Organic carbon export by marine mammal deadfalls in the Nordic Seas

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Abstract

The biological pump is a critical process in the oceanic carbon cycle, transferring organic carbon from the atmosphere and surface waters into the deep ocean and seafloor sediments. Organic carbon stored in living biomass can be exported into deep sea areas via deadfalls, potentially getting stored for hundreds of years, but studies disagree on the amount of carbon they store, and their significance towards the total carbon flux in the ocean. In this study, organic carbon export of marine mammal deadfalls was calculated from existing data on abundance, biomass, residency, mortality rates, and organic carbon content. This study's area is set in the Nordic Seas, a part of the Northeast Atlantic Ocean, and consists of three regions; ICE (Icelandic shelf, Denmark Strait, Iceland Sea), GN (Greenland Sea and Norwegian Sea), and BS (Barents Sea), that has been comprehensively studied for marine mammal abundance estimates. Previous carbon export studies on marine mammals have mainly focused on baleen whales, but the contribution of the more abundant, smaller marine mammals such as pinnipeds and cetaceans, as well as sperm whales, may also be relevant. The total annual organic carbon flux potential was estimated to be 2.68×10^{-5} Pg C yr^{-1} (95% CI $1.23-5.23 \times 10^{-5}$ Pg C yr^{-1}), which equals ~26 887 tonnes C yr^{-1} for all species across the three study regions. Fin whales (*Balaenoptera physalus*) were the largest single species contributor with ~8 653 tonnes C yr^{-1} (95% CI 5 234−12 072 tonnes C yr^{-1}). Harp seals (*Pagophilus groenlandicus*) were the second largest with ~5 072 tonnes C yr^{-1} (95% CI 3 329, 6 815 tonnes C yr^{-1}) and common minke whales (*Balaenoptera acutorostrata*) were the third with 3 613 tonnes C yr^{-1} (95% CI 2 252, 4 974 tonnes C yr^{-1}). The largest organic carbon flux took place in the ICE region, with over half (51%) of the total contribution of organic carbon located within this region. Compared to organic carbon export by dissolved organic carbon (DOC) and particulate organic carbon (POC), the carbon flux potential derived from marine mammal deadfalls in this study are about 0.03−0.07% and 0.019−0.042% of these values, respectively. While regional storage potentials are low compared to other sources of organic carbon flux, local effects on organic carbon accumilation are massive, with an increase of ~2.14×10^{10} % per m^2 compared to POC export. This study provides the first estimate of organic carbon export via marine mammal deadfalls in the Northeast Atlantic and is the first study to consider the wide range of marine mammals, from pinnipeds and small cetaceans to large whales, in a deadfall carbon export calculation. The study shows the importance of understanding the role of marine mammals in the oceanic carbon cycle, and to quantify the

carbon export contribution from different components of the ecosystem in today's climate crisis.

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Acknowledgements

1 Introduction

The concentration of carbon dioxide (CO_2) in the atmosphere has increased dramatically during the last 300 years. The success of the industrial revolution (from 1760 to around 1830) caused large emissions of CO_2 and other greenhouse gases that continues to this day (Lei *et al.*, 2020). Ecosystems have a large role in atmospheric carbon dioxide regulation and can act as a carbon dioxide source or sink depending on the rates of photosynthetic activity and respiration (Martin *et al.*, 2021). The ocean is one such important carbon sink and has absorbed roughly 30% of anthropogenic emissions since the industrial revolution (Gruber *et al.*, 2019). Carbon in the ocean occurs in inorganic and organic forms, the latter referring to carbon that is part of living or decomposing organisms (Middelburg, 2019). In the oceanic ecosystem primary production originates from photosynthetic phytoplankton that capture carbon dioxide from the environment and produces oxygen by photosynthesis to the surrounding water column. This primary production is limited by the availability of nutrients, and the most important limiting factors are nitrogen, phosphorus, and iron (Martin & Fitzwater, 1988). These nutrients are critical for phytoplankton growth, and their availability is regulated by seasonal variability and physical processes such as vertical mixing, upwelling, and atmospheric deposition (Pershing *et al.*, 2010). Upwelling brings nutrient-rich waters from the depths to the surface, enhancing phytoplankton blooms. Conversely, nutrient depletion can occur in areas where there is strong stratification of water layers or overconsumption of nutrients by phytoplankton populations (Middelburg, 2019).

Carbon sequestration is the capture, removal, and long-time storage of carbon to environmental carbon sinks (Masson-Delmotte *et al.*, 2021). CO_2 is removed from the atmosphere and kept away from the atmospheric carbon cycle, thus playing a role in mitigating the greenhouse effect and regulating the Earth's climate (Follett *et al.*, 2014). Carbon that is transferred through food webs, enter sediments, or sink below the surface layer (photic zone or mixed layer depth, whichever is deeper) have the potential to be stored (Pearson *et al.*, 2022). The carbon must stay away from the atmospheric over a large timescale (>100 years) to be considered sequestered for climate-relevant timescales (Baker *et al.*, 2022; Pearson *et al.*, 2022). The deep ocean is a significant reservoir of carbon on Earth, containing approximately 38,000 Pg C, which is roughly 15-20 times more than that sequestered by land plants (Ricour *et al.*, 2023). This carbon includes both particulate and

dissolved forms, with dissolved organic carbon (DOC) representing 20% of the annual organic carbon flux to the deep seas (Carlson *et al.*, 1994). DOC in the ocean includes a wide range of compounds with varying biological reactivities, from very labile (quickly consumed by microbes) to highly refractory (resistant to microbial degradation and can persist for millennia) (Six & Maier-Reimer, 1996). The refractory fraction of DOC in the ocean, which is biologically unavailable, is estimated to be around 660 Pg and constitutes the ocean's long-term sequestration capacity (Hansell & Carlson, 2014). This fraction plays a crucial role in the ocean's ability to regulate atmospheric CO_2 levels over millennial time scales. Understanding the dynamics of organic carbon storage in the deep ocean, including the processes that control the accumulation and removal of DOC, is essential for accurately modelling the global carbon cycle and predicting the impacts of climate change (Follett *et al.*, 2014).

The biological pump transfers organic carbon, mostly in the form of particulate organic matter (POM) from the atmosphere and surface waters into the deep ocean and seafloor sediments (Nowicki *et al.*, 2022). The global amount of organic carbon exported to the deep seas annually is about 10 Pg C yr^{-1} (1 Pg = 1 Gt = 10^{15} grams), while only 2 Pg C yr^{-1} reaches the seafloor and as little as ~0.2–0.4 Pg C yr^{-1} gets sequestered into deep sea sediments (Middelburg, 2019). It's important to note that these numbers come with uncertainties, and the actual amount of carbon sequestered in deep sea sediments can vary widely depending on numerous factors. Some examples include the efficiency of the biological pump, which is influenced by the types of organisms involved, the water depth, the temperature and chemistry of the ocean, the subsequent timescale of ventilation (release of the remineralized carbon back into the atmosphere), and the region and depth at which the carbon is remineralized (Baker *et al.*, 2022). Carbon burial is also more effective the more anoxic the environment is. The lack of oxygen slows degradation of carbon and increases the likelihood of sequestration (Barber, 1968; Middelburg, 2019).

New research suggests that large baleen whales, as well as other marine mammals, may play an important role in the storage of organic carbon at the ocean floor (Pershing *et al.*, 2010; Roman *et al.*, 2014). When marine mammals die at sea and sink to the seafloor, the organic carbon they contain have the potential to get stored in deep sea sediments for ~100 to potentially millions of years, as well as provide vital nutrients to deep-sea communities (Li *et al.*, 2022; Smith, 1992; Smith & Baco, 2003). The carcass of a great whale is the largest form

of detritus falling from the ocean surface, and they sink rapidly compared to DOC particles, limiting the decomposition that occurs in the upper oceanic layers (Smith, 2006). The longer-lived and larger species of marine mammals, like the baleen whales, have a greater potential for carbon storage considering their large body mass and long lives (~50-200 years). The organic carbon contained within their body accumulate in substantial amounts and may be one of the largest stable carbon pools in the pelagic ocean (Pearson *et al.*, 2022). The global amount of carbon estimated to be exported annually via baleen whale falls vary between studies and methods used. Some estimate that baleen whales store between $2.9–6.2 \times 10^{-5}$ Pg C yr^{-1} (Pearson *et al.*, 2022; Pershing *et al.*, 2010), while others estimate as much as 2×10^{-3} Pg C yr^{-1} of storage potential just in the Southern Ocean (Durfort *et al.*, 2020).

In addition to contributing with carbon export to deeper waters, whale falls create a unique deep-sea ecosystem and provides an abundance of important nutrients to an otherwise nutrient-poor deep sea, supporting diverse and unique biological communities that can thrive for decades (Li *et al.*, 2022; Liu, 2015; Smith & Baco, 2003; Wang, 2021). A single 30 tonne whale fall can support the survival of more than 100 macrofauna species, where several of them are whale fall specialists and are found nowhere else (Liu, 2015; Smith *et al.*, 2014). A whale fall can support these deep-sea communities for up to 100 years and consists of multiple decomposition stages, from scavengers feasting on soft tissues to microorganisms breaking down bones (Smith & Baco, 2003; Smith *et al.*, 2014). This process makes whale falls crucial for understanding evolution, ecological succession, development of life, and nutrient cycling in extreme deep-sea habitats (Wang, 2021).

Other marine mammals, including sperm whales, small cetaceans and pinnipeds may also contribute to the export of carbon to deep seas via deadfalls, but their relative contribution is unknown. One of the main challenges of studying marine mammals is the lack of precise abundance data (Taylor *et al.*, 2007), which have led to their inclusion in carbon export potential studies difficult. Despite their smaller body size compared to baleen whales, small cetaceans and pinnipeds are often more abundant (Leonard & Øien, 2020a; Pike *et al.*, 2019) and should therefore not be overlooked when calculating carbon export potential of marine mammals.

The Nordic Seas (Iceland, Greenland, Norwegian, and Barents Seas) are a part of the North Atlantic ocean, and consists of high latitude areas that are highly productive and energy-rich (Skern-Mauritzen *et al.*, 2022). Many marine mammal species inhabit these seas, including several baleen whale species, such as common minke whales (*Balaenoptera acutorostrata*), fin whales (*Balaenoptera physalus*), humpback whales (*Megaptera novaeangliae*), and blue whales (*Balaenoptera musculus*). These great whales migrate to this region to forage during the highly productive spring and summer months before returning to breeding areas located in warmer tropical regions during the winter (Leonard & Øien, 2020a; Moore *et al.*, 2019). Other species, such as sperm whales (*Physeter macrocephalus*), long-finned pilot whales (*Globicephala melaena*) and ice-breeding seals can be found in the study area year-round (Kovacs *et al.*, 2009). Whale abundance surveys for commercially exploited species (e.g. minke whales in Norway and fin whales in Iceland) have resulted in extensive studies of valuable abundance estimates for these and other whale species (Leonard & Øien, 2020a; Pike *et al.*, 2019). As a results, the Nordic Seas are one of the most thoroughly surveyed areas on the globe in terms of abundance estimates. The most abundant marine mammal species in the Nordic Seas are the pinnipeds, with the harp seal (*Pagophilus groenlandicus*) constituting a total of ~2.66 million individuals (Hammill & Stenson, 2014; ICES, 2019), followed by hooded seals (*Cystophora cristata*) with 667 123 individuals, and ringed seals (*Pusa hispida*) with 400 000 individuals. The baleen whales have the highest biomass in the study area, with a total biomass of ~2.38 million tonnes for fin whales, 952 000 tonnes for minke whales, and 696 000 tonnes for humpback whales (Skern-Mauritzen *et al.*, 2022).

To date, studies on carbon storage from marine mammal deadfalls are few and limited to baleen whales. These studies have differing general conclusions regarding magnitude and relative importance, and some suggests that the amount of organic carbon stored by whale falls are substantial, especially if populations are restored to pre-whaling levels (e.g. Butman *et al.*, 1995; Durfort *et al.*, 2022; Pearson *et al.*, 2022; Pershing *et al.*, 2010; Roman *et al.*, 2014). Others estimate that the amount will be relatively small, even with whale populations are restored (e.g. Jelmert & Oppen-Berntsen, 1996; Meynecke *et al.*, 2023; Smith, 2006). The pre-whaling levels will depend on which whale populations are studied and how severe their levels of depletion are. This disagreement in the scientific community shows that carbon storage potential from whale falls is important to study further. Other marine mammal species should also be included in such estimates, as it is currently undetermined how much organic

carbon is exported by marine mammals other than baleen whales, and how large the regional or global impacts are.

This thesis aims to estimate the annual flux of organic carbon exported through marine mammal deadfalls in the Nordic Seas. Estimates are provided for both year-round residents and migratory species of baleen whales (mysticetes), toothed whales (odontocetes), as well as pinnipeds. Building on estimates of marine mammal abundance available for the study area and published literature on species-specific mortality rate estimates, this thesis calculates the expected number of individuals dying each year, their biomass, and their organic carbon content. The importance of marine mammal deadfalls relative to other downward fluxes of organic carbon in the Nordic Seas is also evaluated.

2 Methods

2.1 Study area

The study area is in the Nordic Seas, a part of the Northeast Atlantic Ocean, and include three regions: (1) the Icelandic shelf, Denmark strait and Iceland Sea (ICE), (2) the Greenland and Norwegian Seas (GN) and (3) the Barents Sea (BS) (Figure 1). The regions are located at a high latitude, with nutrient-rich, cold waters that include shallow shelf areas as well as deep-sea oceanic systems. This study aims to estimate marine mammal deadfalls that sinks to the deep ocean where they have the potential to be sequestered. The depth of the ICE region ranges from 500 to 2000 m and has shallower shelf areas along the continental shelf as well as deep-sea areas (Pálsson *et al.*, 2012). The Norwegian Sea consists of the continental shelf and many deep sea areas, with an average depth of about 2000 m and some areas going as deep as 4000 m (Blindheim, 1989). The Greenland Sea features numerous deep areas, with an average depth of 1450 m and the deepest regions reaching approximately 4800 m (Britannica, 2024). The northern part of the Greenland Sea is covered by seasonal ice during winter and spring. This ice are the major breeding grounds for harp seals and hooded seals in the region (Andersen *et al.*, 2013). The Barents Sea has an average depth of 230 meters and is a rather shallow shelf sea. The southern part is mostly ice-free year-round due to the warm North Atlantic drift, while the northern areas in the high Arctic consists of rapidly declining sea ice (Mori *et al.*, 2019), and several species of whales and pinnipeds utilise these waters either seasonally or year-round.

The Nordic Seas are productive ocean areas with high trophic transfer rates (Moore *et al.*, 2019; Sundby *et al.*, 2016; Wassmann *et al.*, 2006). High latitude oceanic regions have high biological production compared to lower latitude oceans, with phytoplanktonic spring blooms that appear after the limited daylight and ice cover that prohibits primary production during the winter months are removed. These spring-blooms are fed heavily upon by zooplankton that serve as energy rich food packs for large quantities of fish and marine mammals, which again serve as key food for top predators of other marine mammals as well as many seabirds (Labansen *et al.*, 2007; Sundby *et al.*, 2016; Wassmann *et al.*, 2006).
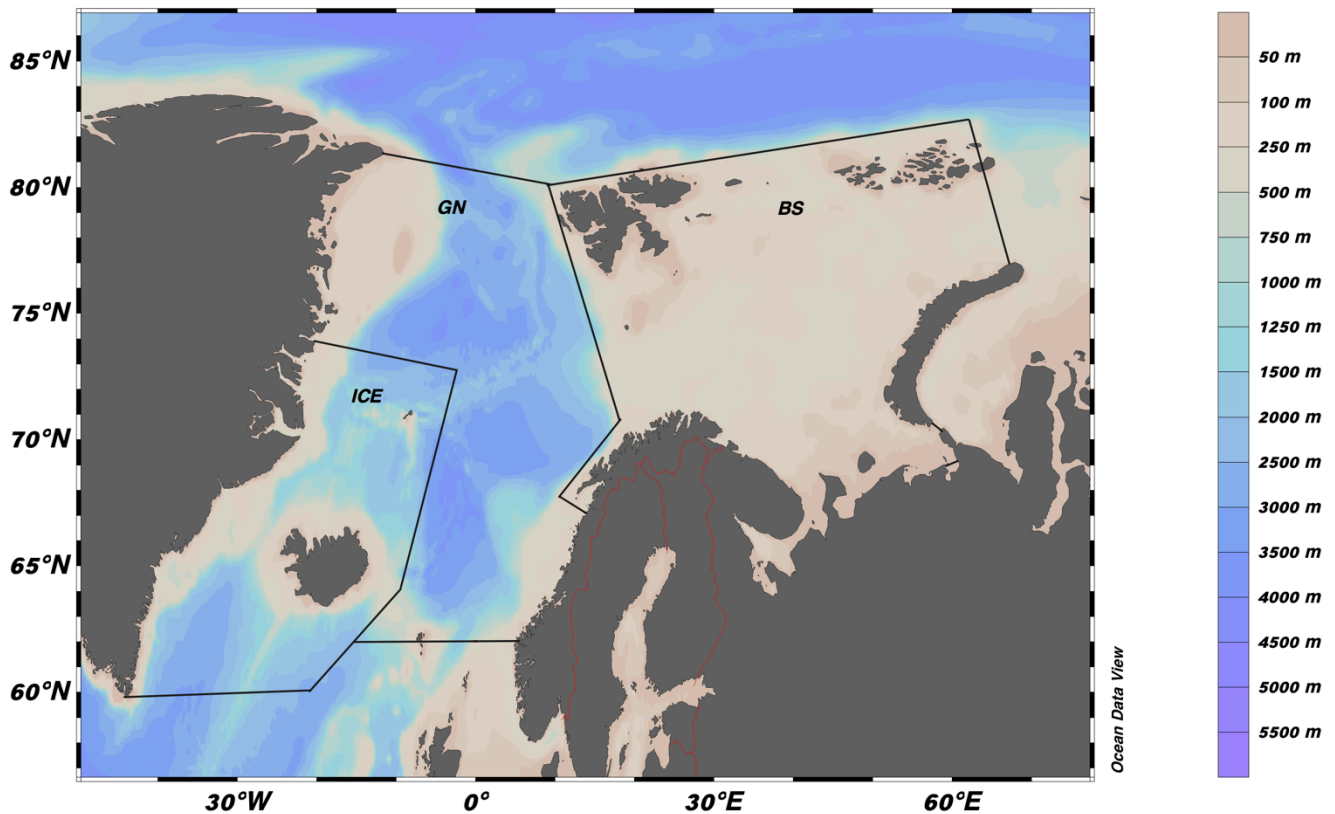
Figure 1: Map of the study area divided into the 3 regions ICE (Icelandic shelf, Iceland sea, and Denmark Strait), GN (Greenland and Norwegian Sea) and BS (Barents Sea). Made with Ocean Data View (version 5.7.0).

