the austral summer. The vegetated area is accessible to the animals through several gentle slope paths (Fig. 5.1). Antarctic fur seals usually occupy a 20 to 40 m-wide band that follows the vegetation line close to shore, on $\approx 26,000 \text{ m}^2$. The colony is tighter and denser at the start of the breeding season (early December) and becomes larger and more patchy as the season progresses to the end of the moulting season (late March). Elephant seals occupy the beach and the vegetated area and can venture further inland than fur seals (up to ≈ 100 meters away from the vegetation limit). The two gentoo penguin colonies are located on either side of the fur seal colony ($\approx 1,000$ to $4,000 \text{ m}^2$), although their occupancy varies throughout the season. The weather at Pointe Suzanne is milder than in Cap Noir, as it is more sheltered from strong winds, with higher temperatures and slower precipitation regime.

5.2.2 Marine predator counts and feces collection

Marine predator populations were surveyed on the two sites as an index of their influence. For Antarctic fur seals, sub-adult and adults were counted together without sex differentiation, as well as pups separately. Elephant seals and penguins were counted without distinction of sex or status. Counts started at dawn at both sites, when a majority of animals were resting on land. On both sites, the beach was not directly visible from the land edge of the colony and needed either a dedicated count (Pointe Suzanne) or binoculars (Cap Noir). Counts were conducted per sector (4 in each site) delimited based on the occupancy patterns of the animals and topographical indicators to estimate relative animal densities. At Cap Noir, an initial count was made by one observer, and a second count was made 10 days later by three observers. Only Antarctic fur seals were counted as they were the only species occupying the vegetated area. At Pointe Suzanne, four counts were carried out over 15 days, by two to three observers independently, and Antarctic fur seals, elephant seals, gentoo penguins and king penguins were counted.

In Cap Noir, only fur seal scats were collected, with a majority being from either adults or subadults ($n = 28$) and a few from pups ($n = 4$) (Table 5.1). In Pointe Suzanne, 32 adults or subadults Antarctic fur seal and 5 elephant seal fecal samples were collected respectively with 8 gentoo penguin guano samples. All samples were collected and stored in clean plastic bags at ambient temperature ($\leq 10\text{-}12^\circ\text{C}$) for 24 to 72 h before being

frozen at -20°C until further processing in the laboratory.

5.2.3 Experimental design, data and sample collection

To test the influence of the proximity to the coast and the presence of marine predators, we defined study plots at each site following a gradient of distance to the coast and animal density (Fig. 5.2). We defined the first plot close to the sea and with the highest animal density, one plot farthest from the sea and with the lowest animal density, and evenly located plots in between to obtain a gradient. We sampled eight plots at Cap Noir and nine at Pointe Suzanne.

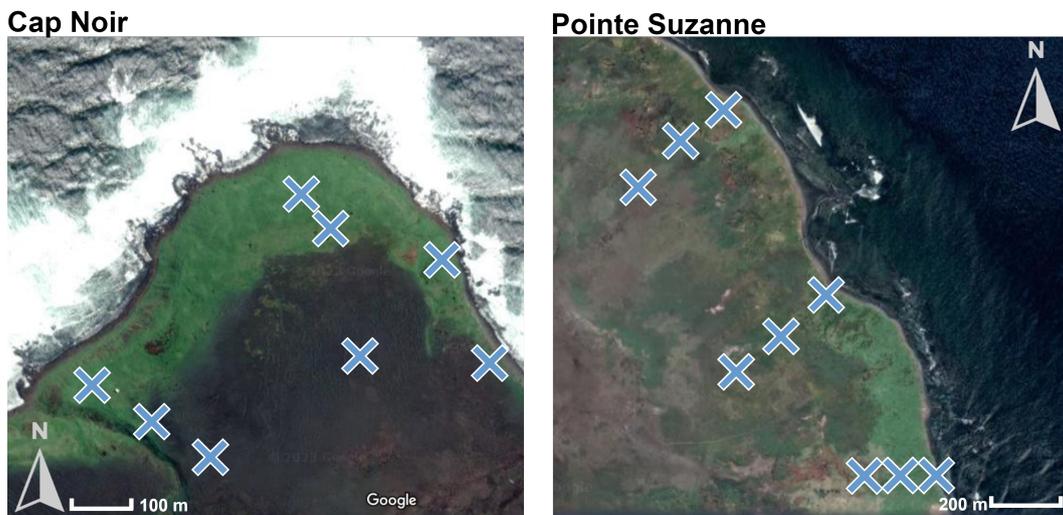


Figure 5.2: Study design on both sites of Cap Noir and Pointe Suzanne (Kerguelen Islands) with location of each sampling plot (blue cross)

Each plot was delimited by a 10-m circle containing five 1 m^2 -quadrats. Abiotic parameters such as wind exposure, orientation, slope were recorded for each plot. Arthropods were identified and counted during a 15-min hunt by two operators using naked-eye observation while searching the vegetation within the plot boundary. The two most abundant species were collected (~ 12 -25 individuals). Plant species were identified and their % of cover, sociability, vigour, height range and phenological stage were estimated. The same parameters were assessed for bryophytes as a separated category, without distinction of species. Five leaves of different plants were collected for the dominant Monocotyledon and Dicotyledon species for isotopic analysis, with up to two species for each group. Then, plant species and their proportion of coverage were assessed within each quadrat. For 4 plants of the dominant Monocotyledon and Dicotyledon species (with again up to two

species for each group), the size of the plant was measured and a leaf was collected for trait measurement analysis. A sample of soil of ~ 10 cm × 10 cm was collected (~ 150 g) on each plot.

Finally, to assess the influence of colonies on the enrichment of marine coastal ecosystems via nutrient leaching, we collected mussels in the tidal foreshore at three points in front of sectors of the colony with different animal densities (bivalve molluscs being water filters). However, we had trouble in finding attached bivalves around the sampling points, mainly due to the nature of the foreshore. Although it was rocky at most points, it sometimes consisted of round rocks with few attached organisms. Most of the samples collected were found unattached to the substrate or attached to seaweed. These samples were collected in clean plastic bags before leaving the site and stored at -20°C within 12h of collection.

Plant samples were kept in clean plastic bags with a sheet of water-saturated absorbent paper, and arthropods were kept in plastic pillboxes with silica bead in kraft paper. These samples remained at ambient temperature on site for up to five days before being processed in the laboratory. Soil samples collected last before leaving colony sites to limit their time at ambient temperature, and were then kept at -20°C. They were kept in clean plastic bags. Samples collected on each site are detailed in [Table 5.1](#).

5.2.4 Sample processing

Plant leaves collected for isotope analysis were dehydrated at 50°C for 48-h minimum in kraft bags and stored at room temperature until analysis. Arthropods were frozen at -20°C overnight, and kept at room temperature afterwards until analysis. Plant leaves collected for trait measurements were carefully cleaned, dried and weighed individually to the nearest 0.1 mg. Leaf surface area was measured using a Portable Leaf Area Meter scanner (CI 202, precision 0.01 cm²). Finally, they were dehydrated at 50°C for 48-h minimum in kraft bags then stored at room temperature before a second weight measurement. Soil samples were stored at -20°C until analysis, and fecal samples were stored at -20°C for 24-h minimum before being freeze-dried, then kept at room temperature in sealed plastic bags until analysis.

Table 5.1: Bioenergetic model parameters settings for Monte-Carlo simulations (n = 5000) with references used (Ref.)

Site	Sample type	n	Dates
Cap Noir	Antarctic fur seal scats	32	2023 January 30-31
	Soil	8	2023 January 16
	Plant leaves <i>for isotope analysis</i>	100-105	2023 January 14-16
	Plant leaves <i>for trait measurements</i>	183	2023 January 14-16
	Arthropods	≈120	2023 January 14-16
	Mussels	6-8	2023 January 16
Pointe Suzanne	Antarctic fur seal scats	32	2022 December 27 to 2023 January 16
	Southern elephant seal scats	5	2022 December 27 to 2023 January 16
	Gentoo penguin guano	8	2022 December 27 to 2023 January 16
	Soil	9	2023 January 5
	Plant leaves <i>for isotope analysis</i>	90	2023 January 1-5
	Plant leaves <i>for trait measurements</i>	228	2023 January 1-5
	Arthropods	≈400	2023 January 1-5
	Mussels	9	2023 January 5

5.3 Future analysis

5.3.1 Biochemical analysis

Marine-derived nitrogen has a unique isotopic signature which can be differentiated from terrestrial-based nitrogen signature (Bokhorst et al. 2019a, Finne et al. 2022, Wang et al. 2020). Stable isotopes of nitrogen will thus be quantified in fecal, mussel, soil, plant and arthropod samples as an indicator of the integration and transfer of marine-derived nutrients into terrestrial ecosystems.

We also aim to assess differential concentration patterns shaped by the predator-mediated deposition of marine nutrients into each compartment. To do so, total concentrations in essential major (phosphorous P, calcium Ca, potassium K, sodium Na, magnesium Mg) and trace nutrients and/or potential contaminants (iron Fe, zinc Zn, copper Cu, manganese Mn, selenium Se, arsenic As, nickel Ni, cobalt Co, cadmium Cd, chromium Cr, molybdenum Mo, lead Pb, strontium Sr, vanadium V and silver Ag) will be measured in fecal, mussel, soil, plant and arthropod samples by inductively coupled plasma atomic emission spectrometry (ICP-OES, Vista-Pro Varian; for major nutrients)

and inductively coupled plasma mass spectrometry (ICP-MS, ICAP-Qc ThermoFisher; for trace nutrients).

Finally, soil microbial biomass will be quantified by a fumigation-extraction method (Wu et al. 1994) as an indicator of soil biological activity and associated remineralisation potential.

5.3.2 Trait measurement

Biological traits are bio-indicators of health and condition of both plants and arthropods. As such, they also indicate the richness and productivity of their environment, and of their ecosystem functioning.

For plants, we will measure plant length, leaf specific area (LSA) and leaf dry matter content (LDMC) as biological traits. LSA is ratio of the leaf surface area and the leaf dry mass, and LDMC is the ratio of the leaf dry mass and the leaf fresh mass. Plant lengths were measured on site, leaf fresh mass and surface were measured in the laboratory, but leaf dry mass measurements require a high sensitivity scale, and will be conducted in the next stage of the study. For arthropods, we will measure length and width of the thorax and abdomen, and the length of the antennae as biological traits.

5.3.3 Statistical analysis

Generalised linear models will be used to test the effect of animal density, distance to the colony sector with the highest density of animal and distance to the coast on each measured variable, similarly to the approach in Bokhorst et al. (2019a). The response variables will thus include soil microbial biomass, plant and arthropod species diversity, plant % cover, sociability, vigour, height and phenology (plot scale), each plant and arthropod trait and soil, plant and arthropod isotope signature and nutrient concentrations. Feces isotopic signature and nutrient concentrations will serve as a reference for result analysis as they are the possible nutrient vectors, but they will not be included as a response variable,.

