




Marine mammal consumption and fisheries removals in the Nordic and Barents Seas

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In this study, we assess prey consumption by the marine mammal community in the northeast Atlantic [including 21 taxa, across three regions: (I) the Icelandic shelf, Denmark Strait, and Iceland Sea (ICE); (II) the Greenland and Norwegian Seas (GN); and (III) the Barents Sea (BS)], and compare mammal requirements with removals by fisheries. To determine prey needs, estimates of energetic requirements were combined with diet and abundance information for parameterizing simple allometric scaling models, taking uncertainties into account through bootstrapping procedures. In total, marine mammals in the ICE, GN, and BS consumed 13.4 [Confidence Interval (CI): 5.6–25.0], 4.6 (CI: 1.9–8.6), and 7.1 (CI: 2.8–13.8) million tonnes of prey year⁻¹. Fisheries removed 1.55, 1.45, and 1.16 million tonnes year⁻¹ from these three areas, respectively. While fisheries generally operate at significantly higher trophic levels than marine mammals, we find that the potential for direct competition between marine mammals and fisheries is strongest in the GN and weakest in the BS. Furthermore, our results also demonstrate significant changes in mammal consumption compared to previous and more focused studies over the last decades. These changes likely reflect both ongoing population recoveries from historic whaling and the current rapid physical and biological changes of these high-latitude systems. We argue that changing distributions and abundances of mammals should be considered when establishing fisheries harvesting strategies, to ensure effective fisheries management and good conservation practices of top predators in such rapidly changing systems.

Keywords: Barents Sea, consumption, competition, ecosystem based fisheries management, Greenland Sea, Iceland Sea, Marine mammals, Norwegian Sea, prey use.

Introduction

There is general agreement that fisheries need to be managed within an ecosystem-based context rather than applying the traditional single-species approach (Pikitch *et al.*, 2004; Essington and Punt, 2011; Nilsson *et al.*, 2016; Arthur *et al.*, 2018). Effective ecosystem-based fisheries management (EBFM) should balance trade-offs between potentially conflicting demands for services that harvested species provide to humans through commercial fisheries vs. the services that species provide ecologically through foodweb interactions (Beddington *et al.*, 1985; DeFries *et al.*, 2004; Leslie and McLeod, 2007). Foreseeing potential interactions and trade-offs between marine mammal prey requirements and fisheries is a classic example of the challenge to EBFM approaches in marine systems around the world (e.g. Beddington *et al.*, 1985; Trites *et al.*, 1997; Read, 2008; Chasco *et al.*, 2017; Arthur *et al.*, 2018).

Impacts of fisheries on marine mammals, impacts of marine mammals on fisheries, and the consequences of associated management interventions, are heavily debated in both scientific and political arenas (e.g. Kaschner and Pauly, 2005; Corkeron, 2009; Morissette *et al.*, 2012; Bowen and Lidgard, 2013; Pauly *et al.*, 2016). These debates are expected to intensify concomitant with marine mammal population recoveries following cessation of historically non-sustainable harvests, and increased human exploitation of marine resources; particularly harvests targeting lower trophic levels (TLs) (e.g. Schipper *et al.*, 2008; Kaschner *et al.*, 2011; Morissette *et al.*, 2012; Magera *et al.*, 2013; Bogstad *et al.*, 2015; SAPEA, 2017). Some modelling studies have suggested that competition between marine mammals and fisheries is theoretically possible, although quantification of the effects has proven problematic (e.g. Stefánsson *et al.*, 1997; Mackinson *et al.*, 2003; Schweder, 2006; Morissette *et al.*, 2012; Hansson *et al.*, 2018). Although it is generally accepted that marine mammals, like other predators, rarely if ever deplete prey stocks to critical levels, they may impede recovery of fish stocks depleted via overfishing (Bundy *et al.*, 2009; O'Boyle and Sinclair, 2012; Cook and Trijoulet, 2016; Swain *et al.*, 2019). Interactions between marine mammals and fisheries are typically system specific and the potential for direct competitive interactions between them is related to harvesting intensity, TLs targeted by the fisheries (e.g. large predatory fish, forage fish, and/or zooplankton), diets and dietary ranges of marine mammals, functional form of marine mammal prey interactions, and ecosystem complexity in terms of number of species and trophic linkages (Mackin-

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Table 1. Marine mammal species regularly occurring in the Nordic and Barents Seas, categorized as year-round residents (Residents) or summer migrants (Migrants).