2.2 Study species

The species included in this thesis are based on the study by Skern-Mauritzen *et al.* (2022) and include pinniped and whale species that occur regularly in the study area and include both residential and migratory species. These species belong to three groups: five pinniped species, nine odontocetes (toothed whales) and six mysticetes (baleen whales) (Table 1). Of the 20 study species, 12 are year-round residents and eight are migrants that forage in the study area during the summer and migrate to reproduce at lower altitudes. The 12 resident species include ringed seals, bearded seals (*Erignathus barbatus*), Atlantic walrus (*Odobenus rosmarus*), white whales (*Delphinapterus leucas*), narwhals (*Monodon monoceros*), and bowhead whales (*Balaena mysticetus*) that live in the High arctic, the two North Atlantic drift-ice breeding seals; harp seals and hooded seals, as well as the north temperate cetacean species; killer whales (*Orcinus orca*), white-beaked dolphins (*Lagenorhynchus albirostris*), Atlantic white-sided dolphins (*Lagenorhynchus acutus*), and harbour porpoises (*Phocoena*

phocoena). Some of the year-round residents perform extensive migrations both within and between the three study regions but do not leave the overall study area (e.g. harp seals, hooded seals, and bowhead whales, Leonard & Øien, 2020a; Lydersen *et al.*, 2012b; Nordøy *et al.*, 2008; Vacquié-Garcia *et al.*, 2017a). The eight seasonal migratory species includes five baleen whale species; common minke whales, fin whales, humpback whales, sei whales (*Balaenoptera borealis*), and blue whales (*Balaenoptera musculus*); and three toothed whale species; sperm whales, long-finned pilot whales, and northern bottlenose whale (*Hyperoodon ampullatus*).

Among pinnipeds, harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) are regular inhabitants of the study area, but were not included in this study because of their coastal affiliation. The geographical range of harbour seals include temperate and polar coastal waters of the northern hemisphere (Teilmann & Galatius, 2018) where they primarily use areas close to the coastline, and forage in shallow waters around 30-50 km from land (Jones *et al.*, 2015; Jones *et al.*, 2017; Sharples *et al.*, 2012; Tollit *et al.*, 1998). Because of this, their carcass would rarely, if at all, reach the deep ocean and be sequestered in sediments. Grey seals take longer foraging trips than harbour seals (20-160 km), but are typically restricted to the continental shelf, which extends from the coast out to the 500 m depth contour (Baylis *et al.*, 2019; Pinet, 2019). This would rarely be deep enough to sequester the organic carbon from deadfalls for long term storage. White-beaked dolphins and Atlantic white-sided dolphins are grouped together in the category *Lagenorhynchus* dolphins. The two species are difficult to differentiate when counting them in the field (Skern-Mauritzen *et al.*, 2022), therefore, to get accurate estimations of abundance, they are considered one taxa for this study. Beaked whales of family Ziphiidae are known to inhabit the study area but are poorly studied and lack sufficient abundance data, and therefore excluded from the study. The exception is the northern bottlenose whale where more studies have been conducted and abundance can be estimated (Christensen, 1973; Leonard & Øien, 2020a; Mead, 1989; Pike *et al.*, 2019). Harbour porpoises are known to mostly inhabit coastal regions along the continental shelf, but have been found to undertake long-range migrations within the North Atlantic ocean, where they stayed in areas with >2500 m depth, and dove as much as 410 m to forage for food (Nielsen *et al.*, 2018). This suggests that harbour porpoises traverse deeper oceanic habitats as well as coastal regions during their lifetime and will therefore play a role in the calculation of organic carbon storage potential by marine mammals in the study region.

2.3 Abundance and body mass data

Abundance estimates are used to measure how large the populations of each species in each study region (ICE, GN, and BS) are. This will give an indication on how much organic carbon potential the populations have, and will be used, together with values of body mass, mortality rate, residence times, and organic carbon content of biomass, to calculate the total organic carbon flux potential for each species in the regions, and for the whole study area. Abundance estimates used in this study (Table 1) are summarized in Skern-Mauritzen *et al.* (2022), and are based on dedicated marine mammal surveys, scientific literature, or expert estimates for populations that lack abundance numbers (see Appendix B for details). The species-specific body mass data (Table 1) are used to calculate the mean biomass for each species in the three study regions. They are retrieved from Skern-Mauritzen *et al.* (2022) and originate from Kovacs *et al.* (2009); Sigurjónsson and Víkingsson (1997); and Smith *et al.* (2015).

Table 1: Residency (annual number of days each species spends in each of the three study regions ICE, GN, and BS), given as one value for all three regions or three separated values for each region. Body mass, abundance (number of individuals) in each of the three regions, adult male and female mortality rates for each of the study species, as well as the sources used for mortality rates. For the other values, the source is the study from Skern-Mauritzen *et al.* (2022) and references therein. Coefficients of variation (CV) are provided with each abundance value in parenthesis, and a CV of 0.20 was assumed for body mass and residency values (Smith *et al.*, 2015). The residency includes the corrected values from Skern-Mauritzen *et al.* (2022) for sei whales, narwals, and bowhead whales.

	SPECIES	Residency (days each year ICE/GN/BS)	Body mass (kg)	Abundance ICE (no. of individuals)	Abundance GN (no. of individuals)	Abundance BS (no. of individuals)	Adult male mortality rate	Adult female mortality rate	Sources mortality rates
PINNIPEDS	RINGED SEAL	365	75	200 000 (0.50)	100 000 (0.50)	100 000 (0.50)	0.160	0.060	Hoenig (2005); Lydersen and Gjertz (1987)
	BEARDED SEAL	365	250	20 000 (0.50)	10 000 (0.50)	10 000 (0.50)	0.096	0.096	Burns and Frost (1979)
	HARP SEAL	150/365/365	120	740 000 (0.50)	426 808 (0.14)	1 497 189 (0.07)	0.115	0.115	Winters (1976)
	HOODED SEAL	30/365/0	250	593 500 (0.11)	73 623 (0.14)	0	0.120	0.120	Jacobsen (1984)
	ATLANTIC WALRUS	0/365/365	1 200	0	1 429 (0.33)	15 000 (0.50)	0.060	0.060	Witting and Born (2005)
	WHITE WHALE	0/0/365	1 350	0	0	5 000 (0.50)	0.070	0.070	Jacobson et al. (2020)
	NARWHAL	365	1 300	2 500 (0.50)	6 444 (0.37)	3 500 (0.50)	0.005	0.005	Garde et al. (2015)
	KILLER WHALE	365	4 400	5 478 (0.36)	6 154 (0.58)	503 (0.71)	0.029	0.023	Kuningas et al. (2014)

ODONTOCETES	**SPERM WHALE**	150	40 000	4 272 (0.55)	2 708 (0.48)	806 (0.71)	0.022	0.022	Evans and Hindell (2004)
	LAGENOR-HYNCHUS DOLPHINS	365	210	136 889 (0.46)	28 168 (0.57)	144 453 (0.55)	0.179	0.148	Hoenig (2005); Sergeant *et al.* (1980)
	PILOT WHALE	270/240/180	1 700	210 000 (0.44)	5 000 (0.50)	500 (0.50)	0.028	0.028	Verborgh *et al.* (2021)
	HARBOUR PORPOISE	365	55	44 821 (0.44)	5 266 (0.47)	85 731 (0.57)	0.133	0.133	Lockyer (2003)
	NORTHERN BOTTLENOSE WHALE	150/150/0	6 000	6 500 (0.55)	617 (0.74)	0	0.084	0.148	Christensen (1973); Hoenig (2005); Mead (1989)
MYSTICETES	**MINKE WHALE**	180	6 600	48 016 (0.23)	48 913 (0.26)	47 295 (0.30)	0.046	0.046	Pershing *et al.* (2010)
	FIN WHALE	180	55 500	29 940 (0.16)	8 504 (0.33)	4 506 (0.54)	0.044	0.044	Pershing *et al.* (2010)
	HUMPBACK WHALE	180	30 400	12 523 (0.30)	1 808 (0.62)	8 563 (0.81)	0.043	0.043	Pershing *et al.* (2010)
	BLUE WHALE	180	100 000	2 450 (0.42)	100 (0.50)	100 (0.50)	0.045	0.045	Pershing *et al.* (2010)
	SEI WHALE	90/90/0	17 000	4 200 (0.70)	100 (0.50)	0	0.042	0.042	Pershing *et al.* (2010)
	BOWHEAD WHALE	0/365/365	80 000	0	173 (0.49)	173 (0.49)	0.040	0.040	Pershing *et al.* (2010)

2.4 Residence times

The residence times for each species in the study area are shown by days per year that the species stays in each of the three regions (Table 1). This is an important value for the calculations of this thesis, as some of the study species stay in the area year-round (365 days), while others migrate for some of the year, and several species intermingle between the three regions but do not leave the study area. Without these values, the potential for organic carbon storage in the study area would be overestimated for migratory species. The residence times are retrieved from the study by Skern-Mauritzen *et al.* (2022) and references therein (see Appendix A for more details). Telemetry studies indicate that harp seals spend roughly 45%, 32%, and 23% of their time in the ICE, GN, and BS regions, respectively (Folkow *et al.*, 2004; Martin Biuw, IMR Norway, unpublished data). Harp seals that breed and molt (shed their skin) in the White Sea area of the Barents Sea (BS), spend all their non-breeding time within the region, while harp seals pupping off East Greenland traverse all study regions (ICE, GN, and BS) for foraging activities. All pinniped species that breed in the study region are year-round residents, and harp seals and hooded seals from the GN region spend some of their time the ICE region during the summer (5 and 2 months, respectively) (Andersen *et al.*,

2013; Sergeant, 1991). Residency for harp seals in the ICE region is therefore set to 150 days. Hooded seals spend about 2 months in the ICE region, but since some of this time is spent moulting hauled out on pack ice (Vacquié-Garcia *et al.*, 2017a), only 1 month (30 days) is included in the residency time for this species in the ICE region. Recent studies suggests that the migration timing of blue whales, fin whales, and minke whales are variable, but generally support the migration patterns demonstrated by Sigurjónsson and Víkingsson (1997) (e.g. Silva *et al.*, 2013; Víkingsson *et al.*, 2015). There is also evidence that some individuals of the migratory mysticetes (i. e. humpback and fin whales) stay in the ICE and BS region throughout the winter, but the information on abundance of overwintering individuals is limited (Jourdain & Vongraven, 2017; Magnúsdóttir *et al.*, 2014; Sigurjónsson & Víkingsson, 1997). Telemetry studies indicate that bowhead whales spend their time equally between the GN and BS region, hence the total stock and residence times were evenly distributed between the two regions (Kit M. Kovacs and Christian Lydersen, NPI, Norway, unpublished data). A CV value of 0.2 for residency times of all species was added to account for uncertainties, following the method by Smith *et al.* (2015).

The residence time for a few of the study species is written incorrectly in the paper by Skern-Mauritzen *et al.* (2022). For sei whales the correct number should be 90 days for the GN region. For narwhals the correct residence time is 365 days for all regions, and for bowhead whales the correct residency for the GN region is 365 days (Mette Skern-Mauritzen, personal communication, March 1, 2024). The correct values are provided in Table 1 and used for the results of this study.

2.5 Mortality rates

Marine mammals generally have low natural mortality rates compared to many other oceanic species, which leads to long lives that can span several decades and even centuries (Pershing *et al.*, 2010). The natural mortality rate (*M*) is used in this study as a proportion of a population that dies of natural causes on an annual basis. This rate encompasses all causes of death excluding anthropogenic factors, such as fishing, hunting, environmental stress, and bycatches (Dimarchopoulou *et al.*, 2024). Natural mortality rates for each of the study species were obtained through literature searches of previously published studies (Table 1). In lack of exhaustive life history data from the study area, mortality rates were obtained from

populations in the whole distribution range of the species. Natural mortality rates for a single species can vary significantly between populations of different geographical regions, and even from one year to the next (Dimarchopoulou *et al.*, 2024; Peatman *et al.*, 2022). Biotic and abiotic factors like mating behaviour, parturition, predation, habitat, migration, and diet are some of the parameters that could impact these variations (Smith & Baco, 2003). It is therefore recognized that the mortality rates are highly uncertain between populations, but for the scope of this study, general estimations of average mortality from previous studies are used.

Some of the mortality rates were calculated using an empirical method developed by Hoenig (2005) for this study (e.g. ringed seals, *Lagenorhynchus* dolphins, and northern bottlenose whales). Hoenig calculated that there is an inverse relationship between longevity and mortality rate for several species-groups, including cetaceans, and created a general regression equation for estimating natural mortality from maximum age (Appendix A). The sex ratios for this study were set to 1:1 for all species based on previous studies by Fedoseev (1975); Helle *et al.* (1976); Johnson *et al.* (1966); Lydersen and Gjertz (1987); McLaren (1958); Øritsland (1964); Øritsland and Benjaminsen (1975); and Smith (1973). It is recognized that some of the study species might display different sex ratios within their populations, and that this can impact the results of this study. Nonetheless, a sex ratio of roughly 1:1 is often displayed for marine mammal populations, and setting this ratio for the species in this study will thus be close to their true values.

2.6   Annual organic carbon export

2.6.1 Number of individuals dying

The values from Table 1 (residence times, body mass, abundance, and mortality rates) were used to calculate the results of this study. To estimate the total flux of organic carbon from marine mammal deadfalls in the study area, the number of individuals dying annually from each species and region needed to be known first. Individuals dying for each species *s* (before residence times are included) was set as ND_s and estimated using this equation:

$$ND_s \ = \ \left(\frac{A_{s\,r}}{2}\right) \times M_{male} + \left(\frac{A_{s\,r}}{2}\right) \times M_{female} \tag{1}$$

Where $A_{s\,r}$ represented the abundance for each species s in the region r. The number was divided by two to separate male and female abundance values, assuming a 1:1 sex ratio for each of the study species. M_{male} and M_{female} were the annual mortality for males and females, respectively, expressed as a proportion of the population that dies annually. The next part was to calculate the total number of deaths (ND_{total}) from all regions using this equation:

$$ND_{total} \ = \ \Sigma\,ND_s \tag{2}$$

Where the total number of deaths (ND_{total}) equals the sum of all individuals dying from each species s (ND_s), calculated using (1). Because some species are seasonal residents, a residency fraction (R) was calculated as:

$$R \ = \ \frac{N_{days}}{365} \tag{3}$$

Where the number of days each species is present in the study regions (N_{days}) were divided by the total number of days in a year (365 days assuming a non-leap year). This residency fraction could be used to calculate the number of individuals dying annually ($ND_{s\,r}$) for each species s inside a region r:

$$ND_{s\,r} \ = \ \left(\left(\frac{A}{2}\right) \times M_{male} \ + \ \left(\frac{A}{2}\right) \times M_{female}\right) \times \left(\frac{N_{days}}{365}\right) \tag{4A}$$

Or more simplified as:

$$ND_{s\,r} \ = \ ND_s \ \times \ R \tag{4B}$$

Here, the number of individuals dying (ND_s) (1) was multiplied by the residency fraction R, estimated from (3), to account for the number of days each species spends in the study region. Finally, to estimate the number of individuals dying outside the regions ($ND_{outside}$) (i.e. when they are migrating to other geographical locations) the following equation was used:

$$ND_{outside} \ = \ ND_{total} - \Sigma\,ND_{s\,r} \tag{5}$$

Where ND_{total} was the total number of individuals dying (before residency), estimated from (2), and ND_r was the total number of individuals dying for each species s within each region r, estimated from (4).

2.6.2 Biomass export

After knowing the number of individuals dying, the amount of biomass exported from each population upon their death will give an indication of the organic carbon contained within their bodies. This carbon has the potential to be stored in deep sea regions as the carcass sinks. The equation for calculating the amount of biomass export per species s in region r ($B_{s\,r}$) was:

$$B_{s\,r} = ND_{s\,r} \times BM_s \qquad (6)$$

Where $ND_{s\,r}$ was the total number of individuals of species s dying in region r, and BM_s was the body mass for each species s. After this was calculated, the biomass exported outside the study area ($B_{outside}$) could be found using:

$$B_{outside} = ND_{outside} \times BM_r \qquad (7)$$

Where $ND_{outside}$ is the total number of individuals dying outside the study area, estimated from (5), and BM_s is body mass for each species s.

2.6.3 Organic carbon export

The estimates of annual organic carbon export per species in each of the three study regions, as well as outside the study area, were found using the previous calculations. Organic carbon export was estimated by using the value for biomass export $B_{s\,r}$ for each species s in region r, estimated from (6), and multiplying by the numerator 0.33 that converts wet weight biomass into dry weight biomass, as the average water content of mammals is about two-thirds (~66%) (Greenspoon *et al.*, 2023; Williams *et al.*, 2004). The organic carbon content of this dry weight is around half (49%) and the conversion factor between carbon and dry weight is

usually set as two for simplicity (Greenspoon *et al.*, 2023). The organic carbon exported from the population upon the individual species' deaths in region *r* ($C_{s\,r}$) was calculated as:

$$C_{s\,r} = \frac{B_{s\,r} \times 0.33}{2} \tag{8}$$

In other to calculate the total organic carbon export outside the study area ($C_{outside}$), the estimate for biomass export outside the study area ($B_{outside}$), estimated in (7), was used:

$$C_{outside} = \frac{B_{outside} \times 0.33}{2} \tag{9}$$

2.6.4 Uncertainty measures

Uncertainty assessments are important to quantify the confidence in results. With uncertainty estimates, the precision and reliability of this studys' findings can be determined, indicating how much the results are expected to vary if the study were repeated under the same conditions. To provide uncertainty measures for the annual carbon export estimates, coefficients of variation (CV) were estimated from previous CV values available from Skern-Mauritzen *et al.* (2022), for the expected number of individuals dying each year (Table 2). These estimates give an indication of variability within the dataset and provides a standard standardized measure of variability which is useful in assessing relative variability in skewed distributions. CVs enable comparisons across datasets with different units or scales, and expresses the standard deviation σ as a percentage of the mean μ.

95% confidence intervals were estimated for expected biomass export and organic carbon export for each species and region. Confidence intervals are used to indicate the reliability of an estimate and provide a range around the sample value to express the degree of uncertainty associated with the sample size used and the variability in the data.

See Appendix D for more information.

3 Results

3.1 Annual deaths and biomass export

Annual deaths per species in the three study regions were calculated using (4), and annual deaths outside the study region were calculated using (5) (Appendix D). Harp seals are the species with the most individuals dying each year in all regions, with 34 891 (CV 0.55) in the ICE region, 49 083 (CV 0.35) in the GN region, and 172 177 (CV 0.10) in the BS region (Table 2). The second highest number of annual deaths are from *Lagenorhynchus* dolphins in the BS region (23 618 individuals, CV 0.60) and ICE region (22 381 individuals, CV 0.51), followed by ringed seals in the ICE region (22 000 individuals, CV 1.12). The largest number of deaths outside the study regions for migratory species are hooded seals (65 522 individuals, CV 0.12) followed by harp seals (50 209 individuals, CV 1.15), and minke whales (3 317 individuals, CV 0.36). Sei whales and blue whales have the smallest number of deaths, with a mean of one individual (CV 0.55) in the GN region for sei whales, and two individuals in GN and BS regions for blue whales (CV 0.55). These results correlate with the fact that the pinniped species have a larger abundance, higher natural mortality rates, and therefore generally live shorter lives than the baleen whales. The abundance for sei whales and blue whales in the study regions is also relatively low compared to many of the other species.