5.4 Discussion

5.4.1 Significance

The nutrient dynamics around the Kerguelen Archipelago are unique in the High Nutrient Low Chlorophyll (HNLC) waters of the Southern Ocean (SO). The Kerguelen plateau is naturally fed by iron through a combination of physical processes involving the up-welling of enriched waters on the Plateau and atmospheric dust, although the sources and supply processes of this natural fertilisation are not yet fully understood (Bucciarelli et al. 2001, van Der Merwe et al. 2015). The area is located under the Antarctic circumpolar current, and is surrounded by three oceanic fronts: the subtropical front, which marks the northern limit of the SO, the sub-Antarctic front and the Antarctic polar front (Bestley et al. 2020a). This singular context makes it a highly productive oasis for marine fauna. These productive habitats contrast with the nutrient-poor terrestrial habitats. The low levels of anthropisation allows us to study the natural nutrient dynamics of the sea-land continuum. The self-organization of systems, including biodiversity adjustments that facilitate synchrony between species, has so far been understudied, especially in the context of cross-boundary animal-mediated nutrient transfers (McInturf et al. 2019, Scherer-Lorenzen et al. 2022). This work will thus provide unique information on the contribution of marine predators and biodiversity to the productivity and the structuring of coastal ecosystems, including plant and invertebrate communities on land.

The study area is also located in a geographical zone where climate-driven changes in environmental conditions are rapid and intense (Lebouvier et al. 2011). These changes are visible both in the marine (shift of seasonal production blooms, increasing water temperatures, increase in wind strengths, *etc.*) (Mayewski et al. 2009) and terrestrial habitats (increase in air temperatures, decrease in precipitation and increase in frequency and intensity of droughts, *etc.*) (Lebouvier et al. 2001, Smith 2002). These changes affect both abiotic and biotic nutrient fluxes, given the influence of the former on the latter (Chapman et al. 2020). In Antarctic terrestrial ecosystems, changes in temperatures and precipitation regimes may shift the productivity limitation context from temperature-limited to nitrogen-limited, so that the influence of marine-derived nutrient enrichment on coastal ecosystems may also evolve (Bokhorst et al. 2022). The ongoing climate changes therefore make it all the more important to improve our knowledge of the functioning of these coastal ecosystems and to identify the mechanisms that structure the biodiversity of the local flora and fauna.

5.4.2 Limitations

While our main hypothesis supposes that nutrient enrichment mediated by coastal predators has a positive effect on ecosystem productivity and biodiversity, this positive effect could be somewhat offset by potential negative effects of land-based marine predator colonies. Indeed, a large number of marine megafauna on colony sites can lead to soil trampling, erosion, soil acidification, over-fertilisation and transfer of contaminants (Convey and Hughes 2023, Poggere et al. 2016, Santamans et al. 2017). In the field we observed that some areas were bare as a result of trampling and acidification from penguin guano. Soil trampling can be intense for predators such as the heavy southern elephant seals with bare lodges where elephant seals rest during their moult. The relative presence and importance of bare ground, soil erosion and signs of animal impact were included in the characterisation of each of our study plots, so that some of the possible negative impacts can be assessed in our approach. We should also be able to assess patterns of contaminant transfer through the multidimensional nutrient analysis in each biological compartment included in the study. However, the balance between the possible positive and negative effects of the presence of marine predators, which is multi-factorial and difficult to quantify, might complicate the interpretation of our results.

In addition, analysing and interpreting many interconnected factors that can influence our measured parameters (in particular species diversity and assemblages) might prove difficult. For example, exposure (wind, sunlight) and slope influence the abundance of species in a given habitat, independent of its nutrient dynamics. Species of bacteria, plants and arthropods also participate in patterns of nutrient concentrations depending on their affinity and metabolism, which we cannot take into account in our analyses. Finally, nutrients can co-vary and interact, either positively or negatively. Thus, studying biological nutrient transfers in a context where the sources of influence are numerous can make it difficult to identify clear patterns (*e.g.* Souza-Kasprzyk et al. 2022). For these reasons, stable isotope analysis will be valuable in demonstrating marine influence and nutrient transfer mediated by marine predators. We also recorded all data characterising the conditions and nature of the environment in the field, so that these factors can be taken into account when interpreting the results.

5.4.3 Future development

This project was set up as a pilot study. Our aim is to identify trends to explore further in the future. We also want to identify biases that could be better accounted for or quantified in a future data collection campaign with improved protocols. For example, study sites without marine predator colonies could be included. This option was considered during the project design phase, but was abandoned for logistical reason. We instead investigated gradient effects at a given marine predator site. However, having blank study sites may provide additional information on nutrient enrichment and ecosystem structure and dynamics along the Kerguelen coastline, and on the contribution of marine predators in shaping the observed patterns. We could also include plots in the tidal area under the direct influence of the colonies in our sampling protocol.

5.5 Contributors

This project is the fruit of a collaboration between four laboratories: the Centre d'Etudes Biologiques de Chizé - CEBC - and the PELAGIS Observatory from CNRS - La Rochelle University (UMR 7372 and UAR 3462, respectively), the Ecobio laboratory from CNRS - Rennes University (UMR 6553) and the Ecologie des Hydrosystèmes Naturels et Anthropisés (LEHNA) laboratory from CNRS - Lyon 1 University (UMR 5023). Lola Gilbert (CEBC/PELAGIS), Tiphaine Jeanniard-du-Dot (CEBC), Jérôme Spitz (CEBC/PELAGIS), David Renault (Ecobio) and Anne-Kristel Bittebière (LEHNA) conceived the study and the field data collection methodology. The field campaign to collect the data and samples was funded through collaboration between two programs of the French Polar Institute (IPEV; 136-SUBANTECO and 109-ORNITHOECO). Field data and sample collection was carried out by Camille Henriët, Nicolas Bonetti (IPEV), Lola Gilbert and Tiphaine Jeanniard-du-Dot with the help of Mathilde Chevally (doctoral student at CEBC) and voluntary operators Pierre Guenot, Eli Castang and Ludovic Ivars.

At the time of writing, we are awaiting a response to a grant application we have submitted to carry out the future analysis described here.

6.1 Putting it all together

6.1.1 Overview of separate findings

In Chapter 1, we provided a global overview of the contribution of cetacean communities to nutrient cycling in different ocean realms, and estimates of their nutrient release in areas where this had never been quantified. We demonstrated the bottom-up link between productivity and cetacean communities, as reflected in cetacean release levels, which were lower in the less productive tropical and subtropical waters than in the temperate and subpolar areas of the Northern Hemisphere. We highlighted the relative contributions of small cetaceans, deep divers and baleen whales to these processes, and show how species of each taxon may play different roles in nutrient cycling, both quantitatively and qualitatively, globally and in a given area.

In Chapter 2, we spatially zoomed in on the Southern Ocean. We focused on a smaller taxonomic scale, *i.e.* on a community of four species of pack-ice seals never studied in this context before. We demonstrated that their contribution is equivalent that of some whales and penguins and should no be overlooked. We thus provide a more complete picture of the role of marine mammals and marine predators in the biological cycling of iron in the Southern Ocean.

In Chapter 3, we again zoomed in spatially, temporally and taxonomically to focus on Antarctic fur seals in the Kerguelen Archipelago during the Austral summer. We investigated the indirect role of potential prey in nutrient cycling, and showed that different prey species do not provide the same relative nutrient mix to predators, highlighting the importance of predators' diet in the nutrient cycling they mediate. Predators switching prey species with different nutrient composition profiles may affect their role as nutrient vectors. We also showed that not all fur seal scats have the same potential to fertilise their environment, with some enriched in trace nutrients and others in major nutrients.

In Chapter 4, we used the individual fecal composition data from Chapter 3 for a population-scale approach, still focusing on Antarctic fur seals from the Kerguelen Islands during the Austral summer. We provided the first estimates of nutrient release by

marine predators in this area, which is of high conservation interest due to its singular biogeochemical context in the high nutrient-low chlorophyll Southern Ocean. We showed that Antarctic fur seal defecation may cause significant local enrichment when they are at sea even in the naturally fertilised waters of the Kerguelen Plateau. In the terrestrial ecosystems used by fur seals on their colonies, the marine nutrient supply they mediate and the spatially and temporally-defined concentration of animals likely have a structuring effect on the Kerguelen coastal lands. In addition, we demonstrated the relative importance of individual variation in fecal composition in nutrient release patterns generated at the colony and population scales.

6.1.2 Complementary approaches

Overall, our approaches and their different spatio-temporal and taxonomic scales of study revealed different facets of the role of marine mammals and nutrient cycling, and provided complementary information on their variability. Ecological processes and patterns, whether abiotic or biotic, are hierarchical and vary over different spatial and temporal scales. For example, ocean currents can be described at the scale of an entire ocean, or at the mesoscale of eddies, and structures such as fronts are notoriously subject to high spatio-temporal variability (*e.g.* Bestley et al. 2020b, Yelekçi et al. 2017). Similarly, biological processes can be described from the individual level to group, population or community levels, each of which are correlated to physical patterns of different scales (*e.g.* up-welling, thermal fronts) (Bakun 1997, LaRue et al. 2021), *e.g.* cetacean communities and productivity patterns in large ocean basins, or cetacean communities and habitats (Chapter 1). The role of marine mammals in nutrient cycling and ecosystem functioning is therefore likely to extend across different spatial and temporal scales, depending on species and ecosystem characteristics (McInturf et al. 2019, Subalusky and Post 2019).

The estimates presented in Chapters 1 and 2 provide primary information on the broad-scale contributions of focus species in their environment. They serve as background or starting points for identifying future focal studies at smaller spatial and/or temporal scales, as well as taxonomic scale. Although our approaches in Chapters 3 and 4 do not focus on species included in these first chapters, their results shed new light on our methods of investigation, their potential weaknesses and strengths.