	Species	Residency status	Residence time, days yr ^{-1a}	Body mass, kg	Ocean zone	
Pinnipeds	Harbour seal	Resident	365	90	Coastal	
	Grey seal	Resident	365	200	Coastal	
	Ringed seal	Resident	365	75	High Arctic	
	Bearded seal	Resident	365	250	High Arctic	
	Harp seal	Resident	150/365/365	120	Arctoboreal	
	Hooded seal	Resident	30/365/0	250	Arctoboreal	
	Atlantic walrus	Resident	0/365/365	1 200	High Arctic	
Odontocetes	White whale	Resident	0/0/365	1 350	High Arctic	
	Narwhal	Resident	0/365/365	1 300	High Arctic	
	Killer whale	Resident	365	4 400	Arctoboreal	
	Sperm whale	Migrant	150	40 000	Arctoboreal	
	Lagenorhynchus dolphins	Resident	365	210	Arctoboreal	
	Pilot whale	Migrant	270/240/180	1 700	Temperate	
	Harbour porpoise	Resident	365	55	Coastal	
	Bottlenose whale	Migrant	150/150/0	6 000	Arctoboreal	
	Mysicetes	Minke whale	Migrant	180	6 600	Arctoboreal
		Fin whale	Migrant	180	55 500	Arctoboreal
Humpback whale		Migrant	180	30 400	Arctoboreal	
Blue whale		Migrant	180	100 000	Arctoboreal	
Sei whale		Migrant	90/0/0	17 000	Temperate	
Bowhead whale		Resident	0/0/365	80 000	High Arctic	

^aResidence time is given as one value equal for all three regions, or separate values for the three regions: Icelandic shelf, Denmark Strait, and Iceland Sea/Greenland and Norwegian Seas/Barents Seas.

son *et al.*, 2003; Kaschner and Pauly, 2005; Morissette *et al.*, 2012). Furthermore, marine mammals are sensitive to ecosystem fluctuations, including climate-related changes in prey or habitat availability, which may increase their vulnerability to the impacts of fisheries (Haug *et al.*, 1991; Trites *et al.*, 2007; Hátún *et al.*, 2009; Lassalle *et al.*, 2012; Øigård and Smout, 2013; Truchon *et al.*, 2013; Williams *et al.*, 2013; Bogstad *et al.*, 2015; Laidre *et al.*, 2015). Lastly, marine mammals are involved in various direct interactions with fisheries, some of which can negatively impact either commercial fisheries or marine mammal health/survivorship (Buren *et al.*, 2014; Northridge, 2018).

The Nordic Seas (i.e. Iceland, Greenland, and the Norwegian Seas) and the Barents Sea are high latitude, shallow shelf seas that have fisheries targeting TLs ranging from zooplankton, to pelagic forage fish, to large demersal predatory fish. They also include deep oceanic systems with fisheries targeting predominantly small pelagic fish. These productive spring-bloom systems have high trophic transfer rates (e.g. Wassmann *et al.*, 2006; Sundby *et al.*, 2016; Moore *et al.*, 2019). At least 22 species of seals and whales regularly inhabit these seas (Table 1), 14 of which are year-round residents, including High Arctic species (ringed seals *Pusa hispida*, bearded seals *Erignathus barbatus*, walrus *Odobenus rosmarus*, white whales *Delphinapterus leucas*, narwhals *Monodon Monoceros*, and bowhead whales *Balaena mysticetus*); the two North Atlantic drift-ice breeding seals (harp seals *Pagophilus groenlandicus* and hooded seals *Cystophora cristata*) and north temperate species (grey seals *Halichoerus grypus* and harbour seals *Phoca vitulina*); killer whales *Orcinus orca*; white-beaked dolphins *Lagenorhynchus albirostris*; Atlantic white-sided dolphins *Lagenorhynchus acutus*; and harbour porpoises *Phocoena phocoena* (Kovacs *et al.*, 2009). The remaining eight species are seasonal migrants that take advantage of high spring and summer production levels, including five baleen whale species, the abundant common minke whales *Balaenoptera acutorostrata*, fin whales *Bal-*

aenoptera physalus, humpback whales *Megaptera novaeangliae*, less-abundant sei whales *Balaenoptera borealis*, and blue whales *Balaenoptera musculus*, and three-toothed whale species (sperm whales *Physeter macrocephalus*, long-finned pilot whales *Globicephala melas*, and northern bottlenose whale *Hyperoodon ampullatus*).