The amount of annual biomass export potential for each study species in the three study regions, and outside the study area were estimated using (6) and (7). The export potential indicates the possible amount of biomass that can be exported to deep seas via marine mammal deadfalls on an annual basis. Fin whales have the highest biomass export in ICE and GN regions, with 36 557 tonnes C yr^{-1} (95%CI 21 732−58 375) and 10 383 tonnes C yr^{-1} (95%CI 4 211−19 985), respectively (Table 2). The second highest biomass export estimate in the ICE region is from humpback whales (8 185 tonnes C yr^{-1}, 95%CI 3 728−15 175), followed by pilot whales (7 497 tonnes C yr^{-1}, 95%CI 2 778−16 584). In the GN region, the second highest biomass is from minke whales (7 425 tonnes C yr^{-1}, 95%CI 3 340−12 981), and the third is from harp seals (5 890 tonnes C yr^{-1}, 95%CI 3 301−9 120). Harp seals are the largest contributor in the BS region with 20 661 tonnes C yr^{-1}, (95%CI 11 960−30 418),

followed by minke whales (7 179 tonnes C yr^{-1}, 95%CI 3 105−13 342), and humpback whales (5 597 tonnes C yr^{-1}, 95%CI 1 041−18 955).

3.2 Uncertainties on annual deaths

Common for several of the study species are high uncertainties (CVs) in abundance values (Table 1), which will influence uncertainties for all calculations thereafter. The CV values for number of individuals dying was estimated using (11) while individuals dying outside the study area was estimated using (11) and (12) (Appendix D). The CV for pilot whales dying outside the study area is extremely high (CV 2.21), indicating significant variability relative to the magnitude of the sum of the means and the high CVs of the original values (Table 2). The number of northern bottlenose whales dying has a very high level of variability as well, influenced by the high CV values (CV 0.60 and 0.78), which indicates a high level of uncertainty behind the results for this species. This also transfers to the CV of total deaths outside the study area (CV 0.94) for bottlenose whales. Humpback whales has a very high CV for number of deaths, especially in the GN and BS regions (CV 0.66 and 0.85 respectively). Killer whales and sperm whales have a high CV in the BS region (CV 0.75), and sei whales in the ICE region (CV 0.74), indicating a high variability in these estimates. For harp seals dying outside the study area, the high variability (CV 0.93) stems from both the relative sizes of the standard deviations and the means of the original values. For hooded seals this value is much lower (CV 0.12) due to the low CVs of the individual values and the relatively high mean of the total number of deaths outside the ICE region (71 220) compared to the number of deaths within the region (5 698). The species with the lowest CV values are all species that has gotten a lot of research attention, i.e. harp seals in the BS region (CV 0.10), hooded seals (CV 0.23), fin whales (CV 0.26), and minke whales in the ICE region (CV 0.31), that would naturally have a lower uncertainty behind the values because of the extensive research performed. For the number of individuals dying outside the study area, fin whales have a CV of about 0.35. This moderate CV indicates a relatively reasonable level of variability relative to the magnitude of the combined sum of the means, demonstrating that while each individual difference has significant variability (CV 0.41, 0.77, and 1.23), their combined effect balances out to a more stable total.

Table 2: The number of individuals dying each year from each study species in the three regions ICE, GN, and BS, as well as outside the study area. The amount of biomass export potential each year in the three regions and outside the study area. The total amount of biomass export per region and outside the study area is displayed at the bottom of the table. Values are rounded to the closest whole number, or one decimal for small numbers. CV values are provided for annual deaths, while 95% CI values are provided for biomass export (95% CI for bottlenose whales in GN region were not available).

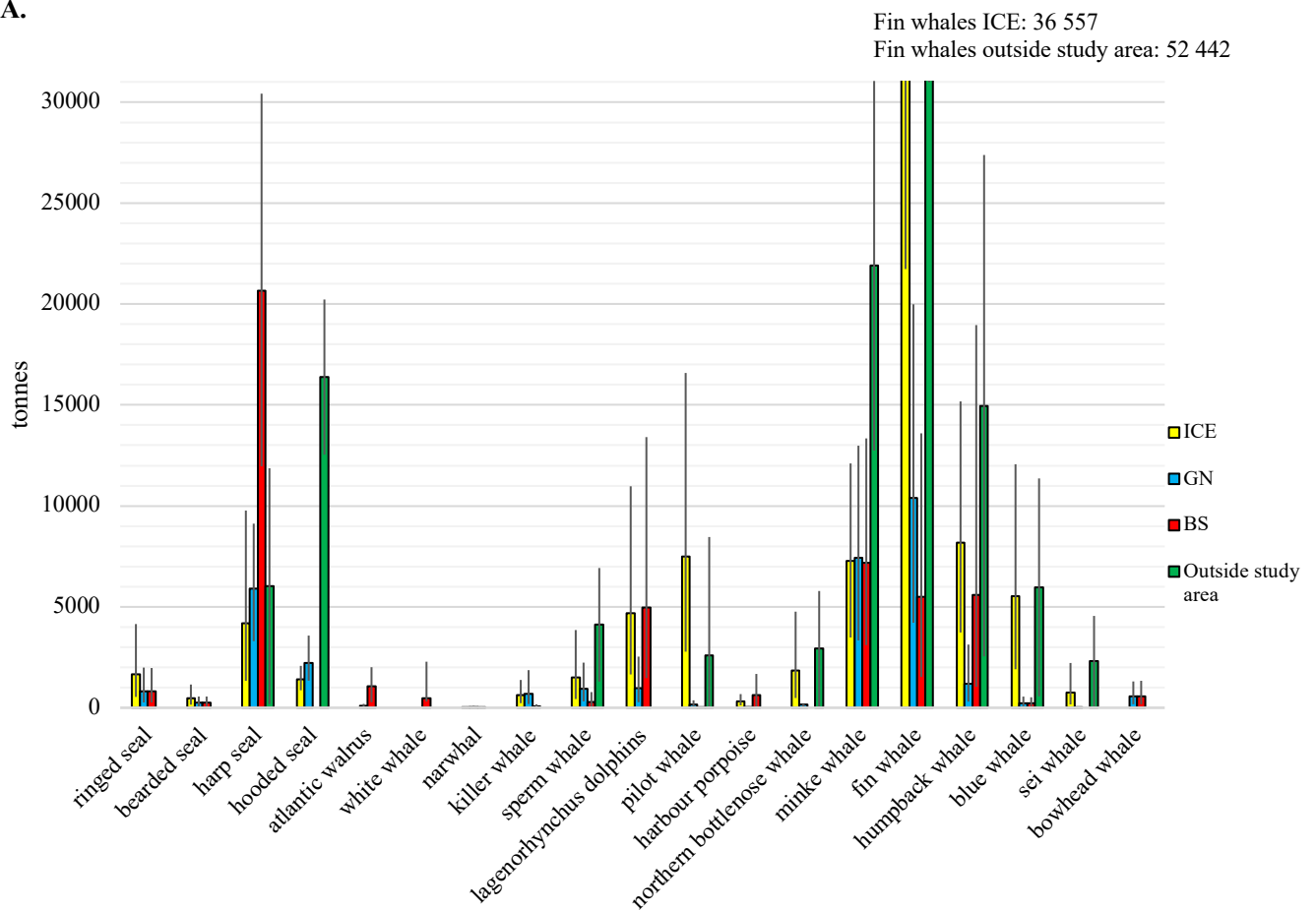|	SPECIES	N of individuals dying each year ICE	N of individuals dying each year GN	N of individuals dying each year BS	N of individuals dying each year outside study area	Biomass export each year ICE (tonnes)	Biomass export each year GN (tonnes)	Biomass export each year BS (tonnes)	Biomass export each year outside of study area (tonnes)
PINNIPEDS	RINGED SEAL	22 000 (1.12)	11 000 (1.12)	11 000 (1.12)	0	1 650 (539, 4 147)	825 (264, 1 991)	825 (264, 1 969)	0
	BEARDED SEAL	1 920 (1.12)	960 (1.12)	960 (1.12)	0	480 (154, 1 152)	240 (77, 557)	240 (77, 557)	0
	HARP SEAL	34 891 (0.55)	49 083 (0.35)	172 177 (0.10)	50 209 (1.15)	4 187 (1 334, 9 770)	5 890 (3 301, 9 120)	20 661 (11 960, 30 418)	6 025 (-5 093, 17 143)
	HOODED SEAL	5 698 (0.23)	8 835 (0.25)	0	65 522 (0.12)	1 424 (867, 2 076)	2 209 (1 344, 3 576)	0	16 381 (8 803, 23 959)
	ATLANTIC WALRUS	0	86 (0.39)	900 (0.55)	0	0	103 (42, 192)	1 080 (276, 2 010)	0
ODONTOCETES	WHITE WHALE	0	0	350 (0.55)	0	0	0	473 (308, 2 282)	0
	NARWHAL	13 (0.55)	32 (0.43)	18 (0.55)	0	16 (5.0, 37)	42 (15, 87)	23 (7.5, 53)	0
	KILLER WHALE	142 (0.42)	160 (0.62)	13 (0.75)	0	626 (229, 1 378)	704 (187, 1 864)	58 (10, 169)	0
	SPERM WHALE	38 (0.60)	24 (0.53)	7 (0.75)	103 (0.64)	1 504 (434, 3 850)	953 (318, 2 236)	284 (55, 778)	4 111 (-1 252, 9 475)
	LAGENORHYNCHUS DOLPHINS	22 381 (0.51)	4 605 (0.62)	23 618 (0.60)	0	4 700 (1 651, 10 971)	967 (278, 2 534)	4 960 (1 472, 13 407)	0
	PILOT WHALE	4 410 (0.49)	92 (0.55)	7 (0.55)	1 525 (2.21)	7 497 (2778, 16 584)	157 (52, 370)	12 (4.2, 31)	2 592 (-8 914, 14 098)
	HARBOUR PORPOISE	5 961 (0.49)	700 (0.52)	11 402 (0.62)	0	328 (120, 678)	39 (13, 80)	627 (53, 1 676)	0
	NORTHERN BOTTLENOSE WHALE	309 (0.60)	29 (0.78)	0	487 (0.94)	1 855 (485, 4 761)	176 (N/A)	0	2 923 (N/A)
MYSTICETES	MINKE WHALE	1 104 (0.31)	1 125 (0.33)	1 088 (0.37)	3 317 (0.36)	7 289 (3 482, 12 103)	7 425 (3 340, 12 981)	7 179 (3 105, 13 342)	21 893 (3 769, 40 017)
	FIN WHALE	659 (0.26)	187 (0.39)	99 (0.59)	945 (0.35)	36 557 (21 732, 58 375)	10 383 (4 211, 19 985)	5 502 (1 533, 13 594)	52 442 (-3 847, 108 731)
	HUMPBACK WHALE	269 (0.37)	39 (0.66)	184 (0.85)	492 (0.79)	8 185 (3 728, 15 175)	1 182 (305, 3 130)	5 597 (1 041, 18 955)	14 964 (-19 028, 48 955)
	BLUE WHALE	55 (0.47)	2 (0.55)	2 (0.55)	60 (0.86)	5 513 (1 910, 12 062)	225 (74, 554)	225 (72, 520)	5 963 (-8 716, 20 641)
	SEI WHALE	44 (0.74)	1 (0.55)	0	135 (0.94)	750 (166, 2 219)	18 (5.3, 39)	0	2 303 (-3 755, 8 360)
	BOWHEAD WHALE	0	7 (0.54)	7 (0.54)	0	0	554 (176, 1 304)	554 (176, 1 336)	0
	TOTAL:					**82 561**	**32 091**	**48 298**	**129 595**

3.3   Organic carbon export

The total estimation of annual organic carbon export from all three regions is 26 887 tonnes (2.68×10^{-5} Pg C yr^{-1}) (Table 3, Figure 2B). In terms of species, fin whales dominate in the ICE and GN regions, with 44% (6 032 tonnes C yr^{-1}) and 32% (1 713 tonnes C yr^{-1}), respectively, of the total organic carbon in the region (Figure 2B). In fact, fin whales are the largest single species contributor across the three study regions with ~8 653 tonnes C yr^{-1}, roughly one third (32.2%) of the total organic carbon export. Harp seals are the biggest contributor in the BS region, with 3 409 tonnes C yr^{-1}, about 43% of the total, and the second largest overall contributor with 5 072 tonnes C yr^{-1}, about 19% of the total. Common minke whales are the second largest in the GN and BS regions (1 225 tonnes C yr^{-1}, 23% and 1 185 tonnes C yr^{-1}, 15% respectively), and the third largest contributor overall (3 612 tonnes C yr^{-1}, 13.4%). A large portion of annual organic carbon export are outside the study area for fin whales, minke whales, humpback whales, and hooded seals (Table 2, Table 3, Figure 2). For fin whales, as much as 8 653 tonnes C yr^{-1} is estimated to be outside the study area, which is half of the total contribution and resonates with the residency time of 180 days in the study region. The mean body mass of harp seals is low (120 kg, CV 0.20) compared to the large whale species (Table 1), but due to their high mortality rate (0.115) and large abundance (~2.66 million) they still make the second largest contribution (5 071 tonnes C yr^{-1}) to the total organic carbon export (figure 2B).

Table 3: Estimated annual organic carbon export per species in each of the three study regions ICE, GN, and BS, as well as outside the study area. The total organic carbon export for all study species and regions is presented at the last row. 95% CI are displayed in parenthesis (95% CI for bottlenose whales in GN region were not available). All values are rounded to the closest whole number, or one decimal for the smallest values.

	SPECIES	Organic carbon export per year ICE (tonnes)	Organic carbon export per year GN (tonnes)	Organic carbon export per year BS (tonnes)	Organic carbon export outside study area (tonnes)
PINNIPEDS	**RINGED SEAL**	272 (89, 684)	136 (44, 329)	136 (44, 325)	0
	BEARDED SEAL	79 (25, 190)	40 (13, 92)	40 (13, 92)	0
	HARP SEAL	691 (220, 1 612)	972 (545, 1505)	3 409 (1 973, 5 019)	994 (-840, 2 829)
	HOODED SEAL	235 (143, 342)	364 (222, 590)	0	2 703 (1 452, 3 953)
	ATLANTIC WALRUS	0	17 (6.9, 32)	178 (46, 332)	0
	WHITE WHALE	0	0	78 (51, 377)	0
	NARWHAL	2.7 (0.8, 6.0)	6.9 (2.4, 14)	3.8 (1.2, 8.7)	0
	KILLER WHALE	103 (38, 227)	116 (31, 308)	9.5 (1.7, 28)	0

ODONTOCETES	**SPERM WHALE**	248 (72, 635)	157 (52, 369)	47 (9.1, 128)	678 (-207, 1 563)
	LAGENORHYNCHUS **DOLPHINS**	776 (272, 1 810)	160 (46, 418)	818 (243, 2 212)	0
	PILOT WHALE	1 237 (458, 2 736)	26 (8.5, 61)	2.0 (0.7, 5.1)	428 (-1 471, 2 326)
	HARBOUR PORPOISE	54 (20, 112)	6.4 (2.2, 13)	103 (8.8, 277)	0
	NORTHERN BOTTLENOSE WHALE	306 (80, 786)	29 (N/A)	0	482 (N/A)
MYSTICETES	**MINKE WHALE**	1 203 (575, 1 997)	1 225 (551, 2 142)	1 185 (512, 2 201)	3 612 (622, 6 603)
	FIN WHALE	6 032 (3 586, 9 632)	1 713 (695, 3 297)	908 (253, 2 243)	8 653 (-635, 17 941)
	HUMPBACK WHALE	1 351 (615, 2 504)	195 (50, 517)	923 (172, 3 127)	2 469 (-3 140, 8 078)
	BLUE WHALE	910 (315, 1 990)	37 (12, 91)	37 (12, 86)	984 (-1 438, 3 406)
	SEI WHALE	124 (27, 366)	2.9 (0.9, 6.4)	0	380 (-620, 1 379)
	BOWHEAD WHALE	0	91 (29, 215)	91 (29, 220)	0
	TOTAL:	13 622 (6 536, 25 630)	5 295 (2 311, 10 013)	7 969 (3 368, 16 681)	21 383 (-8 441, 50 241)
	TOTAL ALL REGIONS:	**26 887 (12 215, 52 324)**			

A.

Fin whales ICE: 36 557
Fin whales outside study area: 52 442

B.

Fin whale outside study area: 8 653
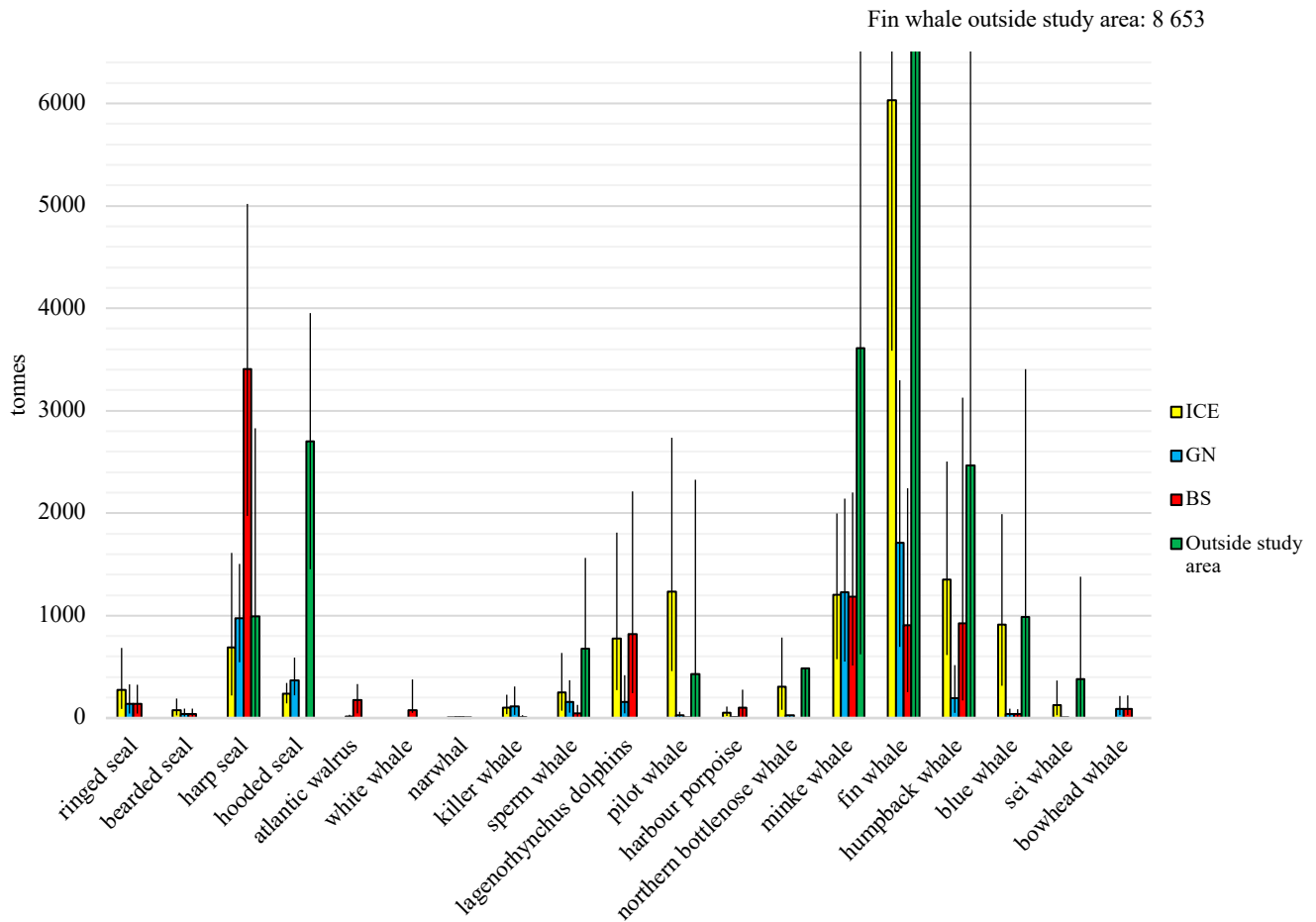
Figure 2: A. Estimated annual biomass export from each species and the three study regions ICE, GN, and BS, as well as total biomass export outside the study area. 95% CI values are presented as error bars for biomass export. Note that the values for fin whales in ICE and outside the study area go beyond the y-axis. **B.** Total number of tonnes of organic carbon export from each species, region and outside the study area. 95% CI values are presented as error bars for organic carbon export (95% CI values were not available for bottlenose whales). Note that values for fin whales outside the study area go beyond the y-axis.