Large spatial scale studies such as the ones in Chapters 1 and 2 are limited by the availability and the heterogeneity of data, and the resulting need in averaging and/or extrapolation of parameters. This was the case for diet and prey composition data, which

led us to use coarse descriptions of diet for each species, without spatial variation. In Chapter 3, we not only added to the global database of multi-nutrient prey species composition, but also confirmed the non-equivalence of different prey in terms of nutrient composition. Furthermore, given the large variability observed in individual Antarctic fur seal fecal composition, likely due to individual dietary variation, these results support our decision to define diets using functional prey groups in Chapters 1 and 2. By grouping prey items and generating variability in their composition, we accounted both for individual diet variation and prey composition. In Chapter 1, the number of prey groups was high (9; [Section 1.2.3](#)), and our results suggested a large variability in the relative composition of the nutrient mix released daily by individual cetaceans ([Fig. 1.5](#)). This concurs with our results on fur seal scats. In Chapter 2, however, we used taxonomic prey groups rather than functional ones (*e.g.* fish and cephalopods) and only 5 categories ([Section 2.2.2](#)). This was chosen because of the scarcity of prey composition data and quantitative diet data for these Southern Ocean species. The results obtained for forage fish in Chapter 3 suggest that our estimates mask some variability in nutrient release at the individual and hence population level. Nevertheless, the greatest variability in individual nutrient release was found for the species with the most diverse diet (leopard seal) and the least for the most specialised species (crabeater seal; [Fig. 2.1](#)). Consequently, these patterns likely reflect existing differences in variability. Furthermore, given the large uncertainty associated with population estimates for these species, the variability in levels of individual nutrient release has little impact on the uncertainty at the population level ([Fig. 2.1](#)). The bias introduced by coarse diet descriptions and prey composition groups is therefore likely small for the population estimates.

In both Chapters 1 and 2, population abundance was the most influential parameter for population nutrient release levels, together with diet composition (energy and nutrients). In this respect, Chapter 4 demonstrated how variability in individual diets (reflected in scat nutrient composition), can override the effect of abundance for population nutrient release levels. These results emphasized the importance of taking into account individual variability in nutrient cycling (McInturf et al. 2019). As they were obtained for just one species and two colonies on the same island, it suggests a potentially large spatial variability between sub-populations in a given area, and between populations in different areas. Multiple colonies of Antarctic fur seals are spread out around the sub-Antarctic Southern Ocean (Goldsworthy 2008, Shirihai 2008), with spatial and temporal variability in individual and population diets (Casaux et al. 2006, Reid et al. 2006). Our study therefore provides a

first glimpse of the spatial, temporal, quantitative and qualitative heterogeneity in the contribution of this species to the Southern Ocean nutrient cycles.

In addition, the more localised approach adopted in Chapter 4 provided an opportunity to compare the nutrient concentrations in fur seal scats with the biochemical conditions of their potential recipient ecosystems. This highlights how local approaches may be better suited to assess the ecosystem response to marine mammal-mediated nutrient cycling. Such fine-scale comparisons would be more challenging in larger-scale studies, such as those in Chapters 1 and 2, given the patchiness and variability of biochemical conditions in the marine environment and the patchiness of marine mammal distributions.

When the study outlined in Chapter 5 is completed, we will assess whether the localised terrestrial enrichment estimated in Chapter 4 is detected. We will also estimate whether the fecal composition patterns observed in the 2022 samples are observed in 2023. In addition, this approach will include other effects of marine predators' presence on land (*e.g.* soil trampling). It will include the contribution of pups, which indirectly participate in the transfer of marine nutrients through the digestion of their mothers' milk, adding an ontogenic level to our approach. The local scale of the study and the simultaneous presence of several marine predator species at the sites led us to include elephant seals and seabirds in the analysis, which will provide a more complete and complex picture of their relative contribution to nutrient cycling processes and ecosystem functioning at the colony land sites.

Finally, a strength of our work was the inclusion of a wide range of essential nutrients. We selected 8 nutrients in Chapter 1, 13 in Chapter 3 and 7 in Chapter 4. We did not use the same sets of nutrients in Chapters 3 and 4 as we had to reduce the number of dimensions analysed in Chapter 4 due to logistical constraints. Nevertheless, Chapters 1, 2, 3 and 4 include nutrients potentially limiting in marine ecosystems and, in the case of Chapter 2, of primary importance in the Southern Ocean. The presence of common nutrients across chapters (iron, zinc, copper, manganese, selenium, cobalt) allowed consistent unique patterns to be identified.

For example, the levels of copper released by cetaceans were the most homogeneous across regions worldwide at the community level, and the most distinctive between small cetaceans, deep divers and baleen whales at the individual level. Interestingly, we found a spatial pattern in the copper content of Antarctic fur seal scats between the two colonies sampled. Patterns of nutrient concentrations in potential prey items and marine mammal feces in Chapter 3 also provided insight into possible differential absorption rates of

nutrients, some of which are bioconcentrated in feces (*e.g.* iron and manganese) and some of which are not (sodium, potassium, arsenic). These multi-nutrient analyses are necessary to include negative or positive co-variations of different nutrients in different ecosystems and in different ecosystem compartments. In Chapter 2, differences between the release patterns of pack ice seals at the individual and population scales may extend to nutrients other than iron. The simultaneous release of multiple nutrients by marine mammals is a key functional aspect that may determine their role in ecosystem functioning, given the diversity of organisms with different metabolisms, nutrient requirements and affinities in ecosystems. Although it inherently complicates analyses by multiplying the number of dimensions and possible interaction effects, this work highlights the importance of multi-nutrient analyses for ecologically relevant studies.

6.1.3 Marine mammal ecological diversity in the spotlight

We investigated the role of marine mammals in nutrient cycling on the basis that they share common characteristics that make their contribution singular ([General introduction](#) and references therein), *e.g.* they are large and they release their waste into the upper water layer after feeding at depth. However, marine mammals are also different for most of these characteristics. While they have large sizes compared to most marine fauna, their body mass ranges from 30-40 kg (*e.g.* porpoises) to 200 tons (blue whales) in cetaceans and from 20 kg (fur seals) to 5 tons (elephant seals) in pinnipeds (Berta 2017, Wursig and Perrin 2009). They feed on all trophic levels from zooplankton to mammals (Trites and Spitz 2018a). They have relatively high metabolic rates (*e.g.* delphinids) or low ones (*e.g.* beaked whales) (Spitz et al. 2012). Some species are migratory, others resident, and can be fully marine or amphibious (Wursig and Perrin 2009). Some marine mammals dive at 20 m depth to forage (*e.g.* Antarctic fur seals), others at 2,000 m (*e.g.* sperm whales, elephant seals). Some are mostly solitary (*e.g.* blue whales), some are highly social (*e.g.* pilot whales), some can be solitary during a season and social in another (*e.g.* Antarctic fur seals).

The diversity of marine mammals has been highlighted as functionally determinant of their ecological importance, including for nutrient cycling and transport processes (Hall et al. 2007, Kiszka et al. 2015, 2022, Pimiento et al. 2020, Rupil et al. 2022, Tavares et al. 2019). This drove one of our working hypothesis, *i.e.* that marine mammals' contribution to nutrient cycling was unlikely to be homogeneous and equally ecologically relevant ([General introduction](#)). We therefore included these differences in our approaches, and

quantified the absolute and relative compositions of marine mammals' wastes, both of which are determinant for the ecosystem response to this nutrient supply (Marcarelli et al. 2011, Subalusky and Post 2019). We showed that they vary between functional groups for cetaceans, different species of Antarctic pack-ice seals, and different populations and individuals of Antarctic fur seals. We also showed that differences between individuals determine the contribution of populations or communities depending on their relative abundances in a given region. This highlights the functional weight of individual diversity within a population or community. In addition, we highlighted the possible ecological importance of foraging tactics and diving depth, habitat use or aggregation behaviour for nutrient cycling and transfer processes. These additional characteristics add another level of diversity in the nutrient transfers and deposition patterns that marine mammals may generate.

We therefore showed that, beyond their commonalities, marine mammals' role in nutrient cycling can be as diverse as their ecology and biology. There may be as many shades of brown as there are species of marine mammals, even more so given the inter-population and intra-species variability. It was beyond the scope of this research project to investigate the ecosystem responses to the variety of marine mammal-mediated nutrient enrichment, except for the uncompleted study presented in Chapter 5. However, if ecosystem responses to marine mammal nutrient inputs reflect their qualitative and quantitative diversity - *i.e.* if, by fertilising their ecosystem with different quantities and qualities of nutrient cocktails, they promote the growth of a diversity of microbial and phytoplankton communities - then marine mammal biodiversity may be important for increasing habitat complexity, resource use efficiency and biodiversity at lower trophic levels, in line with positive correlations between ecosystem processes and biodiversity (Cardinale et al. 2011, van der Plas 2019).

6.2 Limitations

6.2.1 Potential negative effects of marine mammal-mediated nutrient cycling

Our main assumption is that marine mammal-mediated nutrient cycling is beneficial to ecosystem functioning, *i.e.* either positively affecting ecosystem productivity, efficiency, complexity and/or diversity. However, the deposition of recycled nutrients by marine

mammals may also have negative and/or neutral effects (Grant et al. 2022, Subalusky and Post 2019). Most trace nutrients are essential at very low concentrations, but can be toxic if their concentrations in the environment or in the organism get too high (He et al. 2005), with each organism and species having different requirements and tolerances in this respect. This is why some of our essential nutrients are considered as limiting for ecosystem productivity (e.g. zinc (Wing et al. 2017)), or as contaminants (e.g. iron, copper, zinc or arsenic (Celis et al. 2012, Espejo et al. 2014, Metcheva et al. 2011, Szteren et al. 2023, Wing et al. 2014)). In addition, the release of essential nutrients can be associated with the release of contaminants (*i.e.* with no identified physiological function but with deleterious effects on the organism, e.g. lead or mercury). These compounds are found in high concentrations in potential predator prey in some environments (e.g. Chouvelon et al. 2022c, Goutte et al. 2015, Mille et al. 2018, Ogundiran et al. 2014), and in the feces of marine predators such as seabirds, even in the remote Southern Ocean (Celis et al. 2023, Espejo et al. 2014). The simultaneous release of essential nutrients and contaminants could complexify the ecosystem response to marine mammal nutrient release, as positive effects of essential nutrients could be masked or neutralised by the presence of contaminants.

In the ocean, defecation and urination by marine mammals likely relates more to a nutrient input than a contamination. Nutrients are rapidly dispersed (horizontally and vertically) in the water mass and, given their local scale and relatively low biomass, are not comparable to the continuous discharge of contaminated water from anthropogenic industrial activities, for example. In terrestrial ecosystems, however, toxic effects may occur due to the relative persistence of fecal and urinary enrichment in time, their lower potential for spatial dispersion (and thus, dilution), and the spatio-temporal concentration of animals on and around pinniped (and seabird) colonies (Grant et al. 2022, Santamans et al. 2017). In any environment, the effect of nutrient enrichment, whether positive or negative, will depend strongly on the characteristics of the recipient ecosystem at the time of deposition (Subalusky and Post 2019). Nevertheless, the cycling and transfer of contaminants should be considered together with that of essential nutrients to provide a complete picture of the role of marine mammals in nutrient cycling and ecosystem functioning. The study presented in Chapter 5 should be informative in this regard, as it includes the quantification of contaminants and the assessment of their transfer along the food web, together with the potential negative effects of the presence of marine predators unrelated to their role as vectors of marine nutrients (e.g. soil trampling).