Comprising a significant component of the animal biomass within these systems, marine mammals consume millions of tonnes of prey annually (Sigurjónsson and Víkingsson, 1997; Bogstad *et al.*, 2000). Their diverse diets span multiple TLs and include important commercial species, such as herring *Clupeus harengus*, capelin *Mallotus villosus*, and Northeast Atlantic cod *Gadus morhua* (Nilssen *et al.*, 1995a, b). Consequently, marine mammal interactions with fisheries may be direct or indirect, and also synergistic or antagonistic (e.g. Lindstrøm *et al.*, 2009).

To date, studies of marine mammal consumption in the Nordic and the Barents Seas have focused predominantly on only a few commercially harvested species, primarily common minke whales and harp seals (e.g. Sigurjónsson and Víkingsson, 1997; Stefánsson *et al.*, 1997; Bogstad *et al.*, 2000; Folkow *et al.*, 2000; Nilssen *et al.*, 2000; Lindstrøm *et al.*, 2009), and considered consumption of only a few key fish species such as Northeast Atlantic (NEA) cod, herring, and capelin. However, the broad array of marine mammal species inhabiting these systems, together with the volume and range of fishery removals, warrants a more comprehensive assessment of marine mammal–fisheries interactions. In this paper, we assess prey consumption of the 22 seal and whale species that regularly inhabit the Nordic and Barents Seas, and compare their level of consumption with removals by fisheries. We treat the *Lagenorhynchus* dolphins as a single species complex and, therefore, report on 21 taxa. Estimating marine mammal consumption is a challenge due to uncertainties in estimates of abundance, residence times in high latitude ecosystems for migratory species, energy requirements, diets, and energy content of prey species (e.g. Leaper and Lavigne, 2007). Nevertheless,

we argue that it is timely to review and summarize available information in the Nordic and the Barents Seas to support the development of EBFM approaches in these regions. Quantifying trade-offs and synergies between marine mammals and fisheries necessitates the use of multispecies or ecosystem models that include both direct and indirect food-web mediated interactions (Goedegebuure *et al.*, 2017). Several models have been developed for these ecoregions but, thus far, none of them includes the full range of marine mammal species inhabiting these regions (Howell and Filin, 2014; Hansen *et al.*, 2016; Skaret and Pitcher, 2016; Skogen *et al.*, 2018; Sturludottir *et al.*, 2018). A review of available information and estimated prey consumption levels provides guidance for parameterizing these models and identifying significant food web interactions that should be included. Available information on marine mammal consumption relative to fishery removals is used herein to identify interactions of relevance to fisheries management, which should be further monitored and quantified in food web models.

We adopt approaches recommended by Leaper and Lavigne (2007) and Smith *et al.* (2015) to estimate plausible ranges of marine mammal consumption, using bootstrapping procedures that include uncertainty in input parameters (abundance, residence time, body weight, energy requirements, and diet). We explore which parameter uncertainties have the largest influence on estimates of marine mammal consumption. We assess how marine mammal consumption compares to fisheries removals across different groups of prey. Finally, we explore the potential for competition between marine mammals and fisheries, using three metrics for diet similarities: (i) TL overlap, (ii) Morisita's overlap index (Krebs, 2008), and (iii) overlap in the cumulative biomass–TL relationship (CB–TL) between marine mammal consumption and fisheries removals (Pranovi *et al.*, 2014; Link *et al.*, 2015).

Material and methods

The Nordic and Barents Sea ecosystems

The study region includes the Icelandic Shelf and the deep Denmark Strait, the Iceland Sea (ICE), Norwegian and Greenland seas (GN), and the shallow Barents Sea (BS) (Figure 1). Both the Nordic Seas and the Barents Sea are strongly influenced by northward flowing warm, saline water in the North Atlantic Current, which meets cold Arctic waters forming productive ocean fronts (e.g. Moore *et al.*, 2019). These marine systems are typical spring bloom systems because low light conditions due to ice cover and limited daylight limit primary production in winter (e.g. Wassmann *et al.*, 2006; Sundby *et al.*, 2016). Zooplankton feed heavily during the short phytoplankton production season and deposit large stores of lipids for over-wintering (Falk-Petersen *et al.*, 2009), which serves to concentrate primary and secondary production into highly energy rich food packs that are efficiently transferred up the food chain to both resident and summer-migrant top predators, including marine mammals (e.g. Wassmann *et al.*, 2006; Labansen *et al.*, 2007; Sundby *et al.*, 2016). The study area was divided into three regions: (I) the ICE, (II) the GN, and (III) the BS, based on the distribution of key prey stocks for both marine mammals and for fisheries, such as capelin, herring, and gadoids, and the geographic extent of fish and mammal surveys that provide abundance estimates and information on species distributions (Øien,