The ICE region is the largest contributor to organic carbon export, with over half (51%) of the total organic carbon, while the GN region represents 20% and the BS region represents 29% of the total (Figure 3). The mysticetes constitutes 71% of the total organic carbon in the ICE region, mostly due to the large abundance of fin whales that occupy this area (Figure 3). They are the second largest animal on the planet, and each individual weighs on average 55.5 tonnes and contains a large amount of organic carbon (about 9 tonnes each). There is also a large amount of minke whales in this area, and although they are the smallest mysticete in this study (6.6 tonnes), they have the largest mysticete population. This makes their contribution to organic carbon export large in all three areas (9% of the total in ICE, 23% in GN, and 15% in BS).
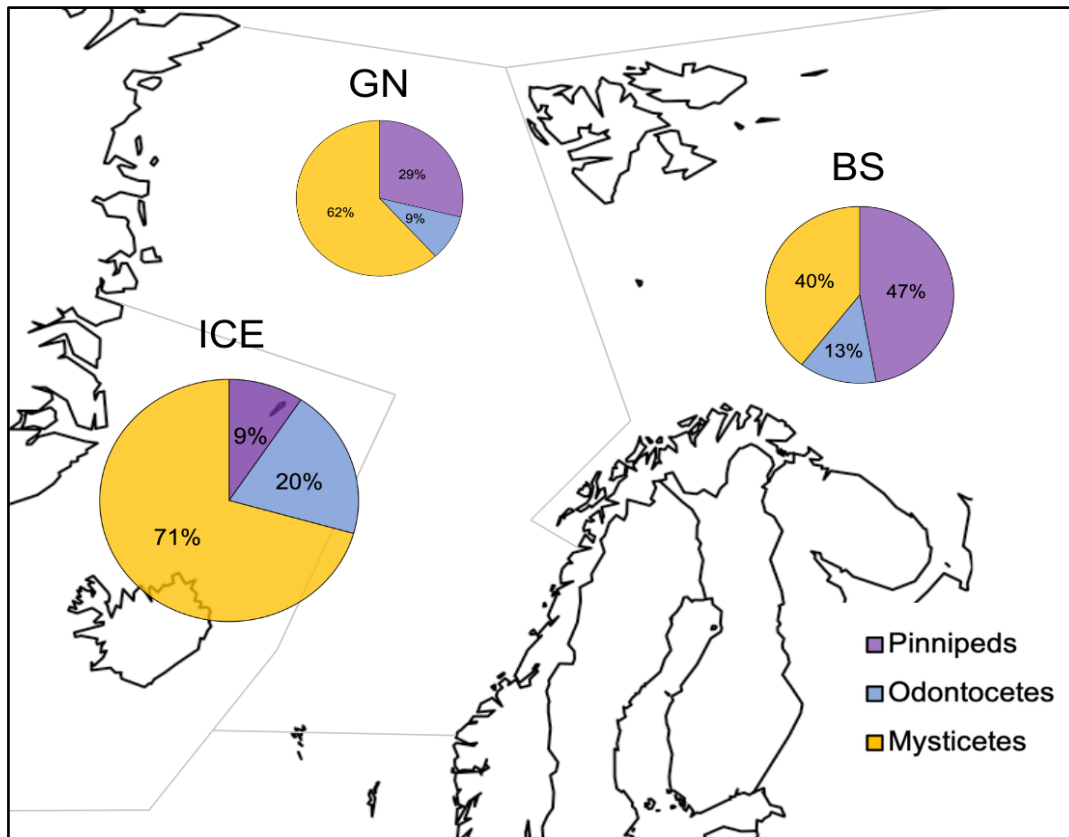
Figure 3: Total contribution of organic carbon export by pinnipeds, odontocetes and mysticetes in the three study regions ICE, GN, and BS. The size of the pie chart represents the total contribution percentage of each region, 51% for ICE, 21% for GN and 29% for BS.

3.4 Uncertainties on annual biomass and organic carbon export

The uncertainty values for biomass and organic carbon export are relatively high for most of the calculations. The highest uncertainty values are for harp seals in the BS region, pilot whales in the ICE region, and humpback whales in the BS region. In addition, almost all uncertainty estimates of biomass and organic carbon export outside the study area are high, many of them with negative lower CI values. This in an indication of the relative uncertainties of input values used for this study, that in most cases keeps adding up to even more uncertain estimates. The species with the lowest uncertainties are ringed seals, harp seals in ICE and GN regions, as well as hooded seals. These species have low uncertainty measures for their abundance values, with reflects in the results.

4 Discussion

To date, studies on carbon export by marine mammals have focused on baleen whale species, and there is a general disagreement on how important marine mammal deadfalls are for the carbon cycle. Marine mammals possess the capacity to sequester atmospheric carbon by the organic carbon contained within their bodies. Upon their death, the carcass may descend to deep-sea environments, where this carbon can be stored for centuries to millennia post-mortem. This process can help mitigate the effects of climate change and give important nutrients to deep sea communities. This study provides the first estimate of organic carbon export via marine mammal deadfalls in the Northeast Atlantic, and the first study to cover the full set marine mammal species, from ice-breeding seals and walruses, to odontocetes, and baleen whales. The results in this study are indications of organic carbon export potential from marine mammal deadfalls in the study area. The results are based on estimates of abundance, body mass, mortality rates, as well as residency in the regions. The total amount of carbon loss estimated in this study is ~26 887 tonnes C yr^{-1} or 2.68×10^{-5} Pg C yr^{-1} (95% CI 12 215−52 324 tonnes C yr^{-1}). Fin whales are the largest overall contributor, with around a third of the total organic carbon export with ~8 653 tonnes C yr^{-1}, (95% CI 5 234−12 072 tonnes C yr^{-1}). Harp seals are the second largest contributor overall, and the largest in the BS region with ~5 072 tonnes C yr^{-1} in total, (95% CI 3 329−6815 tonnes C yr^{-1}), while minke whales are the third largest with ~3 613 tonnes C yr^{-1} (95% CI 2 252−4 974 tonnes C yr^{-1}). Most of the carbon export potential is in the ICE region, with over half (51%) of the total carbon loss.

The results indicate that smaller marine mammals play a large role in carbon cycle estimates and should not be overlooked when analysing organic carbon storage in deep sea areas. Previous studies of baleen whales may therefore have underestimated the total organic carbon potential in the region by not including these smaller marine mammal species. In addition to harp seals, other pinniped and odontocete species (i.e. hooded seals, pilot whales, and *Lagenorhynchus* dolphins) have surprisingly high rates of organic storage potential, surpassing several of the great whale species (i.e. blue whales, sei whales, and bowhead whales) (Figure 2B). For the BS region, as much as 47% of the total organic storage potential comes from pinniped species, and they also have a significant contribution to the GN region (29%) (Figure 3). In addition, odontocetes contribute a surprisingly 20% of the total

contribution in the ICE region. These results show that if the study had been conducted with just the baleen whale species (mysticetes), such as previous studies, the carbon export potential would have been underestimated by 29%, 38%, and 60%, respectively, for the three study regions ICE, GN, and BS.

4.1 Results compared to other forms of carbon storage

The Nordic Seas are major oceanic carbon sinks, and have a highly effective biological carbon pump with large levels of carbon sequestration because of high latitude, cold waters, and large spring-bloom events (Goris *et al.*, 2018). The Nordic Seas are arguably one of the most important sites for deep water formation on earth (Aagaard *et al.*, 1985) and contains a high amount of dissolved organic carbon (DOC) throughout the water column (Amon & Benner, 2003; Børsheim, 2000). Amon *et al.* (2003) estimated that the annual vertical DOC export to deep seas was about 0.036 Pg C yr^{-1} for the Nordic Seas and Arctic ocean. Carlson *et al.* (2010) estimated that DOC export rate from the surface to mesopelagic (200-1000 m) and bathypelagic zones (1000-4000 m) in the North Atlantic Ocean were around 0.081 Pg C yr^{-1}, while Fontela *et al.* (2016) estimated that the contribution of DOC to carbon sequestration in the North Atlantic were 0.062 Pg C yr^{-1}. Considering these values (0.036 Pg C yr^{-1}−0.081 Pg C yr^{-1}), the results of total organic carbon export for this study (2.68 × 10^{-5} Pg C yr^{-1}) is about 0.03−0.07% of the organic carbon contribution by DOC in the study area.

Another important aspect of the biological carbon pump is sinking particulate organic matter (POM) that are transferred from the surface to the deep ocean. The majority of this particulate organic carbon (POC) is remineralized by metabolic processes, but a fraction reaches the deep ocean and gets sequestered (Nowicki *et al.*, 2022). Estimated vertical flux of POC in the Nordic Seas is 15-25 gC m^{-2} yr^{-1} at 100 m depth, and ~2.5 gC m^{-2} yr^{-1} at 2000 m depth (Henson *et al.*, 2012). The notation gC m^{-2} yr^{-1} stands for grams of carbon per square meter per year, and is often used in ecological and environmental sciences to quantify the amount of carbon fixed, stored, or transferred in an area of one square meter over the period of one year. Nowicki *et al.* (2022) estimated that the total amount of organic carbon sequestration by POC and DOC in the North Atlantic is 37.7 gC m^{-2} yr^{-1}, and POC export accounts for ~78% of this. When considering the estimates for DOC export from the previous studies (0.036 Pg C

yr^{-1}−0.081 Pg C yr^{-1}), and the percentage of contribution from POC, POC export could contribute as much as 0.064−0.144 Pg C yr^{-1} in the North Atlantic. Considering these values for POC export, the result from this study is 0.019−0.042% when comparing to North Atlantic levels. The Nordic Seas are a part of the North Atlantic Ocean but does not cover all of it. Therefore, these percentages are overestimated and more realistic values when considering the same study area might be less than 50% of estimated values. Despite this, any contribution to carbon export is important under the present climate challenges. Quantifying the contribution to carbon export from different components of the ecosystem is important, especially for high trophic levels that have received little attention in previous contribution estimates.

Although the estimated organic carbon fluxes in this thesis are low compared to DOC and POC fluxes, a baleen whale fall, which covers an average 50 m^2 and weighs roughly 40 tonnes, will have a massive localised effect on organic carbon accumilation estimates. Considering the results of this study and the fact that ~2.5 gC m^{-2} yr^{-1} is the carbon sequestered from POC in the study area, the carbon from a whale fall will be as much as 5.36×10^8 gC m^{-2} yr^{-1} in the same area. This reflects a tremendous increase in organic carbon of 2.144×10^{10} %.

4.2   Uncertainties on model inputs

This study provides an indication of expected carbon flux from deadfalls in the study area, but as other modelling research, it is based on several assumptions and uses data with high levels of uncertainty. Many of the variables used can be hard to quantify, e.g. abundance, exact days spent in each region, the percentage of carcasses that sink and reach deep sea areas, and precise natural mortality rates. Because of the uncertainty of these input parameters, the uncertainty values (CVs and 95% CIs) for the results of this study are large for most species. Several of the lower CI values for biomass export and organic carbon export outside the study area (Table 2 and 3) are negative values, and they generally have a large interval between the lower and upper CI values. This is mostly due to the multiplication and addition of many highly variable CI values that have large standard deviations (Appendix D), and a large difference in means.

The current understanding of population structures varies significantly between species of marine mammals within the Nordic Seas. While the abundance of marine mammal populations often are difficult to assess due to insufficient survey data (Taylor *et al.*, 2007), the Nordic Seas has one of the most robust abundance estimates for cetacean populations in the world (Skern-Mauritzen *et al.*, 2022). Some of the study species are extensively researched, e.g. minke whales, fin whales, and harp seals (Hammill & Stenson, 2014; Leonard & Øien, 2020a; Moore *et al.*, 2019; Pike *et al.*, 2019; Solvang *et al.*, 2021; Winters, 1976), while others have a largely unknown ecology and life history, e.g. bottlenose whales, Atlantic walrus, and narwhals (Born *et al.*, 1995; Christensen, 1973; Garde *et al.*, 2015; Gowans *et al.*, 2000; Grove *et al.*, 2020; Mead, 1989; Witting & Born, 2005). Species that are relevant for stock assessment regarding hunting or whaling in the study area (e.g. minke whales and harp seals in Norway, fin whales in Iceland), have gotten more research attention than species with low economic value, or that are hard to study due to inaccessibility or rarity. These species lack high quality data, both for abundance estimates and mortality rates (Bentley & Stokes, 2009). This is reflected in the uncertainty values (CVs and 95% CIs) for many of the study species (Table 1) and provides a challenge when estimating the results for this study, as data with moderate to high levels of uncertainty are added together, increasing the overall uncertainty of the results. As displayed in Figure 2A and B, several of the study species have large error bars connected to their biomass export and organic carbon export results. The amount of organic carbon export from all species and regions is 26 887 tonnes C yr^{-1} and the 95% confidence interval is 12 215−52 324 tonnes C yr^{-1} (Table 3). This highlights a significant uncertainty, probably due to the large variability among difference species and regions in the data.

Understanding natural mortality is essential for effective population management and conservation efforts, as it impacts population dynamics and the sustainability of species (Beverton & Holt, 2012). Researchers often rely on field data, historical records, and modelling to estimate natural mortality, but it remains one of the more challenging parameters to measure accurately due to the complexity of natural systems and variability across different species and environmental conditions (Vetter, 1971). For this study, natural mortality rates were not available for some of the study species, and most of the mortality rates found were from global populations outside of the study area. As previously mentioned, natural mortality rates might vary significantly between populations, from year to year, and from one geographical location to the next.

It's interesting to note that narwhals had the lowest mortality rates (0.005) of all the study species. Although they can live very long lives of >100 years, many of the baleen whales are long lived as well, and i.e. bowhead whales can live to more than 200 years. One would assume that bowhead whales would be the species with the lowest mortality rates because they have the highest maximum age of any of the study species, and although their mortality rate is low (0.040), narwhals have a lower rate, as do sperm whales (0.022), pilot whales (0.028), and killer whales (0.029). All mortality rates come from different studies (except the baleen whales who all come from Pershing *et al.* (2010)), each with their own approach and method to estimate mortality rates. For instance, the mortality rate for narwhals, which was the lowest in the study, was found analysing aspartic acid racemization of eye nuclei (Garde *et al.*, 2015), while the mortality rates for bowhead whales were found using a simple population dynamics model (Pershing *et al.*, 2010). Had the same methods been used for both species, or all species for that matter, the comparisons would have been easier to assess, and results for mortality rates could have been different. Other factors than maximum age will also affect natural mortality rates, like disease and predation. For future studies, a similar approach should be used for all estimates of mortality to get a more solidified foundation for comparisons between species, and to eliminate research bias towards some species. Mortality rates should be based on disease and predation prevalence, as well as longevity, to increase the certainty of the values. Uncertainty measures on mortality rates was not included in this study due to their limited availability in the previously published literature. For future studies this should be included on the basis that natural mortality rates are highly variable between populations, years, and geographical locations (Dimarchopoulou *et al.*, 2024).

Estimates of residency given in Table 1 are highly variable between species. There is limited information available on timing of migrations and the overwintering populations of migratory species, so a CV of 0.20 was set for residence times in this study to account for uncertainties, following the studies by Skern-Mauritzen *et al.* (2022) and Smith *et al.* (2015). A CV of 0.20 was also set for mean body mass (Table 1) to approximate typical adult size ranges (Link et al. 2006).

This variety in scientific data quality poses a challenge in calculating the results of this thesis, and increases the uncertainty of the calculations, but an indication of annual carbon flux in the study area can still be derived from the results.

4.3 Ecological factors that impact results

It is important to note that results from this study gives an export potential only, and that the true values for organic carbon export will vary depending on how many carcasses sink to deep oceans or gets stored in sediments. The results of this study assume that the export rates for deadfalls to deep seas are 100%, which is a clear overestimation. Many factors play a role when determining the export rates, including predation, strandings, as well as ocean- and vertical mixed layer depth.

4.3.1 Predation

Predation might account for a significant portion of the natural mortalities in both seals and dolphin species. Marine mammals that become prey will be consumed either fully or partially, and most of the organic carbon they contain will not be stored at depths. Thus, predation rates affect the percentage of carcasses that sink, and should be considered in carbon storage estimates of future studies. Polar bears (*Ursus maritimus*) prey heavily on ice-dependent seals (Cleator, 1996) and are the primary predators of ringed seals and bearded seals in the study regions (Aars *et al.*, 2017; Stirling & Archibald, 1977). Ringed seals are the primary prey of polar bears, but bearded seals are also important due to their larger size (Stirling & Archibald, 1977). Polar bears have also been observed to prey on harp seals, hooded seals, white whales, narwhals, and walruses, but these instances do appear to be much less prevalent than for ringed and bearded seals (Smith & Stirling, 2019; Thiemann *et al.*, 2008). In the Barents Sea (BS), although the number seals killed by polar bears was higher for ringed seals (63% vs 13%), when looking at biomass around 55% of polar bear prey were from bearded seals (Derocher *et al.*, 2002). One third of the bearded seals killed by polar bears were pups, and pups and subadults appear to be more vulnerable to polar bear predation than adults (Stirling & Archibald, 1977). A study by Hammill and Smith (1991) suggests that 75-100% of the polar bear predation in ringed seals in Barrow Strait, Canada were of pups, suggesting that the predation of adult individuals might not be as prevalent. Since this study uses adult abundance and mortality rates, polar bear predation might not impact the results of these prey species in any significant degree but should still be considered when looking at potential flux.

Killer whales are another important predator for seals and small cetaceans. In the Norwegian Sea, killer whales have been observed to feed on harbour porpoises as well as pinnipeds (Jourdain, 2020; Jourdain *et al.*, 2020). Although the predation rate is largely unknown for mammal-eating killer whales, estimations have predicted it could be as high as 0.28 for harbour porpoises as prey in local fjords (Åslein, 2023). In this scenario the killer whales could reduce the harbour porpoise fjord population by 90% over a 20-year period, proving that the predation most likely plays a role in harbour porpoise mortality and should be assessed for future studies.

4.3.2 Deaths on pack ice or by strandings

Another factor that should be considered is that adult ice-breeding seals and walruses might perish on the ice instead of open water areas. Many of the pinniped species spend a good portion of their time on sea ice, especially during molting and breeding season (Burns & Frost, 1979; Nordøy *et al.*, 2008; Vacquié-Garcia *et al.*, 2017b). Deaths that occur during this time (1-2 months a year) might not become deadfalls that sink to the ocean floor if the carcass decomposes or is scavenged on at the surface. Therefore, the realistic amount of organic carbon storage for these species are likely lower than assumed in this study.