6.2.2 Obscured qualitative characteristics of nutrient release

The importance of marine mammal diversity to provide a quantitatively, qualitatively and spatio-temporally heterogeneous nutrient supply to their environment is implicitly based on the assumption that the wastes produced by different taxa, species and individuals have the same biochemical properties. The stimulating and structuring response of primary producer communities to marine mammal fecal enrichment has only been demonstrated for two species of baleen whales (Roman et al. 2016, Smith et al. 2013). However, the only biochemical property of marine mammal wastes that we quantified was their relative nutrient composition (*i.e.* stoichiometry). The contributions of pinnipeds, small cetaceans, deep divers or baleen whales based on sole quantitative and stoichiometric aspects may prove less appropriate for comparison if their feces were radically different in terms of the chemical form of the released nutrients (see Ratnarajah et al. 2017), the concomitant release of microbiota involved in their immediate remineralisation (Lavery et al. 2012b, Roman et al. 2016), or their dispersal and sinking rates. Yet, similar responses were observed penguin (Shatova et al. 2016, 2017), despite their guano being very different than any marine mammal feces. This puts into perspective the importance of these biochemical properties in the fate of the released nutrients. While their omission from our studies does not invalidate our findings, they should be investigated to further assess the roles of marine mammals in nutrient cycling.

6.3 Placing it into the big picture

6.3.1 Marine mammals, nutrient cycling and ecosystem functioning

By focusing on patterns of nutrient release by marine mammals, we have highlighted the complexity of their roles in nutrient cycling and potentially in ecosystem functioning. Yet there are many facets of marine mammals' roles in nutrient cycling that we did not include ([General introduction](#) and references therein). For example, their sinking carcasses transfer nutrients to the ocean depths, creating specific habitats on the seafloor (Smith et al. 2015, Treude et al. 2009), habitats that are at risk from the loss of large whales to industrial whaling (Smith et al. 2019). We did not include the cross-realm nutrient transfers mediated by migrating female whales through their placenta, by nursing their young which in turn release nutrients and through their own bodies when they die on their breeding grounds (Pearson et al. 2023, Roman et al. 2014). We also did not include

the physical alteration of their environments that may generate nutrient transfers, nor the potential risk effects their predatory behaviours may generate (Kiszka et al. 2022). Marine mammal diversity applies to all these facets, and this project therefore provides only a glimpse of the complexity of marine mammals' roles in nutrient cycling.

Furthermore, the roles of marine mammals in nutrient cycling are inextricably linked to their predatory roles and the removal of their prey. After all, there would be no brown nuances to discuss without a meal, and we have highlighted the importance of marine mammal diet and prey composition in determining the composition of their wastes. But the ecological implications of this simplistic correlation are different in nature, *i.e.* prey consumption leading to potential top-down processes (General introduction and references therein) and subsequent nutrient release possibly stimulating bottom-up processes. The bigger picture of the roles of marine mammals in ecosystem functioning encompasses all these processes (Kiszka et al. 2015, 2022), and fully addressing their ecological importance requires integrative approaches (Subalusky and Post 2019).

Moreover, their roles and ecological importance are relative to the other biotic components of ecosystems, from phytoplankton and zooplankton to small and large fish and other marine predators such as sharks, sea turtles and seabirds, and everything in between. All of these play different roles in ecosystems, including the combination of consumption and egestion/excretion roles, and may interact directly or indirectly with marine mammals. Ecosystem modelling frameworks are a promising tool to account for these complex and biodiverse functions (Heithaus et al. 2008, Pimiento et al. 2020), such as those based on meta-ecosystem and functional diversity theories for example (Gounand et al. 2014, Little et al. 2022, Mouillot et al. 2013, Tavares et al. 2019, Villéger et al. 2008). To be effective, they need to unravel as many ecosystem functions as possible, including the nutrient feedback resulting from animal food consumption. The different facets marine mammals' role in nutrient cycling we uncovered could therefore be incorporated into such frameworks to further improve our understanding of the complex workings of these natural systems, highlighting the inherent need for combined and complementary theoretical and empirical approaches (Gounand et al. 2018).

6.3.2 In the time of biodiversity loss and climate changes

Marine mammals also face multiple anthropogenic pressures, ranging from direct threats to their populations (*e.g.* fisheries bycatch and entanglement, culling) to indirect and insidious threats (*e.g.* climate change and pollution) (Albouy et al. 2020, Avila et al. 2018).

On the other hand, quantifying their contribution to carbon cycling and sequestration through their roles in nutrient cycling was beyond the scope of this work. While it has received a lot of attention from the scientific community and the general public worldwide as an argument for whale conservation (Meynecke et al. 2023), studies such as ours provide a glimpse of how complex these processes can be. Including marine mammals into climate policies as a potential lever to mitigate the increase of atmospheric carbon dioxide would require them to be based on the best available science (Pearson et al. 2023). However, waiting for more research should not distract from more immediate and well-identified actions to mitigate climate change, when it is already a threat to marine mammal populations (Meynecke et al. 2023, Pearson et al. 2023).

Furthermore, obtaining robust estimates of the contribution of marine mammals to carbon sequestration would not only be challenging given our current understanding of these processes, but may ultimately carry little weight in climate policy for their conservation. In large parts of the world, most of these marine predators already benefit from protected status for their importance in ecosystem functioning (Enquist et al. 2020, Gamfeldt et al. 2008, Hammerschlag et al. 2019, Pimiento et al. 2020, Scherer-Lorenzen et al. 2022), including their contribution to ocean productivity and carbon cycling (Atwood et al. 2015, Lavery et al. 2010, 2014, Pershing et al. 2010, Savoca et al. 2021). There is always more to investigate given the complexity of ecological systems and the multiple pathways through which an organism can interact with its abiotic environment and its biological components, and the domino effect that one change can have on the whole chain of interactions (Estes et al. 2011). In the meantime, however, implementing direct management actions to mitigate immediate threats to marine mammal populations, which are usually well identified (Avila et al. 2018), is the most effective way to prevent the possible cascading and irreversible effects of their loss (Ingeman et al. 2022).

6.4 Perspectives: revealing more facets of marine mammals' role in nutrient cycling?

6.4.1 Explore the fate of brown nuances in the big blue (but in the lab)

Biochemical characteristics of marine mammal wastes could be estimated in the laboratory. For a given area, samples from different local species should in this case be analysed

using a similar methodology, taking into account the biochemical characteristics of the recipient ecosystem in terms of nutrient background, nutrient limitation patterns, light, temperature, but also the relative abundance and composition of primary producers and microbial communities.

First, the relative bioavailability of nutrients in wastes can be determined (*e.g.* dissolved or particulate) using current methods of nutrient concentrations measurements in oceanic waters (see Ratnarajah et al. 2017 for iron). Second, the potential for nutrient dispersal, *i.e.* the volume of water affected by changes in nutrient concentrations after a defecation, could be determined, as well as the temporal pattern of enrichment in that volume, as in Ratnarajah et al. (2017), Roman et al. (2014), Roman and McCarthy (2010). Finally, fertilisation experiments should be conducted together with control treatments to track both quantitative (*e.g.* chlorophyll a concentration, photosynthetic efficiency) and qualitative responses (relative abundance and succession of species, cell size), similarly to Roman et al. (2014), Shatova et al. (2016, 2017), Smith et al. (2013).

The number of nutrients included in such experiments may have to be reduced due to practical and analytical constraints, but should be selected based on the ecological context of the area. However, it would be valuable to combine these experiments with an analysis of fecal samples multi-nutrient composition. In the case of fertilisation experiments, the use of a control treatment in which only a single nutrient (the one of interest) is added can, by comparison, provide information on the effect of the simultaneous release of multiple nutrients in fecal matter, as demonstrated in Shatova et al. (2016) with penguin guano.

There is a growing interest in assessing the contribution of small cetaceans to nutrient cycling, and at the time of writing, several such experiments are underway using fecal material collected from strandings (Dr H. Pearson personal comment). However, to our knowledge, no such work is planned using fecal material from deep-diving species, although their contribution may be all the more unique because of their foraging ecology and diet, or from pinnipeds, although from simple observations of their shape and texture they are likely to have distinct characteristics from cetaceans.

6.4.2 Replicability of our methods across scales, species, populations and regions

Our approaches are replicable and require little adaptation to apply on different species, populations and/or regions where data are available.

The contribution of pinnipeds to nutrient cycling has rarely been assessed outside the Southern Ocean (but see Fariña et al. 2003, Theobald et al. 2006), and the focus has often been on the sea-to-land nutrient transfers they mediate rather than on their overall contribution, both at sea and on land. However, similarly to cetaceans, pinnipeds occur in multiple and ecologically diverse ocean regions (Berta 2017). Numerous species interact with human activities and urbanised coastlines, so they are also experiencing strong changes in their habitats (Blanchet et al. 2021, Kovacs et al. 2012). Arctic and sub-Arctic species are both facing severe changes in their habitats due to intense climate change and increased human use (Kovacs et al. 2012). In addition, pinniped populations in the northern hemisphere are subject to conflict with fisheries (Butler et al. 2011, Lavigne 2003, Olsen et al. 2018). In any case, their presence on coastal colonies facilitates access for monitoring and research (Teilmann and Galatius 2018). Thus, estimating nutrient release by pinniped populations in different regions of the world, similarly to cetaceans in Chapter 1, may provide new insights into their contribution to ecosystem dynamics beyond their consumption of prey.

Similarly, our local approach in Chapter 4 could be applied to a wide range of pinniped or cetacean populations. Abundance, seasonal distribution or even daily movement patterns of well-known coastal species are often available, along with population structure, diet and foraging ecology. In this case, fine-scale estimates of nutrient release patterns could be compared with local biochemical and productivity patterns, and with other sources of nutrient cycling and/or supply. Potential case studies range from small cetaceans such as bottlenose dolphins (*e.g.* Moray Firth population, Scotland (Arso Civil et al. 2019, Wilson et al. 1999)) to larger humpback whales *Megaptera novaeangliae* (*e.g.* North Atlantic populations (Fleming and Jackson 2011, Stevick et al. 2003)) or ubiquitous pinnipeds such as harbour seals (*e.g.* multi-colony population in the Northeast Atlantic (Andersen and Olsen 2010, Härkönen et al. 2002, Planque et al. 2021)). To illustrate this point, we develop in the next section a potential case study that would provide an original opportunity to combine several of the above approaches in a specific socio-environmental context.