2009; Víkingsson *et al.*, 2015; Eriksen *et al.*, 2017; Pike *et al.*, 2019; Leonard and Øien, 2020a, b).

Marine mammal species

This study focuses on seal and whale species that are regularly sighted in the study area, which include seven pinniped species, nine odontocetes taxa, and six mysticetes (Table 1). Several additional species (besides the northern bottlenose whale) of beaked whales (Ziphiidae) are known to inhabit the area, but these species are poorly known and hence not included herein. Of the 22 taxa we are reporting on, 8 species are summer migrants that forage in these areas but reproduce outside at lower latitudes, while 14 species are year-round residents (Table 1). However, some of the year-round residents perform extensive annual migrations both within and between the three study regions without leaving the overall study area (e.g. harp seals, hooded seals, and bowhead whales, Folkow *et al.*, 2004; Nordøy *et al.*, 2008; Lydersen *et al.*, 2012; Vacquie-Garcia *et al.*, 2017a, b; Kovacs *et al.*, 2020). Six species inhabit the High Arctic, while the other 16 taxa are predominantly associated with arcto-boreal water masses, although some of these species are dependent on sea ice for birthing (e.g. harp and hooded seals, Lavigne, and Kovacs, 1988), or they feed in Arctic waters close to the sea ice (e.g. minke, fin and humpback whales, hooded seals, and killer whales, Vacquie-Garcia *et al.*, 2017a; Storrie *et al.*, 2018; Table 1). Harbour seals, grey seals, bearded seals, harbour porpoise, and white whales feed predominantly in coastal habitats, while the others tend to feed offshore.

Abundance estimates

Available survey-based abundance estimates for the marine mammal species included in this study are given in Table 2 (more detailed information is provided in Supplementary Table S1). However, some marine mammal species lack abundance estimates. For these species, we have used “guesstimates” obtained from either scientific literature or from regional experts (Table 2, numbers in italics, Supplementary Tables S1a–c) and added coefficients of variations ($C.V.s.$) = 0.5, following Smith *et al.* (2015). We specifically assessed the proportion of the total marine mammal consumption accounted for by the species with guesstimates, to assess their potential overall importance in terms of consumption.

Estimating daily per capita consumption

Marine mammal energetic requirements are based on experimental measurements from animals in captivity, field observations of feeding rates, stomach content and evacuation rates, respiration rates, and energy storage while on feeding grounds (Leaper and Lavigne, 2007). These data were used for parameterizing simple models based on Kleiber's Law scaling basal metabolic rate (BMR) to body mass (Kleiber, 1932) to more complex models such as multispecies models and end-to-end ecosystem models, that include prey availability and marine mammal functional responses (e.g. Koen-Alonso and Yodzis, 2005; Lindstrøm *et al.*, 2009; Hansen *et al.*, 2016). Due to limited knowledge of many species included in this study, we base our estimations on the generalized form of the Kleiber equation, scaling average daily consumption C to body mass M :