Several of the study species also experience strandings, and stranded animals that die and decompose at shore and will not account towards deep sea carbon flux estimates. Some of the study species have common mass-stranding events (e.g. bottlenose whales, *Lagenorhynchus* dolphins) (Grove *et al.*, 2020). The cause of these mass strandings is unknown, some researchers suggest that they follow prey towards shore, and might get stuck during low tides (Sampson *et al.*, 2012). Other suggests that illness could lead some individuals to swim towards shore and that the rest of the pod might follow them (Rogan *et al.*, 1997). Some also suggest extreme weather, acoustic disturbance, or geomagnetic anomalies as possible causes (NAMMCO, 2020). Harbour porpoises are frequently seen stranded, but usually strand individually, and not in large mass strandings. Interactions with fishing gear as bycatch has been identified as the cause of many of these strandings (47-86%) (Culik *et al.*, 2015), where harbour porpoises dead from entanglement are dropped from fishing boats, and later wash up on shore. Because bycatches are anthropogenic sources of mortality, they are not included in natural mortality estimates and strandings of harbour porpoises should therefore have little impact on organic carbon flux for this species. Baleen whales and large toothed whales (e.g.

sperm whales, killer whales) are also known to experience strandings, but this accounts for a relatively small proportion of the population and will usually not have a large effect on mortality estimates (Rugh *et al.*, 2005; Smith, 2006). These stranding events appear to be random or without any predictable pattern, and their frequency can be hard to estimate. Because of this, strandings for larger whales does not seem to be of any large significance to the results of this study, but their occurrence should be noted, nonetheless. One interesting exception is the sperm whales. Stranding records shows that between 1-8 individuals of sperm whales have stranded yearly in the North Sea since 2000, and in 2016 as many as 28 individuals stranded (Pierce *et al.*, 2018; Smeenk, 1997). Considering the estimations of this study are that 69 individuals of sperm whales die annually in the three study regions (Table 2), these strandings have the potential to account for 40% of total deaths. 2016 was a record year for sperm whale strandings and the estimation of 40% is clearly overestimated, but strandings they could still account for a percentage (1.5-11.6%) of sperm whale deaths in the region every year and should be included in carbon flux estimates of deadfalls.

4.3.3 Sequestration depth and decomposition

The true amount of carbon sequestered in deep sea sediments can vary widely depending on numerous factors. The efficiency of the biological pump is influenced various factors, including the types of organisms involved, the water depth, ocean temperature and chemistry, the timescale of ventilation (the release of remineralized carbon back into the atmosphere), and the region and depth at which carbon is remineralized (Baker *et al.*, 2022). Carbon burial becomes more effective in anoxic environments, as the absence of oxygen slows the degradation of carbon, thereby increasing the likelihood of its sequestration (Barber, 1968; Middelburg, 2019). The study area encompasses a range of depths, predominantly consisting of deep-sea regions, but also includes some shallower waters (Figure 2). In terms of sequestration, the largest sequestration inventories and longest sequestration times are usually found in the northern high latitudes (Nowicki *et al.*, 2022). The sequestration depth depends on the mixed-layer depth and can vary greatly between regions (Martin *et al.*, 2021). For future studies the sequestration depth of the study regions should be included in estimates to get more accurate values of organic carbon storage.

One of the reasons marine mammal deadfalls have the capacity to store organic carbon is due to their relatively rapid sinking towards the deep sea, which, compared to other vertical fluxes of organic carbon (e.g. DOC or POC), experience little decomposition in the upper layers of the water columns (Smith, 2006). There is also a scarcity of scavengers for whales in midwater (Britton and Morton, 1994), and one can assume that most of the tissue is intact when the carcass reaches the ocean floor (Smith & Baco, 2003). One notable exception to this might be bowhead whales, as they were dubbed "right whales" by whalers due to their natural buoyancy after death and may float in surface waters for long periods of time, increasing decomposition from scavengers. Due to this, bowhead whales might have a lower organic carbon flux estimate than other baleen whales.

4.4   Uncertainties estimating organic carbon content

One uncertainty in this study is that an approximation for mammalian water content is used (66%) when calculating the organic carbon content, and the same value is used for all species. For the results to increase in accuracy, each species' water content and therefore organic carbon content should be analysed individually. The study by Brodie (1975) showed that about 50% of the body of baleen whales contains muscles, and that these contain 75% water. In another study the blubber of stellar sea lions (*Eumetopias jubatus*) was showed to contain only 24.4-24.9% water (Williams *et al.*, 2004), showing that the calculations will depend on the amount of muscle, blubber etc. within each of the study species. This will in turn impact the values for organic carbon loss, and the results might have been different than the results of this study. It is a time-consuming project to investigate the composition of each study species, one that would be too large for the scope of this study, and it relies on the fact that each species would have at least one published study where body composition is analysed. The fact is that many of the study species does not have these studies conducted, and therefore a general assumption on body composition and water content must be used instead. You could argue that for the species that have body composition analyses published, i.e baleen whales (Adamczak *et al.*, 2023; Brodie, 1975; Williams *et al.*, 2004), the accurate values could be used, while a general assumption could be used for the rest of the species. This is true but would again increase the scope of this study tremendously. For the future such analyses should be performed and incorporated into the calculations. Williams *et al.* (2004) shows that marine mammals such as sea otters (*Enhydra lutris*), stellar sea lions, and

northern fur seals (*Callorhinus ursinus*) has a water percentage between 64.0-66.6%, which is close to the approximate value of 66% used in this study. Although every study species will have a unique composition of water content based on the percentage of muscle, lipids, and bones they contain, it is safe to assume that the water content would be quite similar between all species. Therefore, although not completely accurate, the organic carbon content estimated in this study will be close to the true estimates, and an indication of organic carbon loss potential can be surmised. Compared to the other uncertainties previously mentioned in this study, the variation around water content is quite low, and will not have a significant effect on the results.

4.5   Impacts on deep sea communities and other whale carbon fluxes

Although the total contribution of organic carbon from marine mammal deadfalls in this study is relatively small compared to export of DOC and POC in the study area, the local impact on deep-sea communities are massive (Roman *et al.*, 2014; Smith, 2006; Smith & Baco, 2003; Smith *et al.*, 2014). The organic carbon that a sinking marine mammal carcass imports to the deep sea provides a massive food fall to the nutrient-lacking deep-sea and can sustain a large number of organisms from decades to millennia (Smith, 2006). In fact, the sediments that lie directly underneath a sunken baleen whale carcass (which covers roughly 50 m^2) experience a flux of organic carbon equivalent to 2000 years of background organic flux from marine snow (Smith & Baco, 2003). The impacts on deep-sea ecosystems are massive and vital to deep-sea life, and many species are dependent on the organic carbon supply from whale falls. Several species are also whale fall specialists and found nowhere else on earth (Smith, 1992; Smith *et al.*, 1989). These species face extinction as the reduction of whale-populations due to commercial whaling has reduced the number of whale falls in several areas (Pearson *et al.*, 2022).

Whales and marine mammals also contribute to the carbon cycle in other ways. Although not a part of this study, the contribution of whales in fertilizing the oceans and stimulate primary production should not be overlooked when looking at the full contribution of whales to carbon storage. Whale excretions contain nutrients (e.g. nitrogen, phosphorus, and iron) that are important for the photosynthetic activity of phytoplankton (Freitas *et al.*, 2023; Gilbert *et*

al., 2023). These primary producers gather carbon dioxide during this process, thus contributing to the reduction of greenhouse gases. Much of this carbon is stored either as living organic carbon or as particulate or dissolved organic carbon that slowly sinks to the seafloor and can be stored at depth or in sediments (Six & Maier-Reimer, 1996). This is another part of the biological carbon pump, often known as the whale pump, and shows that whales and other marine mammals contribute to carbon storage in more ways than just deadfalls. The results from this study will compliment such studies and help to provide a holistic understanding on the contribution of marine mammals to the oceanic carbon cycle.

5 Conclusion

There is still much we do not know about organic carbon export by marine mammal deadfalls. This study enhances our understanding and highlights the importance of better comprehension of the fate of marine mammal deadfalls, and improving the input parameters to get more accurate estimates of the proportion of deadfalls that will reach the sequestration depths of the deep ocean. This knowledge can contribute to blue carbon estimates for climate conservation research and improve the current knowledge of the oceanic carbon cycle and its ecological factors, which is crucial in addressing today's climate crisis.

This study estimated a total annual organic carbon flux potential in the study area of 2.68×10^{-5} Pg C yr$^-$1. Fin whales were the largest contributor to organic carbon export, followed by harp seals and minke whales. These findings emphasize the need to include smaller marine mammals in future studies of carbon sequestration, as, despite their small size, their significant contribution is due to their large abundance. Compared to other forms of organic carbon export, such as dissolved organic carbon (DOC) and particulate organic carbon (POC), the carbon flux potential from marine mammal deadfalls in this study constitutes about $0.03-0.07\%$ and $0.019-0.042\%$ of these values, respectively. While the regional storage potentials are low compared to other sources of organic carbon flux, the local effects on organic carbon accumilation are substantial, with an increase of approximately 2.14×10^{10} % per m^2 compared to POC export.

This study is impacted by significant uncertainties in many of the estimated values. Improved research on population parameters, such as abundance estimates and mortality rates, especially for species with the highest uncertainties, is needed to refine these estimates. Ecological factors such as predation, strandings, and depth analyses of the study area should also be incorporated into downward flux estimates. Despite its limitations, this study provides an indication of organic carbon flux in the study area and highlights the importance of understanding the role of marine mammals in the oceanic carbon cycle.

References

Aagaard, K., Swift, J., & Carmack, E. (1985). Thermohaline circulation in the Arctic Mediterranean seas. *Journal of Geophysical Research: Oceans*, *90*(C3), 4833-4846.

Aars, J., Marques, T. A., Lone, K., Andersen, M., Wiig, Ø., Bardalen Fløystad, I. M., Hagen, S. B., & Buckland, S. T. (2017). The number and distribution of polar bears in the western Barents Sea. *Polar Research*, *36*(1), 1374125.

Adamczak, S. K., McHuron, E. A., Christiansen, F., Dunkin, R., McMahon, C. R., Noren, S., Pirotta, E., Rosen, D., Sumich, J., & Costa, D. P. (2023). Growth in marine mammals: a review of growth patterns, composition and energy investment. *Conservation Physiology*, *11*(1), coad035. https://doi.org/10.1093/conphys/coad035

Amon, R. M., & Benner, R. (2003). Combined neutral sugars as indicators of the diagenetic state of dissolved organic matter in the Arctic Ocean. *Deep Sea Research Part I: Oceanographic Research Papers*, *50*(1), 151-169.

Amon, R. M. W., Budéus, G., & Meon, B. (2003). Dissolved organic carbon distribution and origin in the Nordic Seas: Exchanges with the Arctic Ocean and the North Atlantic. *Journal of Geophysical Research: Oceans*, *108*(C7). https://doi.org/10.1029/2002JC001594

Andersen, J. M., Wiersma, Y. F., Stenson, G. B., Hammill, M. O., Rosing-Asvid, A., & Skern-Maurizen, M. (2013). Habitat selection by hooded seals (*Cystophora cristata*) in the Northwest Atlantic Ocean. *ICES Journal of Marine Science*, *70*(1), 173-185.

Åslein, E. H. (2023). *Killer whale (Orcinus orca) predation on harbour porpoise (Phocoena phocoena) in Hardangerfjord, Western Norway*

Baker, C. A., Martin, A. P., Yool, A., & Popova, E. (2022). Biological carbon pump sequestration efficiency in the North Atlantic: a leaky or a long-term sink? *Global biogeochemical cycles*, *36*(6), e2021GB007286.

Barber, R. T. (1968). Dissolved Organic Carbon from Deep Waters resists Microbial Oxidation. *Nature*, *220*(5164), 274-275. https://doi.org/10.1038/220274a0

Baylis, A. M., Þorbjörnsson, J. G., Dos Santos, E., & Granquist, S. M. (2019). At-sea spatial usage of recently weaned grey seal pups in Iceland. *Polar Biology*, *42*(11), 2165-2170.

Bentley, N., & Stokes, K. (2009). Contrasting paradigms for fisheries management decision making: how well do they serve data-poor fisheries? *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, *1*(1), 391-401.

Beverton, R. J., & Holt, S. J. (2012). *On the dynamics of exploited fish populations* (Vol. 11). Springer Science & Business Media.

Blindheim, J. (1989). Ecological features of the Norwegian Sea. Proc. 6th Conf. Com. Arct. Int,

Borchers, D. L., & Burt, M. L. (1997). Sei and fin whale abundance in the North Atlantic, estimated from NASS-95 shipboard survey data. Paper NAMMCO/SC/5/AE/1 presented at the NAMMCO Scientific Committee Working Group on Abundance Estimates meeting in Reykjavik, February 1997. 12.

Born, E., Boertmann, D., Heide-Jørgensen, M. P., Dietz, R., Witting, L., Kyhn, L., Fossette, S., Rigét, F. F., Laidre, K., & Ugarte, F. (2009). Abundance of Atlantic walrus (*Odobenus rosmarus rosmarus*) in East Greenland. *NAMMCO/SC/17/WWG/07*, 37.

Born, E. W., Gjertz, I., & Reeves, R. R. (1995). *Population assessment of Atlantic walrus (Odobenus rosmarus rosmarus L.)*.

Børsheim, K. Y. (2000). Bacterial production rates and concentrations of organic carbon at the end of the growing season in the Greenland Sea. *Aquatic Microbial Ecology*, *21*(2), 115-123.

Britannica, T. (2024, February 15). *Greenland Sea*. Encyclopedia Britannica. Retrieved April 2, 2024 from https://www.britannica.com/place/Greenland-Sea

Brodie, P. (1975). Cetacean energetics, an overview of intraspecific size variation. *Ecology*, *56*(1), 152-161.

Burns, J. J., & Frost, K. J. (1979). The natural history and ecology of the bearded seal, *Erignathus barbatus*. *Environmental Assessment of the Alaskan Continental Shelf, Final Reports*, *19*, 311-392.

Butman, C. A., Carlton, J. T., & Palumbi, S. R. (1995). Whaling effects on deep-sea biodiversity. *Conservation biology*, *9*(2), 462-464.

Carlson, C. A., Ducklow, H. W., & Michaels, A. F. (1994). Annual flux of dissolved organic carbon from the euphotic zone in the northwestern Sargasso Sea. *Nature*, *371*(6496), 405-408.

Carlson, C. A., Hansell, D. A., Nelson, N. B., Siegel, D. A., Smethie, W. M., Khatiwala, S., Meyers, M. M., & Halewood, E. (2010). Dissolved organic carbon export and subsequent remineralization in the mesopelagic and bathypelagic realms of the North

Atlantic basin. *Deep Sea Research Part II: Topical Studies in Oceanography*, *57*(16), 1433-1445. https://doi.org/10.1016/j.dsr2.2010.02.013

Christensen, I. (1973). Age determination, age distribution and growth of bottlenose whales, *Hyperoodon ampullatus* (Forster), in the Labrador Sea. *Norwegian Journal of Zoology*, *21*, 331-340.

Cleator, H. J. (1996). The status of the bearded seal, *Erignathus barbatus*, in Canada. *Canadian Field Naturalist*, *110*(3), 501-510.

Culik, B., von Dorrien, C., Müller, V., & Conrad, M. (2015). Synthetic communication signals influence wild harbour porpoise (*Phocoena phocoena*) behaviour. *Bioacoustics*, *24*, 201-221. https://doi.org/10.1080/09524622.2015.1023848

Derocher, A. E., Wiig, Ø., & Andersen, M. (2002). Diet composition of polar bears in Svalbard and the western Barents Sea. *Polar Biology*, *25*, 448-452.

Dimarchopoulou, D., Tsikliras, A., Froese, R., & Pauly, D. (2024). Fish Stocks. In S. M. Scheiner (Ed.), *Encyclopedia of Biodiversity (Third Edition)* (pp. 388-403). Academic Press. https://doi.org/10.1016/B978-0-12-822562-2.00001-3

Durfort, A., Mariani, G., Troussellier, M., Tulloch, V., & Mouillot, D. (2020). The collapse and recovery potential of carbon sequestration by baleen whales in the Southern Ocean.

Durfort, A., Mariani, G., Tulloch, V., Savoca, M. S., Troussellier, M., & Mouillot, D. (2022). Recovery of carbon benefits by overharvested baleen whale populations is threatened by climate change. *Proceedings of the Royal Society B*, *289*(1986), 20220375.

Evans, K., & Hindell, M. A. (2004). The age structure and growth of female sperm whales (Physeter macrocephalus) in southern Australian waters. *Journal of Zoology*, *263*(3), 237-250.

Fedoseev, G. A. (1975). Ecotypes of the ringed seal (*Pusa hispida* Schreber, 1777) and their reproductive capabilities. *Rapports et Proces-verbaux des Reunions. Conseil International pour l'Exploration de la Mer*, *169*, 156-160.

Folkow, L. P., Nordøy, E. S., & Blix, A. S. (2004). Distribution and diving behaviour of harp seals (*Pagophilus groenlandicus*) from the Greenland Sea stock. *Polar Biology*, *27*, 281-298.

Follett, C. L., Repeta, D. J., Rothman, D. H., Xu, L., & Santinelli, C. (2014). Hidden cycle of dissolved organic carbon in the deep ocean. *Proceedings of the National Academy of Sciences*, *111*(47), 16706-16711. https://doi.org/10.1073/pnas.1407445111

Fontela, M., García-Ibáñez, M. I., Hansell, D. A., Mercier, H., & Pérez, F. F. (2016). Dissolved Organic Carbon in the North Atlantic Meridional Overturning Circulation. *Scientific reports*, *6*(1), 26931. https://doi.org/10.1038/srep26931

Freitas, C., Gundersen, K., Lindblom, L., Biuw, M., & Haug, T. (2023). Nutrient concentrations in minke whale faeces and the potential impact on dissolved nutrient pools off Svalbard, Norway. *Progress in Oceanography*, *210*, 102927.

Garde, E., Hansen, S. H., Ditlevsen, S., Tvermosegaard, K. B., Hansen, J., Harding, K. C., & Heide-Jørgensen, M. P. (2015). Life history parameters of narwhals (*Monodon monoceros*) from Greenland. *Journal of mammalogy*, *96*(4), 866-879.

Gilbert, L., Jeanniard-du-Dot, T., Authier, M., Chouvelon, T., & Spitz, J. (2023). Composition of cetacean communities worldwide shapes their contribution to ocean nutrient cycling. *Nature Communications*, *14*(1), 5823.

Gilles, A., Gunnlaugsson, T., Mikkelsen, B., Pike, D. G., & Víkingsson, G. (2020). Summer abundance of harbour porpoises (*Phocoena phocoena*) in the coastal waters of Iceland and the Faroe Islands. *NAMMCO Scientific Publications*, *11*. https://doi.org/10.7557/3.4939

Goris, N., Tjiputra, J. F., Olsen, A., Schwinger, J., Lauvset, S. K., & Jeansson, E. (2018). Constraining Projection-Based Estimates of the Future North Atlantic Carbon Uptake. *Journal of Climate*, *31*(10), 3959-3978. https://doi.org/10.1175/JCLI-D-17-0564.1

Gowans, S., Whitehead, H., Arch, J. K., & Hooker, S. K. (2000). Population size and residency patterns of northern bottlenose whales (*Hyperoodon ampullatus*) using the Gully, Nova Scotia. *J. Cetacean Res. Manage.*, *2*(3), 201-210.

Greenspoon, L., Krieger, E., Sender, R., Rosenberg, Y., Bar-On, Y. M., Moran, U., Antman, T., Meiri, S., Roll, U., & Noor, E. (2023). The global biomass of wild mammals. *Proceedings of the National Academy of Sciences*, *120*(10), e2204892120.

Grove, T., Senglat, C., Petitguyot, M., & Kosiba, D. (2020). Mass stranding and unusual sightings of northern bottlenose whales (*Hyperoodon ampullatus*) in Skjálfandi Bay, Iceland.