6.4.3 The common dolphin in the Bay of Biscay: a potential case for a specific integrative approach

Socio-ecological context

The case of the common dolphin *Delphinus delphis* population in the Bay of Biscay (Northeast Atlantic) may represent an interesting opportunity to develop an integrative mesoscale approach for a small cetacean species. The Bay of Biscay, located between the northern coast of Spain and the western coast of France, combines human activities that threaten the habitat and food webs on which local marine mammals depend (García-Barón et al. 2019, Lassalle et al. 2012), including intense fishing activities (Gascuel et al. 2011, Lorance 2011, Ruiz et al. 2021), freight traffic and coastal urbanisation. The common dolphin is the most abundant small cetacean in the region (Laran et al. 2017). In the 1990s, the French Stranding Network (Réseau National Echouage RNE) detected abnormal stranding signals for common dolphins identified as the result of fisheries bycatch (Canneyt Van et al. 1998, Peltier et al. 2021). The levels of bycatch were quickly recognised as a potential threat to the population, and together with high bycatch levels of harbour porpoise in the northern part of Europe, they led to coordinated efforts to assess and monitor small cetacean populations in this part of Europe. With the Agreement on the Conservation of Small Cetaceans of the Baltic, North-East Atlantic, Irish and North Seas (ASCOBANS, 1992), large scale abundance surveys (the Small Cetaceans in European Atlantic waters and the North Sea (SCANS); Hammond et al. 2021, Macleod 2008) were conducted in 1994 (SCANS-I), 2005-2007 (SCANS-II), 2016-2017 (SCANS-III) and 2022 (SCANS-IV), covering both the neritic and oceanic parts of the Bay of Biscay (Gilles et al. 2023, Hammond et al. 2021). Some smaller-scale surveys focusing on the French waters were also conducted seasonally in 2012 (Laran et al. 2017).

This original socio-ecological situation makes the area uniquely data rich. Fishing activities have led to ichthyological and oceanographic research to understand patterns of productivity, fish distribution, abundance and trends (Arias et al. 2023, Doray et al. 2018). On the other hand, strandings of common dolphins have provided important data on the ecology and health of the population, while their abundance was repeatedly estimated from European surveys over a large area. The Bay of Biscay and common dolphin populations are both prone to past, present and future changes. The levels of exploitation by fisheries in the Bay of Biscay has already led to several shifts in fish stocks (Gascuel et al. 2011, Guénette and Gascuel 2012, Mesnil 2008). The abiotic conditions in the Bay of Biscay

are also largely influenced by the Gulf Stream, which is expected to know a regime shift as a result of climate changes (Bryden et al. 2005). Anthropogenic activities may also be changing, with several offshore windfarm projects underway along the French coast of the Bay of Biscay. The common dolphin bycatch issue has been intensifying since 2016 (Peltier et al. 2021), probably in part due to a shift in the population seasonal distribution and habitat use. This context thus provides an opportunity to improve our understanding of a small cetacean species in the functioning of its ecosystems, while subject to conflicts with fisheries, and to changes in its environment at different spatio-temporal time scales.

Population scale: nutrient release level estimate

Firstly, the bioenergetic model used in Chapter 1 could be used to estimate the level of nutrient release by the Bay of Biscay common dolphin population. Population abundance and average diet have been assessed in both the oceanic and neritic parts of the Bay, allowing separate estimates for each habitat. The metabolism of this species has been formally quantified using muscle power indicators (Spitz et al. 2012), and body mass can be estimated from historical stranding data. The prey composition data used in Chapter 1 are from the Bay of Biscay (Chouvelon et al. 2022b,c), and local dietary assessments for the population Marçalo et al. (2018), Pusineri et al. (2007), Santos et al. (2013) suggest that more than half of the prey species in the diet have been analysed. This percentage may increase to between 60 and 78% with some taxonomic groupings, and functional prey groups could be adapted to more accurately describe the diet of common dolphins. The parameters of the bioenergetic model may therefore be more finely tuned than the settings used in Chapter 1 and 2, as a result of focusing on a specific species in a data-rich area. As in Chapter 1, both the absolute and relative amounts of nutrients released could be assessed at the annual population level (or shorter time scale) and at the daily individual level.

Individual scale: waste nutrient analysis combined with dietary assessment

Secondly, a finer-scale approach can be developed to assess effective nutrient release at the individual level, *i.e.* to assess the nutrient content of common dolphin feces. Collecting feces from live common dolphins in the wild is virtually impossible. For this reason, collecting feces that have not yet been released as the content of the end of the colon of dead animals can be an indirect sampling method. A caveat associated with sampling stranded carcasses is that the stranded animals may not be representative of the live

population as they may have died of either disease, starvation or old age (Ten Doeschate et al. 2018). However, the intense local bycatch issue results in many strandings of healthy individuals, with nearly all age classes represented (Rouby 2022). Most carcasses identified as bycatch by either internal necropsy or external signs (e.g. net marks) show evidence of recent feeding (Pelagis Observatory team, personal comm.), making them particularly suitable for studying nutrient cycling processes.

Such sampling of stranded common dolphin egesta was initiated at the beginning of this PhD project, with \approx 40 samples collected between 2020 and 2022. Given the current rates of strandings and internal necropsies by the RNE (Dars et al. 2021), this number could double in a year (Willy Dabin, personal comm.). Multi-nutrient analysis of these samples could provide primary information on the absolute and relative composition of a small cetacean's egesta. In addition, stomach contents are routinely collected during necropsies and have therefore been collected from the same individuals for which we have fecal samples. Dietary assessment of these individuals can provide almost simultaneous pictures of the prey mix consumed and the nutrient released from it, depending on the state of digestion of the items found in the stomach and used for assessment. Although these data should be interpreted with caution because of the biases introduced by the differential digestion of different prey items and/or parts of prey and the unknown temporality of digestion, such simultaneous sampling is rare in wild species, even allowing for these biases. Individual dietary data could be compared with population mean data estimates and their inter-individual variability could be assessed. Similarly, the absolute and relative composition of individual common dolphin feces could be assessed and compared with estimates from the bioenergetic model using average diet data and approximate nutrient release rates.

In addition, the same samples could be incorporated into a framework similar to that used in Chapter 4 to estimate the levels of nutrient released by the common dolphin population without the biases of average diet and uncertain release rates. Estimates from both methods could be compared and provide primary information on their respective strengths and weaknesses.

Lab experiments

Finally, common dolphin colon content samples may be used to conduct some or all of the experiments described in Section 6.4.1. Experiments could be carried out taking into account the biochemical conditions of both the shelf and the oceanic part of the

Bay of Biscay, in collaboration with local institutes involved in the characterisation of the microflora and fauna of the region and their biochemical characterisation, such as the Institut Français de Recherche pour l'Exploitation de la Mer (Ifremer) and with oceanographers specialised in biochemistry, such as the Microbial Oceanography Laboratory (LOMIC, UMR 7621 CNRS-Sorbonne University).

6.5 Conclusion

This work has revealed different facets of marine mammals' role in nutrient cycling through waste release, at different spatial, temporal and taxonomic scales, in different ecosystems and for different species. It has expanded the field of knowledge about marine mammals and the functioning of their ecosystems, and demonstrated the diversity of marine mammal contributions to nutrient cycling as a result of their diverse ecology and biology. It provided only a glimpse of this diversity by focusing on one nutrient cycling pathway, but it adds to the body of evidence suggesting that losses in marine mammal populations may have consequences for the functioning of their ecosystems. While we cannot formally quantify the ecological importance of nutrient cycling mediated by marine mammals through waste release compared to the better documented effects of marine mammal predation and prey removal, we have provided quantitative arguments for how the former may be functionally relevant. This work has also highlighted some of the many unknowns that remain to be elucidated and opens the door to studies that could be undertaken to improve our understanding of these complex processes.

In the face of climate change and biodiversity loss, it is imperative to embrace the complexity and diversity of ecological interactions and processes in order to deepen our understanding of the past, present and future evolution of the Earth's ecosystem, including the dual role of biota as consumers and as nutrient vectors / recyclers. While it may seem like a tremendous task, our progress in this field has been all the more significant in the past decades. This joint effort not only sheds light on the marvellous yet discreet mechanisms that govern the functioning of natural ecosystems, but also shows the extent to which humans must come to terms with these mechanisms in order to continue to inhabit this extraordinarily rich planet.

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Appendices

Chapter 2 - Supplementary Data 1

[Chapter 2](#) - Statistics (min, lowest quantile, mean, median, highest quantile, max) for all parameters used or calculated in our bioenergetic model using Monte-Carlo simulations (first sheet) and for Sobol sensitivity index for each input parameter of the model (second sheet). This data support results displayed on [Figs. 2.1–2.3](#) of the chapter.

Chapitre 2, Supplementary Data 1 - sheet 1: statistics for model parameters

Species	min	2.5_quant	mean	median	97.5_quant	max	Parameter
Hydrurga leptonyx	10901	12988	41382	39499	81254	102599	Population abundance
Leptonychotes weddellii	221000	265756	669115	655710	1161796	1334919	Population abundance
Lobodon carcinophaga	3699479	3978809	5936041	5911378	8076091	8616004	Population abundance
Ommatophoca rossii	39403	42602	95665	91047	176978	231112	Population abundance
Hydrurga leptonyx	0,70	0,70	0,80	0,80	0,89	0,90	Fe release rate
Leptonychotes weddellii	0,70	0,71	0,80	0,80	0,89	0,90	Fe release rate
Lobodon carcinophaga	0,70	0,71	0,80	0,80	0,90	0,90	Fe release rate
Ommatophoca rossii	0,70	0,70	0,80	0,80	0,89	0,90	Fe release rate
Hydrurga leptonyx	150	215	350	350	488	599	Body mass
Leptonychotes weddellii	120	184	301	300	419	559	Body mass
Lobodon carcinophaga	120	133	202	201	279	361	Body mass
Ommatophoca rossii	100	109	162	161	222	250	Body mass
Hydrurga leptonyx	2,0	2,1	2,9	2,9	3,5	3,5	Beta
Leptonychotes weddellii	1,5	1,5	2,1	2,1	2,9	3,0	Beta
Lobodon carcinophaga	1,5	1,5	2,1	2,1	2,9	3,0	Beta
Ommatophoca rossii	1,5	1,5	2,1	2,1	2,9	3,0	Beta
Hydrurga leptonyx	1603	4219	6948	6954	9673	13119	Diet mean energy content E (kJ.kg ⁻¹ wet weight)
Leptonychotes weddellii	1216	3265	5382	5379	7497	9742	Diet mean energy content E (kJ.kg ⁻¹ wet weight)
Lobodon carcinophaga	1056	3122	5117	5116	7122	9490	Diet mean energy content E (kJ.kg ⁻¹ wet weight)
Ommatophoca rossii	1048	2918	4798	4797	6678	8965	Diet mean energy content E (kJ.kg ⁻¹ wet weight)
Hydrurga leptonyx	14,01	40,62	66,79	66,80	92,77	125,98	Diet mean iron content xFe (mg.kg ⁻¹ wet weight)
Leptonychotes weddellii	4,73	14,07	23,18	23,18	32,28	44,78	Diet mean iron content xFe (mg.kg ⁻¹ wet weight)
Lobodon carcinophaga	2,38	6,92	11,41	11,41	15,89	21,06	Diet mean iron content xFe (mg.kg ⁻¹ wet weight)
Ommatophoca rossii	3,48	9,83	16,21	16,21	22,58	30,29	Diet mean iron content xFe (mg.kg ⁻¹ wet weight)
Hydrurga leptonyx	0,01	0,02	0,03	0,03	0,06	0,17	% of body mass (daily ration)
Hydrurga leptonyx	0,80	0,81	0,89	0,89	0,95	0,95	Assimilation rate
Hydrurga leptonyx	26123	43135	68151	67795	95014	120321	Average Daily Metabolic Rate (kJ)
Hydrurga leptonyx	3,2	6,2	11,6	11,0	20,0	63,1	Daily ration (kg)
Leptonychotes weddellii	0,01	0,02	0,03	0,03	0,06	0,16	% of body mass (daily ration)
Leptonychotes weddellii	0,80	0,81	0,89	0,89	0,95	0,95	Assimilation rate
Leptonychotes weddellii	16685	27344	44587	43659	66535	90445	Average Daily Metabolic Rate (kJ)
Leptonychotes weddellii	2,7	5,1	9,8	9,2	17,6	51,3	Daily ration (kg)