$$C = \alpha M^\beta, \quad (1)$$

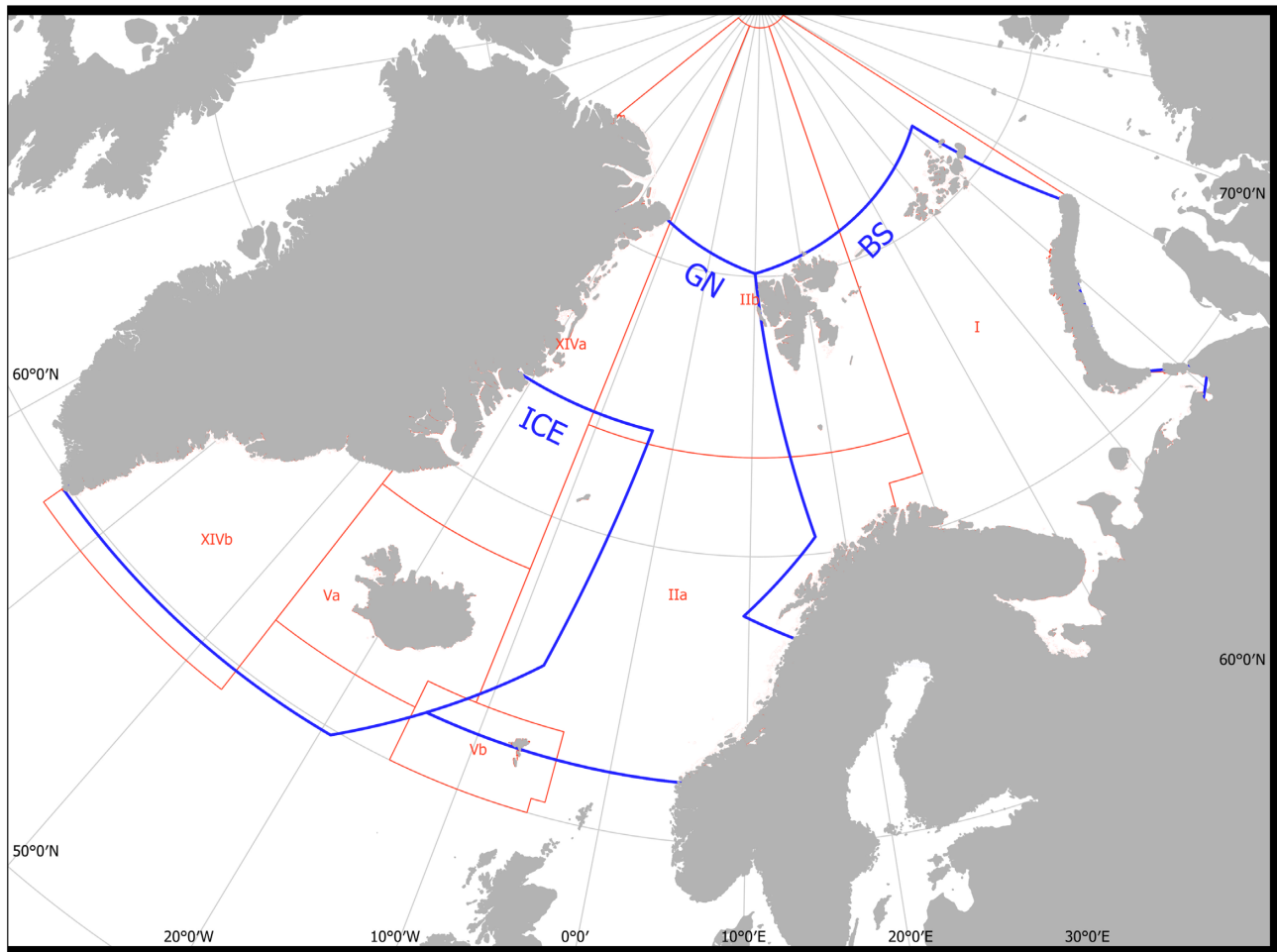


Figure 1. Map of study region. Blue polygons indicate the ICE, GN, and BS regions. The red lines indicate fisheries statistics areas for reported fisheries catches.

Table 2. Abundances and C.V. for marine mammal species included in consumption estimates in the ICE, GN, and BS.