Gruber, N., Clement, D., Carter, B. R., Feely, R. A., van Heuven, S., Hoppema, M., Ishii, M., Key, R. M., Kozyr, A., Lauvset, S. K., Lo Monaco, C., Mathis, J. T., Murata, A., Olsen, A., Perez, F. F., Sabine, C. L., Tanhua, T., & Wanninkhof, R. (2019). The oceanic sink for anthropogenic CO_2 from 1994 to 2007. *Science*, *363*(6432), 1193-1199. https://doi.org/10.1126/science.aau5153

Gunnlaugsson, T., Víkingsson, G. A., & Pike, D. G. (2009). Combined line-transect and cue-count estimate of sperm whale abundance in the North Atlantic, from Icelandic NASS-2001 shipboard survey. *NAMMCO Scientific Publications*, *7*, 73-80.

Hammill, M., & Smith, T. (1991). The role of predation in the ecology of the ringed seal in Barrow Strait, Northwest Territories, Canada. *Marine Mammal Science*, *7*(2), 123-135.

Hammill, M. O., & Stenson, G. B. (2006). *Abundance of Northwest Atlantic hooded seals (1960-2005)*. Fisheries and Oceans.

Hammill, M. O., & Stenson, G. B. (2014). *Changes in ice conditions and potential impact on harp seal pupping*. Canadian Science Advisory Secretariat.

Hansell, D. A., & Carlson, C. A. (2014). *Biogeochemistry of marine dissolved organic matter*. Academic press.

Hansen, R. G., Borchers, D. L., & Heide-Jørgensen, M. P. (2019). Abundance of narwhals summering in East Greenland and narwhals wintering in the North Water and Northeast Water. *NAMMCO SC/26/NEGWG/04*.

Heide-Jørgensen, M., Laidre, K. L., Burt, M. L., Borchers, D. L., Marques, T. A., Hansen, R. G., Rasmussen, M., & Fossette, S. (2010). Abundance of narwhals (*Monodon monoceros*) on the hunting grounds in Greenland. *Journal of mammalogy*, *91*(5), 1135-1151.

Helle, E., Olsson, M., & Jensen, S. (1976). PCB levels correlated with pathological changes in seal uteri. *Ambio*, 261-262.

Henson, S. A., Sanders, R., & Madsen, E. (2012). Global patterns in efficiency of particulate organic carbon export and transfer to the deep ocean. *Global biogeochemical cycles*, *26*(1). https://doi.org/10.1029/2011GB004099

Hoenig, J. M. (2005). Empirical Use of Longevity Data to Estimate Mortality Rates. *Fishery Bulletin*, *82*, 898-903.

ICES. (2019). ICES/NAFO/NAMMCO WORKING GROUP ON HARP AND HOODED SEALS (WGHARP). *ICES Scientific Reports*, *1*(72), 193. https://doi.org/10.17895/ices.pub.5617

Jacobsen, N. O. (1984). Estimates of pup production, age at first parturition and natural mortality for hooded seals in the West Ice. *FiskDir. Ser. Havunders.*, *17*, 483-498.

Jacobson, E. K., Boyd, C., McGuire, T. L., Shelden, K. E., Himes Boor, G. K., & Punt, A. E. (2020). Assessing cetacean populations using integrated population models: an example with Cook Inlet beluga whales. *Ecological Applications*, *30*(5), e02114.

Jelmert, A., & Oppen-Berntsen, D. O. (1996). Whaling and deep-sea biodiversity. *Conservation biology*, *10*(2), 653-654.

Johnson, M. L., Fiscus, C. H., Ostenson, B. T., & Barbour, M. L. (1966). *Marine mammals In Environment of the Cape Thompson region, Alaska.* (N. J. Wilimowsky & J. N. Wolfe, Eds.). United States Atomic Energy Commission.

Jones, E. L., McConnell, B. J., Smout, S., Hammond, P. S., Duck, C. D., Morris, C. D., Thompson, D., Russell, D. J., Vincent, C., & Cronin, M. (2015). Patterns of space use in sympatric marine colonial predators reveal scales of spatial partitioning. *Marine Ecology Progress Series*, *534*, 235-249.

Jones, E. L., Sparling, C. E., McConnell, B. J., Morris, C. D., & Smout, S. (2017). Fine-scale harbour seal usage for informed marine spatial planning. *Scientific reports*, *7*(1), 11581.

Jourdain, E. (2020). Dietary variations and specializations of killer whales (Orcinus orca) in Norway.

Jourdain, E., Andvik, C., Karoliussen, R., Ruus, A., Vongraven, D., & Borgå, K. (2020). Isotopic niche differs between seal and fish-eating killer whales (Orcinus orca) in northern Norway. *Ecology and Evolution*, *10*(9), 4115-4127.

Jourdain, E., & Vongraven, D. (2017). Humpback whale (*Megaptera novaeangliae*) and killer whale (*Orcinus orca*) feeding aggregations for foraging on herring (*Clupea harengus*) in Northern Norway. *Mammalian Biology*, *86*(1), 27-32.

Kovacs, K. M., Aars, J., & Lydersen, C. (2014). Walruses recovering after 60+ years of protection in Svalbard, Norway. *Polar Research*, *33*(1), 26034.

Kovacs, K. M., Haug, T., & Lydersen, C. (2009). Marine mammals of the Barents Sea. In E. Sakshaug, G. H. Johnsen, & K. M. Kovacs (Eds.), *Ecosystem Barents Sea* (pp. 453-496). Tapir Academic Press.

Kuningas, S., Similä, T., & Hammond, P. S. (2014). Population size, survival and reproductive rates of northern Norwegian killer whales (*Orcinus orca*) in 1986–2003. *Journal of the Marine Biological Association of the United Kingdom*, *94*(6), 1277-1291.

Labansen, A. L., Lydersen, C., Haug, T., & Kovacs, K. M. (2007). Spring diet of ringed seals (*Phoca hispida*) from northwestern Spitsbergen, Norway. *ICES Journal of Marine Science*, *64*(6), 1246-1256.

Lei, R., Feng, S., & Lauvaux, T. (2020). Country-scale trends in air pollution and fossil fuel CO_2 emissions during 2001–2018: confronting the roles of national policies and economic growth. *Environmental Research Letters*, *16*(1), 014006.

Leonard, D. M., & Øien, N. I. (2020a). Estimated abundances of cetacean species in the Northeast Atlantic from Norwegian shipboard surveys conducted in 2014–2018. *NAMMCO Scientific Publications*, *11*. https://doi.org/10.7557/3.4694

Leonard, D. M., & Øien, N. I. (2020b). Estimated abundances of cetacean species in the Northeast Atlantic from two multiyear surveys conducted by Norwegian vessels between 2002-2013.

Li, Q., Liu, Y., Li, G., Wang, Z., Zheng, Z., Sun, Y., Lei, N., Li, Q., & Zhang, W. (2022). Review of the Impact of Whale Fall on Biodiversity in Deep-Sea Ecosystems. *Frontiers in Ecology and Evolution*, *10*. https://doi.org/10.3389/fevo.2022.885572

Liu, J. (2015). Whale fall, an alternative ecosystem in the deep sea. *Sci. Public: Middle School Students China*, *6*, 41-43.

Lockyer, C. (2003). Harbour porpoises (*Phocoena phocoena*) in the North Atlantic: Biological parameters. *NAMMCO Scientific Publications*, *5*, 71-89.

Lydersen, C., Chernook, V. I., Glazov, D. M., Trukhanova, I. S., & Kovacs, K. M. (2012a). Aerial survey of Atlantic walruses (*Odobenus rosmarus rosmarus*) in the Pechora Sea, August 2011. *Polar Biology*, *35*, 1555-1562.

Lydersen, C., Freitas, C., Wiig, Ø., Bachmann, L., Heide-Jørgensen, M. P., Swift, R., & Kovacs, K. M. (2012b). Lost highway not forgotten: satellite tracking of a bowhead whale (*Balaena mysticetus*) from the critically endangered Spitsbergen stock. *Arctic*, 76-86.

Lydersen, C., & Gjertz, I. (1987). Population parameters of ringed seals (*Phoca hispida* Schreber, 1775) in the Svalbard area. *Canadian Journal of Zoology*, *65*(4), 1021-1027.

Magnúsdóttir, E. E., Rasmussen, M. H., Lammers, M. O., & Svavarsson, J. (2014). Humpback whale songs during winter in subarctic waters. *Polar Biology*, *37*, 427-433.

Martin, A. H., Pearson, H. C., Saba, G. K., & Olsen, E. M. (2021). Integral functions of marine vertebrates in the ocean carbon cycle and climate change mitigation. *One Earth*, *4*(5), 680-693.

Martin, J. H., & Fitzwater, S. E. (1988). Iron deficiency limits phytoplankton growth in the north-east Pacific subarctic. *Nature*, *331*(6154), 341-343.

Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., & Gomis, M. (2021). Climate change 2021: the physical science basis. *Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change*, *2*(1), 2391.

McLaren, I. A. (1958). *The biology of the ringed seal (Phoca hispida Schreber) in the eastern Canadian Arctic* (Vol. 118). Fisheries Research Board of Canada Ottawa.

Mead, J. (1989). Bottlenose whales *Hyperoodon ampullatus* (Forster, 1770) and *Hyperoodon planifrons* (Flower, 1882). *Handbook of marine mammals*, *4*, 321-348.

Meynecke, J.-O., Samanta, S., de Bie, J., Seyboth, E., Prakash Dey, S., Fearon, G., Vichi, M., Findlay, K., Roychoudhury, A., & Mackey, B. (2023). Do whales really increase the oceanic removal of atmospheric carbon? *Frontiers in Marine Science*, *10*. https://doi.org/10.3389/fmars.2023.1117409

Middelburg, J. J. (2019). *Marine carbon biogeochemistry: A primer for earth system scientists*. Springer Nature.

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

Mori, M., Kosaka, Y., Watanabe, M., Nakamura, H., & Kimoto, M. (2019). A reconciled estimate of the influence of Arctic sea-ice loss on recent Eurasian cooling. *Nature Climate Change*, *9*(2), 123-129.

NAMMCO. (2020). *Atlantic white-sided dolphin*. Retrieved 05.05.24 from https://nammco.no/atlantic-white-sided-dolphin-2/#1475762140594-0925dd6e-f6cc

Nielsen, N. H., Teilmann, J., Sveegaard, S., Hansen, R. G., Sinding, M. H. S., Dietz, R., & Heide-Jørgensen, M. P. (2018). Oceanic movements, site fidelity and deep diving in harbour porpoises from Greenland show limited similarities to animals from the North Sea. *Marine Ecology Progress Series*, *597*, 259-272.

Nordøy, E. S., Folkow, L. P., Potelov, V., Prischemikhin, V., & Blix, A. S. (2008). Seasonal distribution and dive behaviour of harp seals (*Pagophilus groenlandicus*) of the White Sea–Barents Sea stock. *Polar Biology*, *31*, 1119-1135.

Nowicki, M., DeVries, T., & Siegel, D. A. (2022). Quantifying the Carbon Export and Sequestration Pathways of the Ocean's Biological Carbon Pump. *Global biogeochemical cycles*, *36*(3), e2021GB007083. https://doi.org/10.1029/2021GB007083

Øritsland, T. (1964). Klappmysshunnens forplantningsbiologi. *Fisken Hav.*, *1*, 1-15.

Øritsland, T., & Benjaminsen, T. (1975). Additional data on the sex ration, age composition and mortality of Newfoundland hooded seals, with an estimate of pup production and sustainable yield *ICNAF Res. Doc.*, *75*(122), 1-22.

Pálsson, Ó. K., Gislason, A., Guðfinnsson, H. G., Gunnarsson, B., Ólafsdóttir, S. R., Petursdottir, H., Sveinbjörnsson, S., Thorisson, K., & Valdimarsson, H. (2012). Ecosystem structure in the Iceland Sea and recent changes to the capelin (*Mallotus villosus*) population. *ICES Journal of Marine Science*, *69*(7), 1242-1254.

Pearson, H. C., Savoca, M. S., Costa, D. P., Lomas, M. W., Molina, R., Pershing, A. J., Smith, C. R., Villaseñor-Derbez, J. C., Wing, S. R., & Roman, J. (2022). Whales in the carbon cycle: can recovery remove carbon dioxide? *Trends in Ecology & Evolution*, *38*(3), 238-249.

Peatman, T., Vincent, M. T., Scutt Phillips, J., & Nicol, S. (2022). Times are changing, but has natural mortality? Estimation of mortality rates for tropical tunas in the western and central Pacific Ocean. *Fisheries Research*, *256*, 106463. https://doi.org/10.1016/j.fishres.2022.106463

Pershing, A. J., Christensen, L. B., Record, N. R., Sherwood, G. D., & Stetson, P. B. (2010). The impact of whaling on the ocean carbon cycle: why bigger was better. *PloS one*, *5*(8), e12444.

Pierce, G. J., Ward, N., Brownlow, A., & Santos, M. B. (2018). Analysis of historical and recent diet and strandings of sperm whales, *Physeter macrocephalus*, in the North Sea. *Centro Oceanográfico de Vigo*.

Pike, D. G., Gunnlaugsson, T., Mikkelsen, B., Halldórsson, S. D., Víkingsson, G., Acquarone, M., & Desportes, G. (2019). Estimates of the abundance of cetaceans in the Central North Atlantic from the T-NASS Icelandic and Faroese ship surveys conducted in 2007. *NAMMCO Scientific Publications*, *11*.

Pike, D. G., Gunnlaugsson, T., Mikkelsen, B., Víkingsson, G., & Desportes, G. (2020). Distribution and abundance of killer whales in the Central North Atlantic, 1987-2015. *NAMMCO Scientific Publications*, *11*. https://doi.org/10.7557/3.5579

Pinet, P. R. (2019). *Invitation to oceanography* (8 ed.). Jones & Bartlett Learning.

Ricour, F., Guidi, L., Gehlen, M., DeVries, T., & Legendre, L. (2023). Century-scale carbon sequestration flux throughout the ocean by the biological pump. *Nature Geoscience*, *16*(12), 1105-1113.

Rogan, E., Baker, J. R., Jepson, P. D., Berrow, S., & Kiely, O. (1997). A mass stranding of white-sided dolphins (*Lagenorhynchus acutus*) in Ireland: biological and pathological

studies. *Journal of Zoology*, *242*(2), 217-227. https://doi.org/10.1111/j.1469-7998.1997.tb05798.x

Roman, J., Estes, J. A., Morissette, L., Smith, C., Costa, D., McCarthy, J., Nation, J., Nicol, S., Pershing, A., & Smetacek, V. (2014). Whales as marine ecosystem engineers. *Frontiers in Ecology and the Environment*, *12*(7), 377-385.

Rugh, D. J., Hobbs, R. C., Lerczak, J. A., & Breiwick, J. M. (2005). Estimates of abundance of the eastern North Pacific stock of gray whales (*Eschrichtius robustus*) 1997-2002. *J. Cetacean Res. Manage.*, *7*(1), 1-12.

Sampson, K., Merigo, C., Lagueux, K., Rice, J., Cooper, R., Weber III, E. S., Kass, P., Mandelman, J., & Innis, C. (2012). Clinical assessment and postrelease monitoring of 11 mass stranded dolphins on Cape Cod, Massachusetts. *Marine Mammal Science*, *28*(4), E404-E425. https://doi.org/10.1111/j.1748-7692.2011.00547.x

Sergeant, D. E. (1991). *Harp seals, man and ice* (Vol. 114). Canadian Special Publications of Fisheries and Aquatic Sciences.

Sergeant, D. E., Aubin, D., & Geraci, J. R. (1980). *Life History and Northwest Atlantic Status of the Atlantic White-sided Dolphin, Lagenorhynchus Acutis*. Biological Systems, Incorporated.

Sharples, R. J., Moss, S. E., Patterson, T. A., & Hammond, P. S. (2012). Spatial variation in foraging behaviour of a marine top predator (*Phoca vitulina*) determined by a large-scale satellite tagging program. *PloS one*, *7*(5), e37216.

Sigurjónsson, J., & Víkingsson, G. A. (1997). Seasonal abundance of and estimated food consumption by cetaceans in Icelandic and adjacent waters. *Journal of Northwest Atlantic Fishery Science*, *22*.

Silva, M. A., Prieto, R., Jonsen, I., Baumgartner, M. F., & Santos, R. S. (2013). North Atlantic blue and fin whales suspend their spring migration to forage in middle latitudes: building up energy reserves for the journey? *PloS one*, *8*(10), e76507.

Six, K. D., & Maier-Reimer, E. (1996). Effects of plankton dynamics on seasonal carbon fluxes in an ocean general circulation model. *Global biogeochemical cycles*, *10*(4), 559-583.

Skern-Mauritzen, M., Lindstrøm, U., Biuw, M., Elvarsson, B., Gunnlaugsson, T., Haug, T., Kovacs, K. M., Lydersen, C., McBride, M. M., & Mikkelsen, B. (2022). Marine mammal consumption and fisheries removals in the Nordic and Barents Seas. *ICES Journal of Marine Science*, *79*(5), 1583-1603.

Smeenk, C. (1997). Strandings of sperm whales *Physeter macrocephalus* in the North Sea: history and patterns. *Bull Inst R Sci Nat Belg Biol*, *67*, 15-28.

Smith, C. R. (1992). Whale falls: chemosynthesis on the deep seafloor. *Oceanus*, *35*(3), 74-79.

Smith, C. R. (2006). Bigger is Better: The Role of Whales as detritus in Marine Ecosystems. In Estes J., DeMaster D. P., Doak D. F., Williams T. M., & Brownell R. L. J. (Eds.), *Whales, whaling and ocean ecosystems* (1 ed.). California University Press, Berkeley, CA. http://www.jstor.org/stable/10.1525/j.ctt1ppsvh

Smith, C. R., & Baco, A. R. (2003). Ecology of whale falls at the deep-sea floor. *Oceanography and marine biology*, *41*, 311-354.

Smith, C. R., Bernardino, A. F., Baco, A., Hannides, A., & Altamira, I. (2014). Seven-year enrichment: macrofaunal succession in deep-sea sediments around a 30 tonne whale fall in the Northeast Pacific. *Marine Ecology Progress Series*, *515*, 133-149.

Smith, C. R., Kukert, H., Wheatcroft, R. A., Jumars, P. A., & Deming, J. W. (1989). Vent fauna on whale remains. *Nature*, *341*(6237), 27-28.

Smith, L. A., Link, J. S., Cadrin, S. X., & Palka, D. L. (2015). Consumption by marine mammals on the Northeast US continental shelf. *Ecological Applications*, *25*(2), 373-389.

Smith, T. G. (1973). Population dynamics of the ringed seal in the Canadian Eastern Arctic. *Bulletin - Fisheries Research Board of Canada*, *181*.

Smith, T. G., & Stirling, I. (2019). Predation of harp seals, *Pagophilus groenlandicus*, by polar bears, *Ursus maritimus*, in Svalbard. *Arctic*, *72*(2), 197-202.

Solvang, H. K., Skaug , H. J., & Øien, N. I. (2018). Preliminary abundance estimates of common minke whales in Svalbard 2014, the Norwegian Sea and Jan Mayen 2015, and the Barents Sea 2017 - the first four years of the survey cycle 2014-2019 in the Northeast Atlantic (including extension survey NASS2015 Jan Mayen) [Working paper]. 10.