Lobodon carcinophaga	0,01	0,02	0,04	0,04	0,07	0,21 % of body mass (daily ration)
Lobodon carcinophaga	0,80	0,81	0,89	0,89	0,95	0,95 Assimilation rate
Lobodon carcinophaga	15985	20962	33144	32405	49213	68249 Average Daily Metabolic Rate (kJ)
Lobodon carcinophaga	2,5	4,1	7,6	7,2	13,6	46,9 Daily ration (kg)
Ommatophoca rossii	0,02	0,02	0,04	0,04	0,07	0,21 % of body mass (daily ration)
Ommatophoca rossii	0,80	0,81	0,89	0,89	0,95	0,95 Assimilation rate
Ommatophoca rossii	14081	17853	28072	27468	41449	54877 Average Daily Metabolic Rate (kJ)
Ommatophoca rossii	2,1	3,7	6,9	6,5	12,3	35,0 Daily ration (kg)
Hydrurga leptonyx	116,1	348,6	772,5	727,7	1459,8	4971,5 Individual daily amount of Fe ingested (mg)
Leptonychotes weddellii	32,0	98,8	226,7	211,3	444,3	1646,1 Individual daily amount of Fe ingested (mg)
Lobodon carcinophaga	13,3	38,8	87,1	81,2	169,0	594,4 Individual daily amount of Fe ingested (mg)
Ommatophoca rossii	16,6	49,8	111,9	104,4	217,1	685,7 Individual daily amount of Fe ingested (mg)
Hydrurga leptonyx	92,7	274,9	618,0	580,8	1180,2	3937,4 Individual daily amount of Fe released (mg)
Leptonychotes weddellii	23,9	77,8	181,4	168,7	359,3	1402,3 Individual daily amount of Fe released (mg)
Lobodon carcinophaga	9,6	30,6	69,7	64,8	136,6	477,3 Individual daily amount of Fe released (mg)
Ommatophoca rossii	13,2	39,2	89,5	83,3	175,9	547,0 Individual daily amount of Fe released (mg)
Hydrurga leptonyx	0,59	2,23	9,33	8,12	23,44	63,26 Population annual amount of Fe released (t/yr)
Leptonychotes weddellii	3,79	12,57	44,30	39,15	105,93	316,98 Population annual amount of Fe released (t/yr)
Lobodon carcinophaga	17,79	59,88	150,93	138,27	315,04	1001,73 Population annual amount of Fe released (t/yr)
Ommatophoca rossii	0,25	0,94	3,12	2,73	7,59	25,91 Population annual amount of Fe released (t/yr)

Chapitre 2, Supplementary Data 1 - sheet 2: statistics for Sobol sensitivity indices

Species	Input	Sensitivity	original	bias	std. error	min. c.i.	max. c.i.
Hydrurga leptonyx	Abundance	First order indices	0,531503657	0,000166409	0,006326376	0,518949694	0,543820076
Hydrurga leptonyx	Body mass	First order indices	0,061816455	-9,94764E-05	0,00711883	0,047150695	0,075354447
Hydrurga leptonyx	Beta	First order indices	0,045370821	-0,000132139	0,006868727	0,031674914	0,05844949
Hydrurga leptonyx	Mean energy content of diet	First order indices	0,156071833	-0,000100662	0,00795565	0,140410076	0,171819675
Hydrurga leptonyx	Mean Fe content of diet	First order indices	0,105028657	2,45121E-05	0,006908585	0,090958473	0,118929378
Hydrurga leptonyx	Assimilation rate	First order indices	0,004281808	-0,00017437	0,006889743	-0,009450735	0,017699396
Hydrurga leptonyx	Fe release rate	First order indices	0,011469279	-0,000165184	0,006846591	-0,002349705	0,024402467
Hydrurga leptonyx	Abundance	Total order indices	0,598605133	0,000166409	0,00851279	0,581769572	0,615230768
Hydrurga leptonyx	Body mass	Total order indices	0,078535878	-9,94764E-05	0,001556512	0,075279742	0,081435952
Hydrurga leptonyx	Beta	Total order indices	0,057058172	-0,000132139	0,001005954	0,054921015	0,058993735
Hydrurga leptonyx	Mean energy content of diet	Total order indices	0,198468603	-0,000100662	0,004936359	0,187782195	0,207708412
Hydrurga leptonyx	Mean Fe content of diet	Total order indices	0,143398284	2,45121E-05	0,002741341	0,137830611	0,148786247
Hydrurga leptonyx	Assimilation rate	Total order indices	0,003278389	-0,00017437	6,15372E-05	0,003155559	0,003395536
Hydrurga leptonyx	Fe release rate	Total order indices	0,019278842	-0,000165184	0,000325817	0,018603931	0,019895304
Lobodon carcinophaga	Abundance	First order indices	0,159530352	-9,67831E-05	0,007303705	0,144793465	0,173806012
Lobodon carcinophaga	Body mass	First order indices	0,084195344	-6,12715E-05	0,006871915	0,070470059	0,097576728
Lobodon carcinophaga	Beta	First order indices	0,14071302	0,000161779	0,007018852	0,126564243	0,153914627
Lobodon carcinophaga	Mean energy content of diet	First order indices	0,269909314	-4,60534E-05	0,00844038	0,253081781	0,286520896
Lobodon carcinophaga	Mean Fe content of diet	First order indices	0,192125216	2,76201E-05	0,006975378	0,178840752	0,205049545
Lobodon carcinophaga	Assimilation rate	First order indices	-0,009099707	-6,5997E-05	0,006901786	-0,022500785	0,004130865
Lobodon carcinophaga	Fe release rate	First order indices	0,010058335	-9,07308E-05	0,006992159	-0,003804369	0,024179794
Lobodon carcinophaga	Abundance	Total order indices	0,196363522	-9,67831E-05	0,003351164	0,189838265	0,20240814
Lobodon carcinophaga	Body mass	Total order indices	0,112566052	-6,12715E-05	0,001930351	0,108676637	0,116120691
Lobodon carcinophaga	Beta	Total order indices	0,176502794	0,000161779	0,002908979	0,170185613	0,181662267
Lobodon carcinophaga	Mean energy content of diet	Total order indices	0,319737639	-4,60534E-05	0,005679878	0,308159282	0,330357673
Lobodon carcinophaga	Mean Fe content of diet	Total order indices	0,247097658	2,76201E-05	0,004218351	0,238874166	0,255335024
Lobodon carcinophaga	Assimilation rate	Total order indices	0,005614387	-6,5997E-05	9,46615E-05	0,005426001	0,005800011
Lobodon carcinophaga	Fe release rate	Total order indices	0,031140118	-9,07308E-05	0,00054436	0,02998173	0,032148125
Ommatophoca rossii	Abundance	First order indices	0,430458662	-0,000210002	0,006857888	0,417050836	0,44405676
Ommatophoca rossii	Body mass	First order indices	0,050242268	0,000155961	0,006923224	0,036356295	0,063278711
Ommatophoca rossii	Beta	First order indices	0,085662134	8,22988E-05	0,006934475	0,07160971	0,099023676
Ommatophoca rossii	Mean energy content of diet	First order indices	0,160681545	-0,000264115	0,00782918	0,145680752	0,176580102

Ommatophoca rossii	Mean Fe content of diet	First order indices	0,120924939	3,47722E-06	0,007092473	0,106355202	0,134210722
Ommatophoca rossii	Assimilation rate	First order indices	0,001510574	2,63687E-05	0,006769096	-0,012761817	0,014869182
Ommatophoca rossii	Fe release rate	First order indices	0,016125234	8,26526E-05	0,006886467	0,002446959	0,029490517
Ommatophoca rossii	Abundance	Total order indices	0,511978008	-0,000210002	0,007213511	0,497934749	0,526829149
Ommatophoca rossii	Body mass	Total order indices	0,074326253	0,000155961	0,001356297	0,071672173	0,076950528
Ommatophoca rossii	Beta	Total order indices	0,111754404	8,22988E-05	0,002050846	0,108031042	0,115916918
Ommatophoca rossii	Mean energy content of diet	Total order indices	0,21193793	-0,000264115	0,004082505	0,203968992	0,219708969
Ommatophoca rossii	Mean Fe content of diet	Total order indices	0,155494147	3,47722E-06	0,002831969	0,149939187	0,160836686
Ommatophoca rossii	Assimilation rate	Total order indices	0,003634696	2,63687E-05	6,34077E-05	0,00350716	0,003754461
Ommatophoca rossii	Fe release rate	Total order indices	0,021611456	8,26526E-05	0,00040229	0,020817885	0,022378537
Leptonychotes weddellii	Abundance	First order indices	0,399957171	0,000393528	0,006032952	0,387741477	0,411494177
Leptonychotes weddellii	Body mass	First order indices	0,060506504	0,000490562	0,007285505	0,045757237	0,073779888
Leptonychotes weddellii	Beta	First order indices	0,084158123	0,000502695	0,007287159	0,06988675	0,098046063
Leptonychotes weddellii	Mean energy content of diet	First order indices	0,173284444	0,00027842	0,008360843	0,157205121	0,190412426
Leptonychotes weddellii	Mean Fe content of diet	First order indices	0,122808513	0,000555365	0,007534828	0,108456355	0,137297496
Leptonychotes weddellii	Assimilation rate	First order indices	-0,004833381	0,000455443	0,006989242	-0,018271247	0,008126896
Leptonychotes weddellii	Fe release rate	First order indices	0,008060946	0,000398329	0,007014397	-0,005218131	0,021171042
Leptonychotes weddellii	Abundance	Total order indices	0,463819131	0,000393528	0,006565733	0,451373915	0,47731538
Leptonychotes weddellii	Body mass	Total order indices	0,092440313	0,000490562	0,002023932	0,088431782	0,09631792
Leptonychotes weddellii	Beta	Total order indices	0,117382013	0,000502695	0,002101478	0,113147592	0,121564157
Leptonychotes weddellii	Mean energy content of diet	Total order indices	0,223542765	0,00027842	0,004369055	0,214461566	0,232239282
Leptonychotes weddellii	Mean Fe content of diet	Total order indices	0,160285451	0,000555365	0,003281057	0,153897885	0,166734554
Leptonychotes weddellii	Assimilation rate	Total order indices	0,003793934	0,000455443	7,16374E-05	0,003648059	0,003927415
Leptonychotes weddellii	Fe release rate	Total order indices	0,021425659	0,000398329	0,000407905	0,020563006	0,022202631

Chapter 2 - Supplementary Data 2

[Chapter 2](#) - Iron (Fe) release estimates for several species of marine predators of the Southern Ocean in the literature and in the present study. Full references are provided in the reference list of the article. This data support results displayed on [Fig. 2.2](#) of the chapter.