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

Stirling, I., & Archibald, W. R. (1977). Aspects of predation of seals by polar bears. *Journal of the Fisheries Board of Canada*, *34*(8), 1126-1129.

Sundby, S., Drinkwater, K. F., & Kjesbu, O. S. (2016). The North Atlantic spring-bloom system—where the changing climate meets the winter dark. *Frontiers in Marine Science*, *3*, 28.

Taylor, B. L., Martinez, M., Gerrodette, T., Barlow, J., & Hrovat, Y. N. (2007). Lessons from monitoring trends in abundance of marine mammals. *Marine Mammal Science*, *23*(1), 157-175.

Teilmann, J., & Galatius, A. (2018). Harbor seal: *Phoca vitulina*. In *Encyclopedia of marine mammals* (pp. 451-455). Elsevier.

Thiemann, G. W., Iverson, S. J., & Stirling, I. (2008). POLAR BEAR DIETS AND ARCTIC MARINE FOOD WEBS: INSIGHTS FROM FATTY ACID ANALYSIS. *Ecological Monographs*, *78*(4), 591-613. https://doi.org/10.1890/07-1050.1

Tollit, D., Black, A., Thompson, P., Mackay, A., Corpe, H., Wilson, B., Van Parijs, S., Grellier, K., & Parlane, S. (1998). Variations in harbour seal *Phoca vitulina* diet and dive-depths in relation to foraging habitat. *Journal of Zoology*, *244*(2), 209-222.

Vacquié-Garcia, J., Lydersen, C., Biuw, M., Haug, T., Fedak, M. A., & Kovacs, K. M. (2017a). Hooded seal *Cystophora cristata* foraging areas in the Northeast Atlantic Ocean—Investigated using three complementary methods. *PloS one*, *12*(12), e0187889.

Vacquié-Garcia, J., Lydersen, C., Marques, T. A., Aars, J., Ahonen, H., Skern-Mauritzen, M., Øien, N., & Kovacs, K. M. (2017b). Late summer distribution and abundance of ice-associated whales in the Norwegian High Arctic. *Endangered Species Research*, *32*, 59-70. https://doi.org/10.3354/esr00791

Verborgh, P., Gauffier, P., Esteban, R., & de Stephanis, R. (2021). Demographic parameters of a free-ranging deep-diving cetacean, the long-finned pilot whale. *Marine Mammal Science*, *37*(2), 463-481.

Vetter, E. F. (1971). Estimation of natural mortality in fish stocks: a review. *Fishery Bulletin*, *86*(1-2), 25.

Víkingsson, G. A., Pike, D. G., Valdimarsson, H., Schleimer, A., Gunnlaugsson, T., Silva, T., Elvarsson, B. Þ., Mikkelsen, B., Øien, N., & Desportes, G. (2015). Distribution, abundance, and feeding ecology of baleen whales in Icelandic waters: have recent environmental changes had an effect? *Frontiers in Ecology and Evolution*, *3*, 6.

Wang, B. (2021). An overview of the ecology of whale fall. *Biol. Teach. China*, *46*, 62-63.

Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M. L., Hop, H., Gabrielsen, G. W., Falk-Petersen, S., Denisenko, S. G., & Arashkevich, E. (2006). Food webs and carbon flux in the Barents Sea. *Progress in Oceanography*, *71*(2-4), 232-287.

Williams, T. M., Estes, J. A., Doak, D. F., & Springer, A. M. (2004). KILLER APPETITES: ASSESSING THE ROLE OF PREDATORS IN ECOLOGICAL COMMUNITIES. *Ecology*, *85*(12), 3373-3384. https://doi.org/10.1890/03-0696

Winters, G. (1976). *Estimation of mortality rates and surplus production of Northwest Atlantic harp seals*. International Commission for the Northwest Atlantic Fisheries.

Witting, L., & Born, E. W. (2005). An assessment of Greenland walrus populations. *ICES Journal of Marine Science*, *62*(2), 266-284. https://doi.org/10.1016/j.icesjms.2004.11.001

Appendix A

Table S1: Hoenig longevity calculations based on maximum age (years) to find natural mortality rates of cetaceans. Source: Hoenig (2005).

maxage	natmort	maxage	natmort	maxage	natmort
1,00853258	2,46646125	9,04096355	0,6711609	14,9344789	0,20150281
1,00461596	1,4695838	9,01855852	0,4824196	15,9512677	0,45645654
2,02371813	2,3675511	9,00585313	0,39989567	15,9305921	0,38409571
2,00704936	1,90457769	8,99620901	0,34675541	15,9896936	0,2599864
2,48809869	1,10006239	9,03365883	0,2492341	15,8678311	0,22714354
2,98581124	0,69536998	10,0430442	1,41016245	16,913794	0,39272635
2,97628519	1,09909929	10,0091208	0,89892068	16,9889931	0,29306901
2,99778988	1,18471567	9,99953008	0,79125446	18,9997994	0,62505261
3,98808978	1,2009546	10,0638317	0,76783086	18,9100117	0,33277423
3,98561669	1,10579893	10,0570238	0,70170732	18,8557048	0,22695204
3,98157312	0,9660772	10,045121	0,59939662	17,9826735	0,19981473
4,005595	0,8895028	9,96462978	0,49687842	19,9968724	0,19971105
4,49707476	1,31335627	9,95003045	0,40880177	21,9980409	0,27771961
4,93485557	1,31275994	9,99370489	0,3027844	21,8008616	0,20264561
4,99458178	1,11290037	9,94087002	0,14954618	21,7922576	0,19227521
4,99120308	1,01706037	11,0740824	1,10857651	22,0050716	0,11983121
4,95372223	0,90201705	10,9927824	1,00556715	24,7682945	0,60125318
4,94925465	0,79996074	11,0229925	0,59912446	25,0930501	0,24065856
5,48048479	1,10407841	11,0913734	0,5641959	23,1398385	0,19956857
6,01399851	1,1035771	10,8934296	0,30039398	25,0506346	0,19214427
6,00518731	0,90795706	12,0296205	0,69585138	25,0379239	0,17959542
6,00247877	0,8550515	12,0599594	0,40233327	24,0511834	0,17043779
5,96009207	0,80525481	11,9377146	0,25076959	22,9492425	0,16054304
5,9473339	0,60546132	11,9968771	0,20021052	27,0749031	0,14881543
5,97984264	0,51716675	13,0830924	0,51133913	30,731895	0,16152164
6,99490875	0,90049675	12,98265	0,44340405	29,9427005	0,02962754
6,98938854	0,8106891	12,9694786	0,38737833	33,9060051	0,13687323
6,98229753	0,70825558	12,9344201	0,27020732	37,8158862	0,08399155
6,97285404	0,59152199	13,0007214	0,22064115	44,1602841	0,11676516
6,96695834	0,52854741	12,9626542	0,14935225	47,1845983	0,11498843
6,91607069	0,19924944	13,9318687	0,32099784	44,5488071	0,06405525
8,03127057	0,76867821	13,881678	0,19857191	44,8276924	0,06077525
8,02810091	0,72934106	14,9819973	0,74367595	50,3677237	0,09967581
7,9748573	0,30085233	14,8994291	0,35644214	55,2086146	0,08574523
7,95105786	0,20212476	14,9859405	0,31848429	61,6375462	0,06022702
9,06189105	0,91295833	14,9783367	0,29768424	63,6844815	0,05628449
9,05933633	0,87933692	14,9445885	0,2204909	71,9541709	0,08004132

70,9335449	0,06993235
74,3059915	0,06991647
73,7729564	0,06486378
77,2760415	0,06436422
83,5252023	0,05022549
79,0731258	0,04011095
89,6978305	0,04008624
100,522043	0,04655201
110,369876	0,05015711
113,906633	0,04034106
121,728114	0,04063175
80,8922324	0,01000584

Appendix B

Table S2: Abundances and Coefficients of Variation (CV) for marine mammal species in the three regions ICE **(A),** GN **(B)** and BS **(C).**
Numbers in italics represents best guesses. A CV = 0.5 has been assigned to abundances where no CV was available. Source: Skern-Mauritzen *et al.* (2022)

A. ICE

	Species	ICE	Comments	Reference
Pinnipeds	Ringed seal	*200 000 (0.5)*		Aqqalu Rosing-Asvid, Greenland Institute of Natural Resources, pers. comm.
	Bearded seal	*20 000 (0.5)*		Aqqalu Rosing-Asvid, Greenland Institute of Natural Resources, pers. comm..
	Harp seal	740 000 (0.5)	10% of the NW Atlantic harp seal stock migrates into the ICE area annually. Also based on newer telemetry literature.	Hammill and Stenson (2014), Mike Hammill, Department of Fisheries and Oceans, pers. comm.
	Hooded seal	593 500 (0.11)		Hammill and Stenson (2006)
	Atlantic walrus	0		
	White whale	0		
Odontocetes	Narwhal	*2 500 (0.5)*		Hansen *et al.* (2019)
	Killer whale	5 478 (0.36)		Re-estimated, Thorvaldur Gunnlaugsson, MFRI, Iceland, based on Pike *et al.* (2020)
	Sperm whale	4 272 (0.55)		Re-estimated, Thorvaldur Gunnlaugsson, MFRI, Iceland, based on Gunnlaugsson *et al.* (2009)
	Lagenorhynchus dolphins	136 889 (0.46)		Pike *et al.* (2019); Sigurjónsson and Víkingsson (1997)
	Long-finned pilot whale	210 000 (0.44)		Pike *et al.* (2019)
	Harbour porpoise	44 821 (0.44)		Re-estimated, Thorvaldur Gunnlaugsson. MFRI, Iceland, based on Gilles *et al.* (2020)
	Northern bottlenose whale	6 500 (0.55)		Re-estimated, Thorvaldur Gunnlaugsson, MFRI, Iceland, based on Pike *et al.* (2019)

Mysticetes			
	Common minke whale	48 016 (0.23)	Re-estimated, Thorvaldur Gunnlaugsson, MFRI, Iceland, based on Pike *et al.* (2019)
	Fin whale	29 940 (0.16)	Re-estimated, Thorvaldur Gunnlaugsson, MFRI, Iceland, based on Pike *et al.* (2019)
	Humpback whales	12 523 (0.30)	Re-estimated, Thorvaldur Gunnlaugsson, MFRI, Iceland, based on Pike *et al.* (2019)
	Blue whale	2 450 (0.42)	Re-estimated, Thorvaldur Gunnlaugsson, MFRI, Iceland, based on Pike *et al.* (2019)
	Sei whale	4 200 (0.70)	Re-estimated, Thorvaldur Gunnlaugsson, MFRI, Iceland, based on Borchers and Burt (1997)
	Bowhead whale	0	

B. GN

	Species	GN	Comments	Reference
Pinnipeds	Ringed seal	*100 000*		Aqqalu Rosing-Asvid, Greenland Institute of Natural Resources, pers. comm.
	Bearded seal	*10 000*		Aqqalu Rosing-Asvid, Greenland Institute of Natural Resources, pers. comm.
	Harp seal	426 808 (0.14)		ICES (2019)
	Hooded seal	76 623 (0.12)		ICES (2019)
	Atlantic walrus	1 429 (0.33)		Born *et al.* (2009)
	White whale	0		
Odontocetes	Narwhal	6 444 (0.37)		Heide-Jørgensen *et al.* (2010)
	Killer whale	6 154 (0.58)		(Leonard & Øien, 2020a)
	Sperm whale	2 708 (0.48)		Leonard and Øien (2020a)
	Lagenorhynchus dolphins	28 168 (0.57)		Leonard and Øien (2020b)
	Long-finned pilot whale	*5 000 (0.5)*		Bjarni Mikkelsen, pers. com.
	Harbour porpoise	5 266 (0.47)		Leonard and Øien (2020b)
	Northern bottlenose whale	617 (0.74)		Leonard and Øien (2020a)
Mysticetes	Common minke whale	48 913 (0.26)	Recombination of results from survey strata, (Nils Øien, IMR)	Solvang *et al.* (2018)
	Fin whale	8 504 (0.33)	Recombination of results from survey strata, (Nils Øien, IMR)	Leonard and Øien (2020a)
	Humpback whale	1808 (0.62)		Leonard and Øien (2020a)
	Blue whale	*100 (0.50)*	Very few individuals observed	Nils Øien, IMR, Norway, pers. comm.
	Sei whale	0	Very few individuals observed	Nils Øien, IMR, Norway, pers. comm.
	Bowhead whale	173 (0.49)	A total population of 347 shared equally between GN and BS regions	Vacquié-Garcia *et al.* (2017b)

C. BS

	Species	BS	Comments	Reference
Pinnipeds	Ringed seal	*100 000 (0.50)*		Kovacs *et al.* (2009)
	Bearded seal	*10 000 (0.50)*		Kovacs *et al.* (2009)
	Harp seal	1 497 189 (0.07)		ICES (2019)
	Hooded seal	0		
	Atlantic walrus	*14 000 (0.5)*	Svalbard + Pechora Sea + Franz Josef Land	Kit M. Kovacs, Norwegian Polar Institute, pers. com; Kovacs *et al.* (2014); Lydersen *et al.* (2012a)
	White whale	*10 000* (0.50)		Kovacs *et al.* (2009)
Odontocetes	Narwhal	*3 500(0.50)*		Vacquié-Garcia *et al.* (2017b), Hansen *et al.* (2019)
	Killer whale	503 (0.71)		Leonard and Øien (2020a)
	Sperm whale	806 (0.71)		Leonard and Øien (2020a)
	Lagenorhynchus dolphins	144 453 (0.53)		Leonard and Øien (2020a)
	Long-finned pilot whale	*500 (0.5)*	Few groups observed	Nils Øien, IMR, Norway, pers. comm.; Bjarni Mikkelsen, Natural History Museum, The Faroes. pers. comm.; Leonard & Øien (2020a)
	Harbour porpoise	85 731 (0.57)		
	Northern bottlenose whale	*100 (0.5)*	Very few individuals observed	Nils Øien, Insitute of Marine Research, pers. comm
Mysticetes	Common minke whale	47 295 (0.30)		Re-estimated, Nils Øien, IMR, Norway
	Fin whale	4 506 (0.54)		Leonard and Øien (2020a)
	Humpback whale	8 563 (0.81)		Leonard and Øien (2020a)
	Blue whale	*100* (0.50)	Very few individuals observed	Nils Øien, IMR, Norway, pers. comm
	Sei whale	0		
	Bowhead whale	173 (0.49)	A total population of 347 is shared equally between GN and BS regions	Vacquié-Garcia *et al.* (2017)

Appendix C

Table S3: Mean biomass (and 95% CI) in 1000 tons of marine mammals in ICE, GN and BS regions. The columns for ICE and GN regions are swapped in Skern-Mauritzen *et al.* (2022), but have been corrected in this table (pers. comm. Mette Skern-Mauritzen, 26. April 2024).

Species	ICE	GN	BS
Ringed seal	15.4 (4.9, 37.7)	7.5 (2.4, 18.1)	7.5 (2.4, 17.9)
Bearded seal	5.1 (1.6, 12)	2.5 (0.8, 5.8)	2.5 (0.8, 5.8)
Harp seal	89.2 (28.3, 207.2)	51.6 (28.7, 79.3)	182 (104, 264.5)
Hooded seal	147.7 (90.3, 216.2)	19.2 (11.2, 29.8)	0 (0, 0)
Atlantic walrus	0 (0, 0)	1.7 (0.7, 3.2)	14.2 (4.6, 33.5)
White whale	0 (0, 0)	0 (0, 0)	13.5 (4.4, 32.6)
Narwhal	3.2 (1, 7.3)	8.3 (2.9, 17.4)	4.5 (1.5, 10.5)
Killer whale	24.3 (8.8, 53)	27 (7.2, 71.7)	2.2 (0.4, 6.5)
Sperm whale	172.2 (49.3, 437.5)	107.2 (36.1, 254.1)	31.4 (6.3, 88.4)
Lagenorhynchus dolphins	28.9 (10.1, 67.1)	6 (1.7, 15.5)	31.5 (9, 82)
Pilot whale	350.8 (132.3, 789.7)	8.7 (2.8, 20)	0.9 (0.3, 2.2)
Harbour porpoise	2.4 (0.9, 5.1)	0.3 (0.1, 0.6)	4.9 (1.4, 12.6)
Bottlenose whale	38.6 (10.2, 100.1)	0.6 (0.1, 1.8)	0
Minke whale	312.2 (151.4, 526.2)	320.1 (145.2, 564.4)	304 (135, 580.1)
Fin whale	1673.7 (987.8, 2653.4)	476.5 (191.4, 908.4)	250.8 (69.7, 617.9)
Humpback whale	379.4 (173.4, 705.8)	54.3 (14.2, 145.6)	268.1 (48.4, 881.6)
Blue whale	245.5 (84.9, 536.1)	10.2 (3.3, 24.6)	9.9 (3.2, 23.1)
Sei whale	72.1 (15.8, 211.3)	1.6 (0.5, 3.7)	0 (0, 0)
Bowhead whale	0 (0, 0)	14.0 (4.4, 32.6)	14.0 (4.4, 33.4)

Appendix D

Estimating uncertainty measures

Standard Deviation (σ):

The standard deviation is a measure of the amount of variation or dispersion in a set of values. For population estimates, it quantifies the extent to which individual data points in the population differ from the population mean. The standard deviation (σ) for a population is calculated using this formula:

$$\sigma = \sqrt{\frac{1}{N}\sum_{i=1}^{N}(x_i - \mu)^2} \tag{10}$$

In this equation x_i represents each data point in the population, μ represents the mean of the population, and N is the sample size of the population.

Coefficient of variation (CV):

The coefficient of variation (CV) is a statistical measure of the relative dispersion or variability of data points around the mean in a dataset. The CV is defined as the ratio of the standard deviation to the mean of a distribution, often displayed as a percentage. Hence, $CV = \frac{\mu}{\sigma}$ where the μ represents the mean and σ the standard deviation (SD). The CV is used to assess the variability of the results to estimate uncertainty in the dataset. It provides a standardized measure of dispersion, making it particularly useful when comparing the spread of data sets that have different units or vastly different mean values. To calculate the coefficient of variation (CV) for the sum of several values, each with specified means and CVs, their variances must be added together. To estimate the variances from the CV, the standard deviation σ is estimated using $\sigma = CV \times \mu$, and then the variance for each value is calculated using $Var = \sigma^2$. The variances and the means are added together, to find the variance and mean of the sum. The standard deviation of the sum is calculated as the square root of the total variance using $\sigma_{1,2} = \sqrt{Var(XY)}$. The CV of the sum is calculated by:

$$CV = \frac{\sigma_{sum}}{\mu_{sum}} \tag{11}$$

When multiplying two random variables, each with their own mean and CV, the mean of the product is given by $\mu_{1,2} = \mu_1 \times \mu_2$. The sum of the means gives the mean of the sum, and the sum of the variances gives the variance of the sum, assuming independence between the values. The variance of the sum can be calculated using:

$$Var(XY) \approx (\mu_X^2 Var(Y) + \mu_Y^2 Var(X) + Var(X)Var(Y)) \tag{12}$$

95% confidence intervals:

A confidence interval (CI) is a range of values, derived from the sample data, that is used to estimate an unknown population parameter. The interval has an associated confidence level that quantifies the probability that the parameter lies within the interval. For example, a 95% confidence interval, which is the most common interval for scientific studies, suggests that if the same data collection and analysis were repeated numerous times, the interval would capture the true population parameter in 95% of those instances. Confidence intervals are used to indicate the reliability of an estimate and provide a range around the sample value to express the degree of uncertainty associated with the sample size used and the variability in the data. A narrower interval reflects more certainty in the estimate of the population parameter. Confidence intervals are commonly used in both research and statistics for hypothesis testing and to report the robustness of experimental results. To multiply a value with its own mean μ and 95%CI with a constant k, the operation affects both the mean and the bounds of the CI in a straightforward manner. The first step is to multiply the means $\mu_{new} = k \times \mu$ and then the confidence intervals:

$$CI_{new\ lower} = k \times CI_{lower} \text{ and } CI_{new\ upper} = k \times CI_{upper} \tag{13}$$

If k is positive, the relative positions (i.e. lower and upper bounds) of the CI remain the same, and if k is negative, the CI bounds flip because multiplying by a negative number reverses inequalities. Thus, the new CI would become $[k \times CI_{upper}, k \times CI_{lower}]$.

Table S4: Residency fractions for each species in the three study regions ICE, GN, and BS. Biomass multiplied by the residency fraction for each species in the three study regions, as well as the lower and upper 95% confidence intervals.

	SPECIES	RESIDENCY FRACTION ICE	RESIDENCY FRACTION GN	RESIDENCY FRACTION BS	BIOMASS × RESIDENCY ICE (KG)	LOWER 95%CI ICE (KG)	UPPER 95%CI ICE (KG)	BIOMASS × RESIDENCY GN (KG)	LOWER 95%CI GN (KG)	UPPER 95%CI GN (KG)	BIOMASS × RESIDENCY BS (KG)	LOWER 95%CI BS (KG)	UPPER 95%CI BS (KG)
PINNIPEDS	RINGED SEAL	1	1	1	15000000	4900000	37700000	7500000	2400000	18100000	7500000	2400000	17900000
	BEARDED SEAL	1	1	1	5000000	1600000	12000000	2500000	800000	5800000	2500000	800000	5800000
	HARP SEAL	0.41	1	1	36408000	11603000	84952000	51216960	104000000	79300000	179662680	104000000	264500000
	HOODED SEAL	0.08	1	0	11870000	7224000	17296000	18405750	0	29800000	0	0	0
	ATLANTIC WALRUS	0	1	1	0	0	0	1714800	4600000	3200000	18000000	4600000	33500000
ODONTOCETES	WHITE WHALE	0	0	1	0	0	0	0	4400000	0	6750000	4400000	32600000
	NARWHAL	1	1	1	3250000	1000000	7300000	8377200	1500000	17400000	4550000	1500000	10500000
	KILLER WHALE	1	1	1	24103200	8800000	53000000	27077600	400000	71700000	2213200	400000	6500000
	SPERM WHALE	0.4	0.4	0.4	68352000	19720000	175000000	43328000	2520000	101640000	12896000	2520000	35360000
	LAGENORHYNCHUS DOLPHINS	1	1	1	28746690	10100000	67100000	5915280	9000000	15500000	30335130	9000000	82000000
	PILOT WHALE	0.75	0.66	0.5	267750000	99225000	592275000	5610000	150000	13200000	425000	150000	1100000
	HARBOUR PORPOISE	1	1	1	2465155	900000	5100000	289630	400000	600000	4715205	400000	12600000
	NORTHERN BOTTLENOSE WHALE	0.41	0.41	0	15990000	4182000	41041000	1517820	0	738000	0	0	0

MYSTICETES	**MINKE WHALE**	0.5	0.5	0.5	158452800	75700000	263100000	161412900	67500000	282200000	156073500	67500000	290050000
	FIN WHALE	0.5	0.5	0.5	830835000	493900000	1326700000	235986000	34850000	454200000	125041500	34850000	308950000
	HUMPBACK WHALE	0.5	0.5	0.5	190349600	86700000	352900000	27481600	24200000	72800000	130157600	24200000	440800000
	BLUE WHALE	0.5	0.5	0.5	122500000	42450000	268050000	5000000	1600000	12300000	5000000	1600000	11550000
	SEI WHALE	0.25	0.25	0	17850000	3950000	52825000	425000	0	925000	0	0	0
	BOWHEAD WHALE	0	1	1	0	0	0	13840000	4400000	32600000	13840000	4400000	33400000

Table S5: Biomass export for each species in the three study regions ICE, GN, and BS, as well as the lower and upper 95% confidence intervals. Biomass export outside each study region and total biomass export outside the study area. All data values are showed in tonnes, rounded to the closest whole number.

	SPECIES	BIOMASS EXPORT ICE	LOWER 95%CI ICE	UPPER 95%CI ICE	BIOMASS EXPORT GN	LOWER 95%CI GN	UPPER 95%CI GN	BIOMASS EXPORT BS	LOWER 95%CI BS	UPPER 95%CI BS	BIOMASS EXPORT OUTSIDE ICE REGION	BIOMASS EXPORT OUTSIDE GN REGION	BIOMASS EXPORT OUTSIDE BS REGION	TOTAL BIOMASS EXPORT OUTSIDE STUDY AREA
PINNIPEDS	RINGED SEAL	1650	539	4147	825	264	1991	825	264	1969	0	0	0	0
	BEARDED SEAL	480	154	1152	240	77	557	240	77	557	0	0	0	0
	HARP SEAL	4187	1334	9769	5890	3301	9120	20661	11960	30418	6025	0	0	6025
	HOODED SEAL	1424	867	2076	2209	1344	3576	0	0	0	16381	0	0	16381
	ATLANTIC WALRUS	0	0	0	103	42	192	1080	276	2010	0	0	0	0
ODONTOCETES	WHITE WHALE	0	0	0	0	0	0	473	308	2282	0	0	0	0
	NARWHAL	16	5	37	42	15	87	23	8	53	0	0	0	0
	KILLER WHALE	627	229	1378	704	187	1864	58	10	169	0	0	0	0
	SPERM WHALE	1504	434	3850	953	318	2236	284	55	778	2256	1430	426	4111
	LAGENOR-HYNCHUS DOLPHINS	4700	1651	10971	967	278	2534	4960	1472	13407	0	0	0	0
	PILOT WHALE	7497	2778	16584	157	52	370	12	4	31	2499	81	12	2592
	HARBOUR PORPOISE	328	120	678	39	13	80	627	53	1676	0	0	0	0
	NORTHERN BOTTLENOSE WHALE	1855	485	4761	176	5	86	0	0	0	2669	253	0	2923
MYSTICETI	MINKE WHALE	7289	3482	12103	7425	3340	12981	7179	3105	13342	7289	7425	7179	21893

|												
FIN WHALE	36557	21732	58375	10383	4211	19985	5502	1533	13594	36557	10383	5502	52442
HUMPBACK WHALE	8185	3728	15178	1182	305	3130	5597	1041	18954	8185	1182	5597	14964
BLUE WHALE	5513	1910	12062	225	74	554	225	72	520	5513	225	225	5963
SEI WHALE	750	166	2219	18	5	39	0	0	0	2249	54	0	2303
BOWHEAD WHALE	0	0	0	554	176	1304	554	176	1336	0	0	0	0

Table S7: Organic carbon export for each species in the three study regions ICE, GN, and BS, as well as the lower and upper 95% confidence intervals. Organic carbon export outside each study region and total organic carbon export outside the study area. All data values are showed in tonnes, rounded to the closest whole number or one decimal for low numbers.

	SPECIES	ORGANIC CARBON EXPORT ICE	LOWER 95%CI ICE	UPPER 95%CI ICE	ORGANIC CARBON EXPORT GN	LOWER 95%CI GN	UPPER 95%CI GN	ORGANIC CARBON EXPORT BS	LOWER 95%CI BS	UPPER 95%CI BS	BIOMASS EXPORT OUTSIDE ICE REGION	BIOMASS EXPORT OUTSIDE GN REGION	BIOMASS EXPORT OUTSIDE BS REGION	TOTAL BIOMASS EXPORT OUTSIDE STUDY AREA
PINNIPEDS	RINGED SEAL	272	89	684	136	44	329	136	44	325	0	0	0	0
	BEARDED SEAL	79	25	190	40	13	92	40	13	92	0	0	0	0
	HARP SEAL	691	220	1612	972	545	1505	3409	1973	5019	994	0	0	994
	HOODED SEAL	235	143	342	364	222	590	0	0	0	2703	0	0	2703
	ATLANTIC WALRUS	0	0	0	17	6.9	32	178	46	332	0	0	0	0
ODONTOCETES	WHITE WHALE	0	0	0	0	0	0	78	51	377	0	0	0	0
	NARWHAL	3	0.8	6.0	6.9	2.4	14	3.8	1.2	8.7	0	0	0	0
	KILLER WHALE	103	38	227	116	31	308	9.5	1.7	28	0	0	0	0
	SPERM WHALE	248	72	635	157	52	369	47	9.1	128	372	236	7.0	678
	LAGENOR-HYNCHUS DOLPHINS	776	272	1810	160	46	418	818	243	2212	0	0	0	0
	PILOT WHALE	1237	458	2736	26	8.5	61	2.0	0.7	5.1	412	13	2.0	428
	HARBOUR PORPOISE	54	20	112	6.3	2.2	13	104	8.8	277	0	0	0	0
	NORTHERN BOTTLENOSE WHALE	306	80	786	29	0.8	14	0	0	0	440	42	0	482
MYST ICET	MINKE WHALE	1203	575	1997	1225	551	2142	1185	512	2201	1203	1225	1185	3612

FIN WHALE	6032	3586	9632	1713	695	3297	908	253	2243	6032	1713	908	8653
HUMPBACK WHALE	1351	615	2504	195	50	517	923	172	3127	1351	195	923	2469
BLUE WHALE	910	315	1990	37	12	91	37	12	86	910	37	37	984
SEI WHALE	124	27	366	3.0	0.9	6.4	0	0	0	371	8.8	0	380
BOWHEAD WHALE	0	0	0	91	29	215	91	29	220	0	0	0	0

Appendix F
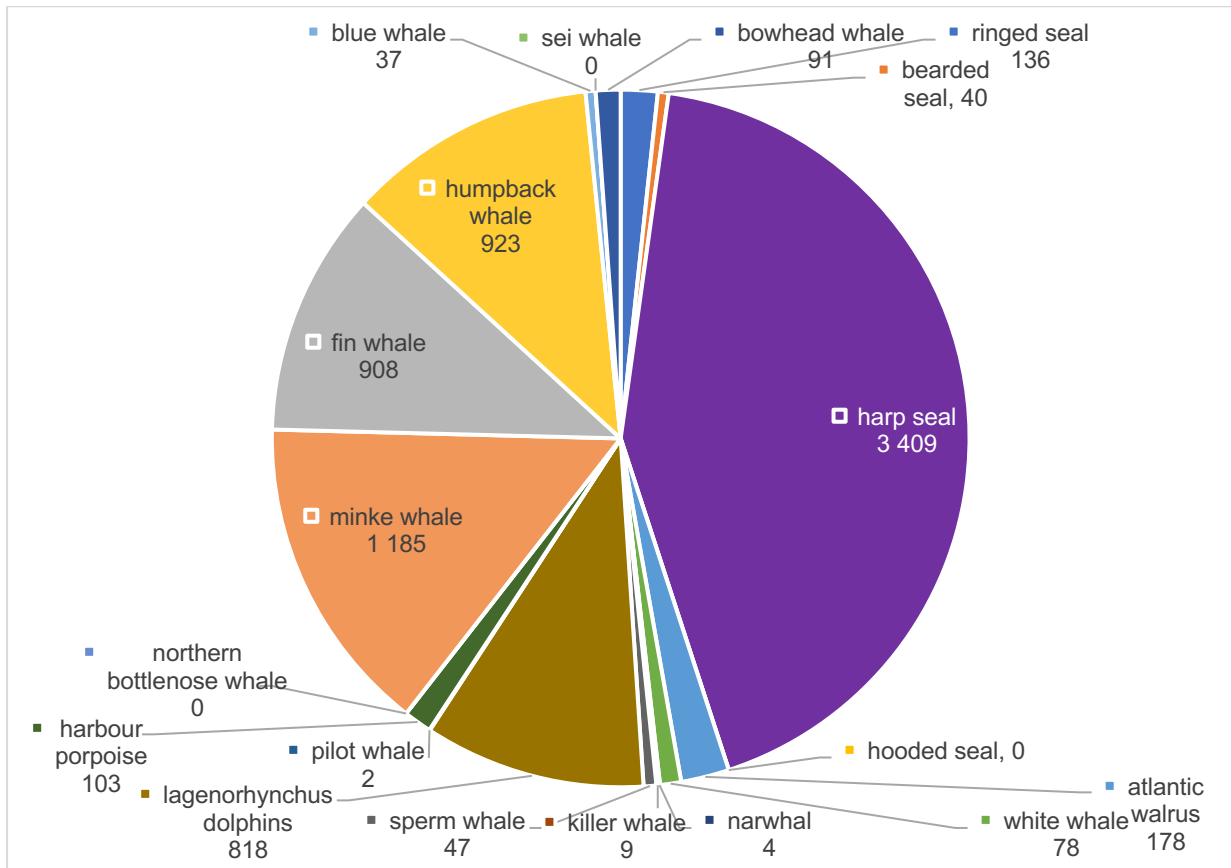
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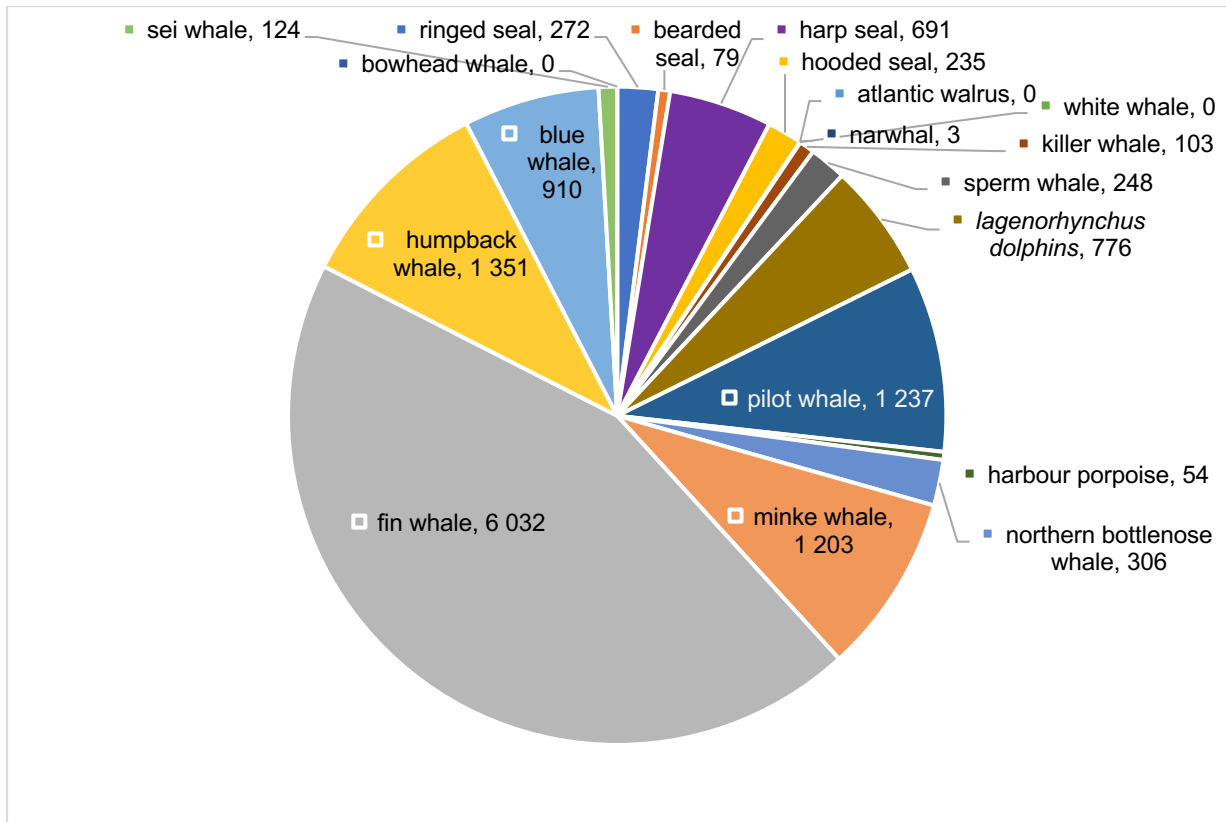
B. GN
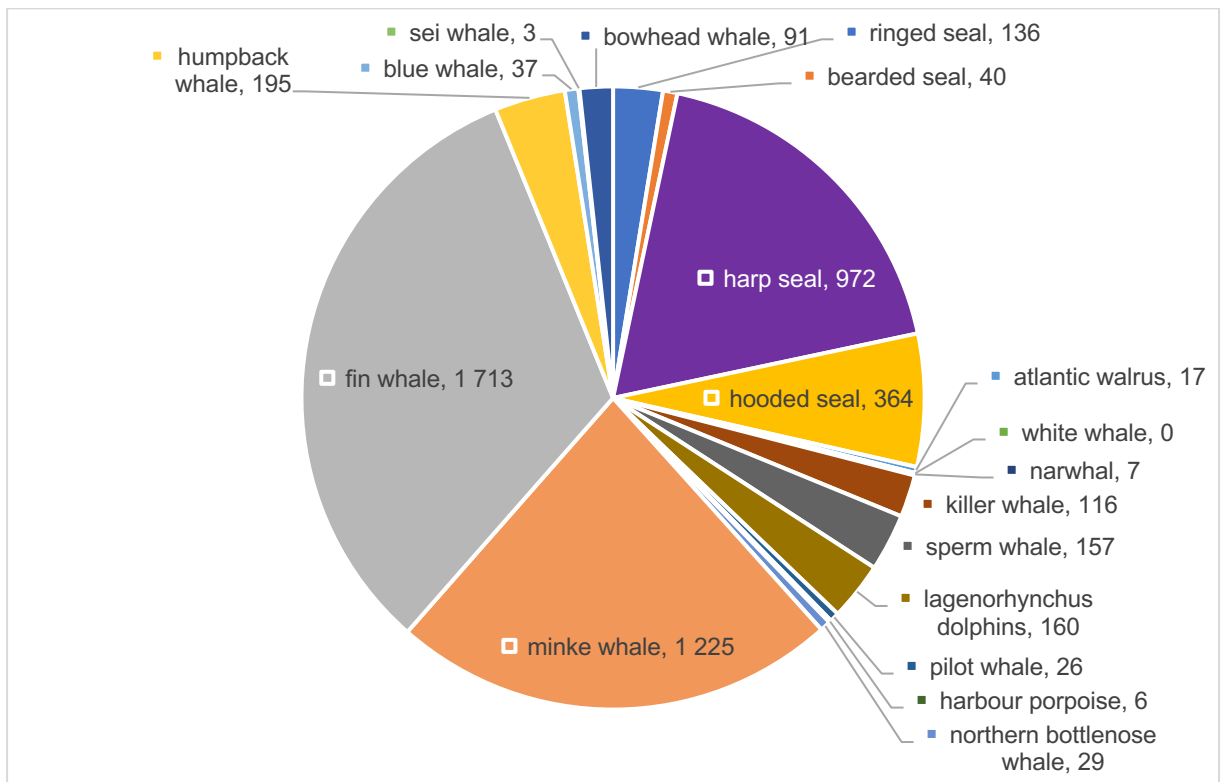
C. BS

Figure S1: Total organic carbon export (tonnes) per species for the three study regions ICE **(A),** GN **(B),** and BS **(C).**