Species	Nb of days of presence considered in the study	Mean Fe yearly release (t/yr)	Confidence interval	Reference	Comment
Sperm whales	365	50		Lavery et al. 2010	
Antarctic blue whales	365	65		Lavery et al. 2014	
Antarctic blue whales	60-180	15	9-24	Savoca et al. 2021	
Humpback whales	60-180	221	144-394	Savoca et al. 2021	
Antarctic fin whales	60-180	367	193-590	Savoca et al. 2021	
Antarctic minke whales	60-180	630	420-937	Savoca et al. 2021	
Chinstrap, Adelie and Gentoo penguins	365	169	deduced from Sparaventi et al. 2021		Estimates from this study were originally calculated for the reproduction period only. They were raised to annual estimates using a simple cross product
Leopard seals	365	9,3	2.2 - 23.4	this study	
Weddell seals	365	44,3	12.6 - 105.9	this study	
Crabeater seals	365	150,9	59.9 - 315	this study	
Ross seals	365	3,1	0.9 - 7.6	this study	

Chapter 4 - Supplementary Table 1

Chapter 4 - Results of statistical tests of comparison between estimates of total nutrient released by lactating Antarctic fur seal females from two colonies on Kerguelen Islands (Southern Ocean) derived from a bioenergetic model with varying simulated scat composition datasets. Scats collected on Cap Noir and Pointe Suzanne were separated into 3 most similar clusters (using a hierarchical clustering). Proportion of these clusters were allowed to vary from 0 to 100%, with scats from other clusters being sampled with equal chances (see [Section 4.2.5.2](#) for methodology details) in the final simulate scat composition dataset used in the bioenergetic model. We compared results from these different generated scat nutrient datasets with baseline values obtained with all scats from the colony being resampled with equal chances (see [Table 4.4](#) "Scats separated by colony site"). For example, where *scenario* = 1, the % of cluster 1 was changed, being set to 0% for *subscenario* = "test 0%", to 10% for *subscenario* = "test 10%" etc to *subscenario* = "test 100%".

The Monte-Carlo simulations precluded the use of usual statistical tests to assess the significance of the differences between two sets of nutrient release estimates because of the high number of simulations. Instead, we quantified the overlap of the two vectors of estimates to compare (as a percentage p). If p is either $> 0,95$ or $< 0,05$, we can say the difference is significant with 5% confidence. Cells colored in red indicated result of comparison test is statistically significant.

Colony site	scenario	subscenario	P	Fe	Zn	Cu	Mn	Se	Co
Cap Noir	1	test_0	1	0	0,66	0	0	0	0
Cap Noir	1	test_10	1	0,01	0,60	0,00	0,00	0,00	0,00
Cap Noir	1	test_20	0,97	0,19	0,54	0,14	0,15	0,12	0,16
Cap Noir	1	test_30	0,03	0,81	0,48	0,86	0,85	0,88	0,84
Cap Noir	1	test_40	0	0,99	0,41	1,00	1,00	1,00	1,00
Cap Noir	1	test_50	0	1	0,35	1	1	1	1
Cap Noir	1	test_60	0	1	0,29	1	1	1	1
Cap Noir	1	test_70	0	1	0,25	1	1	1	1
Cap Noir	1	test_80	0	1	0,20	1	1	1	1
Cap Noir	1	test_90	0	1	0,17	1	1	1	1

Table 1: (continued)

Colony site	scenario	subscenario	P	Fe	Zn	Cu	Mn	Se	Co
Cap Noir	1	test_100	0	1	0,14	1	1	1	1
Cap Noir	2	test_0	0	1	1	1	1	0,62	1
Cap Noir	2	test_10	0	1	0,99	0,99	1	0,56	1
Cap Noir	2	test_20	0,05	0,93	0,74	0,74	0,96	0,52	0,95
Cap Noir	2	test_30	0,92	0,12	0,32	0,29	0,08	0,48	0,09
Cap Noir	2	test_40	1,00	0,00	0,12	0,09	0	0,47	0,00
Cap Noir	2	test_50	1	0	0,03	0,03	0	0,44	0
Cap Noir	2	test_60	1	0	0,02	0,01	0	0,44	0
Cap Noir	2	test_70	1	0	0,01	0,01	0	0,42	0
Cap Noir	2	test_80	1	0	0,00	0,00	0	0,41	0
Cap Noir	2	test_90	1	0	0,00	0,00	0	0,41	0
Cap Noir	2	test_100	1	0	0,00	0,00	0	0,39	0
Cap Noir	3	test_0	0,05	0,04	0,01	0,98	0,01	1	0,03
Cap Noir	3	test_10	0,15	0,12	0,05	0,91	0,08	1	0,11
Cap Noir	3	test_20	0,35	0,33	0,27	0,69	0,31	0,88	0,33
Cap Noir	3	test_30	0,65	0,67	0,73	0,31	0,71	0,13	0,68
Cap Noir	3	test_40	0,91	0,93	0,98	0,05	0,96	0	0,94
Cap Noir	3	test_50	0,99	1,00	1	0,00	1,00	0	1,00
Cap Noir	3	test_60	1	1,00	1	0	1	0	1
Cap Noir	3	test_70	1	1	1	0	1	0	1
Cap Noir	3	test_80	1	1	1	0	1	0	1
Cap Noir	3	test_90	1	1	1	0	1	0	1
Cap Noir	3	test_100	1	1	1	0	1	0	1
Pointe Suzanne	1	test_0	0,99	0,22	0,53	0,26	0,3	0,30	0,24
Pointe Suzanne	1	test_10	0,87	0,34	0,55	0,38	0,4	0,42	0,36
Pointe Suzanne	1	test_20	0,68	0,50	0,56	0,51	0,5	0,53	0,51
Pointe Suzanne	1	test_30	0,49	0,65	0,59	0,64	0,6	0,63	0,65
Pointe Suzanne	1	test_40	0,35	0,80	0,61	0,76	0,8	0,73	0,77
Pointe Suzanne	1	test_50	0,24	0,89	0,62	0,86	0,9	0,82	0,88
Pointe Suzanne	1	test_60	0,17	0,96	0,64	0,92	0,9	0,88	0,94
Pointe Suzanne	1	test_70	0,13	1,00	0,66	0,97	1,0	0,92	0,99

Table 1: (continued)

Colony site	scenario	subscenario	P	Fe	Zn	Cu	Mn	Se	Co
Pointe Suzanne	1	test_80	0,09	1	0,68	1,00	1,0	0,96	1,00
Pointe Suzanne	1	test_90	0,07	1	0,69	1,00	1	0,99	1
Pointe Suzanne	1	test_100	0,05	1	0,70	1	1	1,00	1
Pointe Suzanne	2	test_0	0,21	1	0,75	1,00	1	0,90	1
Pointe Suzanne	2	test_10	0,36	0,94	0,67	0,86	0,92	0,77	0,93
Pointe Suzanne	2	test_20	0,50	0,71	0,60	0,68	0,70	0,63	0,70
Pointe Suzanne	2	test_30	0,64	0,47	0,55	0,51	0,48	0,54	0,48
Pointe Suzanne	2	test_40	0,75	0,31	0,52	0,38	0,34	0,46	0,33
Pointe Suzanne	2	test_50	0,84	0,23	0,50	0,31	0,25	0,40	0,24
Pointe Suzanne	2	test_60	0,88	0,17	0,47	0,26	0,19	0,35	0,19
Pointe Suzanne	2	test_70	0,92	0,12	0,45	0,22	0,16	0,32	0,15
Pointe Suzanne	2	test_80	0,95	0,10	0,44	0,19	0,13	0,29	0,12
Pointe Suzanne	2	test_90	0,97	0,08	0,42	0,17	0,11	0,27	0,10
Pointe Suzanne	2	test_100	0,99	0,07	0,41	0,16	0,09	0,25	0,08
Pointe Suzanne	3	test_0	0,46	0,40	0,52	0,52	0,43	0,60	0,42
Pointe Suzanne	3	test_10	0,51	0,47	0,54	0,54	0,48	0,58	0,48
Pointe Suzanne	3	test_20	0,55	0,54	0,56	0,56	0,54	0,57	0,54
Pointe Suzanne	3	test_30	0,60	0,62	0,59	0,58	0,61	0,57	0,61
Pointe Suzanne	3	test_40	0,67	0,71	0,62	0,61	0,69	0,56	0,70
Pointe Suzanne	3	test_50	0,74	0,80	0,65	0,65	0,77	0,55	0,79
Pointe Suzanne	3	test_60	0,80	0,88	0,70	0,69	0,86	0,55	0,87
Pointe Suzanne	3	test_70	0,88	0,95	0,72	0,73	0,91	0,53	0,92
Pointe Suzanne	3	test_80	0,93	0,99	0,77	0,77	0,98	0,53	0,99
Pointe Suzanne	3	test_90	0,98	1	0,81	0,81	1,00	0,52	1
Pointe Suzanne	3	test_100	1,00	1	0,85	0,86	1	0,51	1

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Dealing with several sources of uncertainty in modelling of community-level processes

Uncertainty is pervasive in ecological sciences and must be quantified properly for ecological assessment and management decisions at the scale of ecosystems. Nutrient fluxes are crucial to ocean productivity. Phytoplankton growth relies on the availability of essential nutrients, and cetacean communities could contribute significantly to the primary production dynamics by releasing nutrient-rich fecal matter in the photic zone. We used a bioenergetic model to estimate the amount of nutrients released by cetaceans, from large whales to small cetaceans, in several large-scale areas around the globe. Model inputs included abundance data from broad-scale multispecies surveys, diet composition studies and analysis of nutrient concentrations in prey. The model also involved bioenergetic parameters such as body mass, metabolic cost factors, energy assimilation efficiency and elemental excretion rates, most of which were never actually measured on cetaceans. We faced several sources of uncertainty for all parameters of the model, from systematic error to natural variation or inherent (epistemic) randomness, sometimes combined. Using Monte Carlo simulations, we assumed a parametric distribution of the parameter to simulate data from statistical descriptors (mean, coefficient of variation, minimum and maximum). Parameters relevant to the composition of preys were associated to limited datasets, and we used bootstrapping (*i.e.* sampling with replacement) to account for variability. We then conducted a sensitivity analysis to assess how the sources of uncertainty in the inputs affected the uncertainty in the output, and identify influential parameters using Sobol indices. Parameters resulting from bootstrapping could not be included in the sensitivity analysis, we were limited to more basic methods to assess the effect of the variability of these parameters on the output. The most influential parameter was the abundance of cetacean populations, the only parameter based on robust statistical survey methods (distance sampling), with inherent uncertainty due to sampling conditions, species and areas. Never measured parameters associated to flat distributions were only slightly influential. Our study illustrates how Monte-Carlo simulations combined with bootstrapping can be used to obtain intervals likely to contain true values of particular interest, considering several sources of uncertainty in parameters.

Context

Aim – Estimate amounts of nutrients released in the enlightened zone of oceans by whole cetacean communities via their waste products (feces, urine)

How? Bioenergetic model estimating prey ingestion, nutrient ingestion and nutrient release

n = nutrient  c = cetacean population 

$$R_{n,c} = \beta_c \times 293,1 \times BM_c \times \frac{1}{AE \times E_c} \times x_{n,c} \times r_n \times A_c \times ndays_c$$

β_c	metabolic parameter	estimated by indirect method for 11 out of 38 species	Individual variation Random error
BM_c	body mass	estimated for 34 out of 38 species from regression equations	Individual variation Random error
AE	Assimilation rate of energy	typically 0.8, rarely measured on cetaceans	Individual variation Epistemic uncertainty
E_c	mean energy	estimated from mean diet inferred from literature + dataset of nutritional content of prey	Individual variation Random error Epistemic uncertainty
$x_{n,c}$	mean nutrient in diet		
r_n	nutrient release rate	never measured on cetaceans, for all nutrients	Individual variation Epistemic uncertainty
A_c	population abundance	estimated from distance sampling surveys	Random error
$ndays_c$	nb of day spent in area	ranges inferred from literature , from few individuals of few species	Individual variation Epistemic uncertainty

Problem – Several sources of uncertainty (random error, natural variation, epidemic uncertainty), few existing data and dataset available

Objectives

1 – Account for uncertainty in model inputs to obtain interval estimates of output

2 – Identify influential model inputs



Dealing with several sources of uncertainty in modelling of community-level processes



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Method

Monte-Carlo simulations

A **distribution** and **variation factor** was assigned to each input, based on literature or common practice:

$$\beta_c, BM_c, AE \rightarrow \text{Normal, e.g. } \beta_c \sim N(\bar{\beta}_c, \frac{(\bar{\beta}_c+0,5) - (\bar{\beta}_c-0,5)}{4})$$

$$r_n, ndays_c \rightarrow \text{Uniform, e.g. } r_{Fe} \sim U(0,85, 0,95)$$

$$A_c \rightarrow A_c \sim \log N(\log(\frac{A_c}{\sqrt{1+CV_{A_c}^2}}), \sqrt{\log(1+CV_{A_c}^2)})$$

Kernel-based bootstrap

Kernel-based procedure to estimate each prey group composition cumulative density function, sample from it and obtain **independent samples**

$$\% \text{ of prey group in diet (constant)} \times \begin{matrix} \text{prey group 1} & \dots & \text{prey group } 10 \\ \dots & \dots & \dots \\ \dots & \dots & \dots \end{matrix}$$

E_c, r_n, c

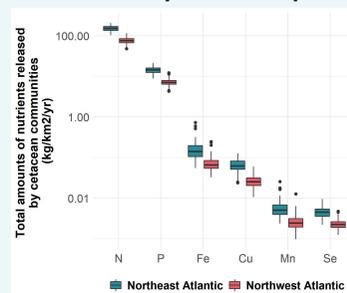
Global sensitivity analysis

- **Global** i.e. effect of an input on the output is estimated with all other inputs varying
- **Variance decomposition** to attribute uncertainty in output to uncertainty in inputs
- **Sobol first-order** and **total** (i.e. including interactions with other inputs) indices with R sensitivity package



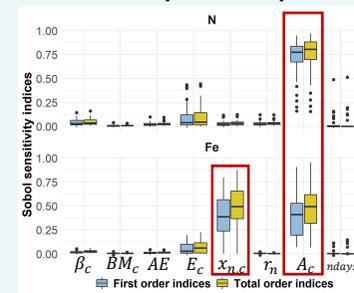
Results

Uncertainty in the output



Ranges of estimates allow comparison between areas

Sensitivity to the inputs



2 influential inputs \neq between macro & micro-nutrients

Discussion

- Accounting for uncertainty has a **computational cost** (nb of simulations)
- Kernel-based bootstrap \rightarrow still a dependence on the **empirical basis** (dataset and nb of samples per prey group)
- Abundance is the **most influential input**, yet it is already resulting of a well proofed **complex statistical design and analysis** \rightarrow hard to be more precise
- Most never measured inputs are only slightly influential
- **Ranges of variation** driven by **researcher's degree of freedom** setting up input variation parameters, but does it **accurately reflect the process of interest** ?

Conclusions

1 – **Monte-Carlo simulations** combined with **kernel-based bootstrap** allowed to **formalize assumptions** and obtain interval estimates of a community-level process associated to many sources of uncertainty

2 – **Global sensitivity analysis** to get a clear understanding of **how the output is affected** by uncertainties in the inputs

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Nuances de brun dans le grand bleu : exploration de facettes du rôle des mammifères marins dans le recyclage des nutriments

Résumé : Les mammifères marins sont présents dans tous les océans et comprennent plus de 130 espèces à la biologie et à l'écologie diverses. Leurs fèces et leurs urines sont riches en nutriments essentiels (azote, fer, etc.) et leurs rejets dans l'environnement peut influencer le fonctionnement des écosystèmes en stimulant la productivité des réseaux trophiques. Cependant, ces processus et leur importance écologique sont peu connus. Ce projet étudie comment les mammifères marins contribuent au recyclage des nutriments dans leurs écosystèmes via la production de fèces et d'urine. Il mobilise des modèles bioénergétiques, des données populationnelles, physiologiques et de régime alimentaire ainsi que des données de composition de proies et de fèces. Nos approches couvrent plusieurs espèces, écosystèmes, nutriments et échelles spatio-temporelles. Nous montrons que la contribution des communautés de cétacés au recyclage des nutriments est hétérogène dans les océans du monde et qu'elle est déterminée par l'abondance relative des petits cétacés, des grands plongeurs et des baleines. Dans l'océan Austral, les espèces de phoques des glaces contribuent au recyclage du fer avec les baleines et les manchots. Le régime alimentaire est déterminant pour la contribution des espèces à l'échelle individuelle et populationnelle, et les variations à fine échelle du contenu des fèces individuelles peuvent avoir une influence sur l'impact global de la population sur le recyclage des nutriments. La contribution des mammifères marins à la dynamique des nutriments dans le contexte biogéochimique unique de l'archipel des Kerguelen (océan Austral) semble significative en mer et sur leurs colonies côtières. Ce travail élargi nos connaissances sur le rôle des mammifères marins dans la dynamique des écosystèmes. Il démontre la diversité des contributions des mammifères marins au recyclage des nutriments et fournit des arguments quantitatifs sur la façon dont ces processus peuvent être fonctionnellement importants dans les écosystèmes.

Mots clés : nutriments ; mégafaune ; sources de nutriments ; transferts de nutriments médiés par les animaux ; diversité ; océan Austral ; azote ; fer ; cétacés ; pinnipèdes ; otaries à fourrure de l'Antarctique

Brown nuances in the big blue: exploring facets of marine mammals' role in nutrient cycling

Summary: Marine mammals are found in all oceans and include over 130 species with diverse biology and ecology. Marine mammal feces and urine are rich in essential nutrients (*e.g.* nitrogen, iron) and their release into the environment seems to influence ecosystem functioning by stimulating productivity at the base of food webs. However, little is known of these processes and their ecological importance. This research project investigates how marine mammals contribute to ecosystem nutrient cycling through defecation and urination. It is based on bioenergetic models, population, physiology and diet data as well as prey and feces nutrient composition data. Our project spans multiple species, ecosystems, nutrients and study scales. We showed that cetacean communities' contribution to nutrient cycling is heterogeneous across the world oceans and is determined by the relative abundance of small cetaceans, deep diving species and large whales. In the Southern Ocean, ice seal species significantly contribute to iron cycling along with whales and penguins. Diet is determinant of the contribution of species at individual and population scales, and fine scale individual variations in the nutrient composition of waste can influence the population impact on nutrient dynamics. The contribution of marine mammals to nutrient dynamics in the unique biogeochemical context of the Kerguelen Archipelago (Southern Ocean) is likely significant both at sea and on their terrestrial colony sites. Overall, this work has expanded our knowledge of marine mammals' role in ecosystem dynamics. It demonstrated the diversity of marine mammal contributions to nutrient cycling, and provided quantitative arguments for the functional relevance of these processes in ecosystems.

Keywords: nutrients; megafauna; nutrient subsidies; animal-mediated nutrient transfers; diversity; Southern Ocean; nitrogen; iron; cetaceans; pinnipeds; Antarctic fur seals



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Abstract

Marine mammals are found in all oceans and include over 130 species with diverse biology and ecology. Marine mammal feces and urine are rich in essential nutrients (*e.g.* nitrogen, iron) and their release into the environment seems to influence ecosystem functioning by stimulating productivity at the base of food webs. However, little is known of these processes and their ecological importance. This research project investigates how marine mammals contribute to ecosystem nutrient cycling through defecation and urination. It is based on bioenergetic models, population, physiology and diet data as well as prey and feces nutrient composition data. Our project spans multiple species, ecosystems, nutrients and study scales. We showed that cetacean communities' contribution to nutrient cycling is heterogeneous across the world oceans and is determined by the relative abundance of small cetaceans, deep diving species and large whales. In the Southern Ocean, ice seal species significantly contribute to iron cycling along with whales and penguins. Diet is determinant of the contribution of species at individual and population scales, and fine scale individual variations in the nutrient composition of waste can influence the population impact on nutrient dynamics. The contribution of marine mammals to nutrient dynamics in the unique biogeochemical context of the Kerguelen Archipelago (Southern Ocean) is likely significant both at sea and on their terrestrial colony sites. Overall, this work has expanded our knowledge of marine mammals' role in ecosystem dynamics. It demonstrated the diversity of marine mammal contributions to nutrient cycling, and provided quantitative arguments for the functional relevance of these processes in ecosystems.