	Species	ICE	GN	BS
Pinnipeds	Harbour seal	9 434 (0.17)	2 370 (0.50)	6 432 (0.50)
	Grey seal	6 300 (0.07)	1 616 (0.22)	6 011 (0.18)
	Ringed seal	200 000 (0.5)	100 000 (0.5)	100 000 (0.50)
	Bearded seal	20 000 (0.5)	10 000 (0.5)	10 000 (0.50)
	Harp seal	740 000 (0.5)	426 808 (0.14)	1 497 189 (0.07)
	Hooded seal	593 500 (0.11)	73 623 (0.14)	0
	Walrus	0	1 429 (0.33)	15 000 (0.5)
	White whale	0	0	5 000 (0.50)
Oddontocetes	Narwhal	2 500 (0.5)	6 444 (0.37)	3 500 (0.50)
	Killer whale	5 478 (0.36)	6 154 (0.58)	503 (0.71)
	Sperm whale	4 272 (0.55)	2 708 (0.48)	806 (0.71)
	<i>L. dolphins</i> ^a	136 889 (0.46)	28 168 (0.57)	144 453 (0.55)
	Pilot whale	210 000 (0.44)	5 000 (0.5)	500 (0.5)
	Harbour porpoise	44 821 (0.44)	5 266 (0.47)	85 731 (0.57)
	Bottlenose whale	6 500 (0.55)	617 (0.74)	0
Mysticetes	Minke whale	48 016 (0.23)	48 913 (0.26)	47 295 (0.30)
	Fin whale	29 940 (0.16)	8 504 (0.33)	4 506 (0.54)
	Humpback whale	12 523 (0.30)	1 808 (0.62)	8 563 (0.81)
	Blue whale	2 450 (0.42)	100 (0.50)	100 (0.50)
	Sei whale	4 200 (0.70)	100 (0.50)	0
	Bowhead whale	0	173 (0.49)	173 (0.49)

^a*Lagenorhynchus* dolphins.

Numbers in italics represents best guesses. A C.V. = 0.5 has been assigned to abundances where no C.V. is available. Additional information about abundance estimates is provided in the supporting material (Tables S1a–c).

where α and β are species or taxonomic group-specific parameters (Kleiber, 1932; Leaper and Lavigne, 2007). We note that this simple approach does not take into account variation in energy requirements across seasons, or due to age structure, sex, or reproductive state (e.g. Víkingsson, 1995; Folkow *et al.*, 2000). This may result in an underestimation of consumption by summer migrants, as particularly anestrus and pregnant female baleen whales may forage more intensively in these areas than when inhabiting lower latitudes in winter (Víkingsson, 1995; Folkow *et al.*, 2000).

In the scientific literature, many pairs of α and β have been used for parameterizing equation (1) for various marine mammals (Leaper and Lavigne, 2007; Smith *et al.*, 2015, Supplementary Table S2). Much of the available information is derived from studies of captive marine mammals, and is therefore, biased towards smaller species of seals and toothed whales (Leaper and Lavigne, 2007). Parameterizations extrapolated to larger whales may therefore result in unrealistic high consumption estimates (Leaper and Lavigne, 2007). Smith *et al.* (2015) made a thorough evaluation of different parameterizations used for pinnipeds, odontocetes, and mysticetes when estimating marine mammal consumption in the northeastern US shelf system. They excluded α and β pairs that resulted in consumption estimates 50% higher than the mean consumption calculated using the remaining parameter pairs. We generally adopted the parameter pairs included by Smith *et al.* (2015) in the current study (Supplementary Table S2). However, further inspection of the model estimates revealed that some models, for some species, produced unrealistically small consumption estimates (i.e. estimated consumption < BMR) and a few models produced unrealistically high estimates (i.e. estimated consumption 10–21 \times BMR), a conclusion also supported by Leaper and Lavigne (2007). These models were removed from our calculations of equation (1) to estimate the daily consumption of pinnipeds, odontocetes, and mysticetes, respectively (Supplementary Table S2). Species-specific body masses M used in equation (1) were retrieved from Sigurjónsson and Víkingsson (1997), Kovacs *et al.* (2009), and Smith *et al.* (2015). To include uncertainties, the weight estimates were associated with a C.V. of 0.2, following Smith *et al.* (2015). An overview of the total estimated biomasses of the marine mammal species is given by regions in Supplementary Table S3.

Residence times

Species' residence times in the study region used for consumption estimation are given in Table 1. While all the pinniped stocks that breed in the study regions are year-round residents, harp seals and hooded seals from the northwest Atlantic also enter the ICE region for around 5 and 2 months, respectively, during summer (Sergeant, 1991; Andersen *et al.*, 2013, G. Stenson, DFO Canada, pers. comm., M. Hammill, DFO Canada, pers. comm.). However, because hooded seals spend 1–2 months moulting, with low foraging activity during this period (G. Stenson, DFO Canada, pers. comm.), we included only 1 month of residency time for this species in our calculations. Among the odontocetes, there is limited information available on the timing of migrations, and hence residency times. According to Sigurjónsson and Víkingsson (1997), sperm whales and northern bottlenose whales are in the study area for \sim 5 months. Observations of pilot whales in-

dicating residence times of 9, 8, and 6 months for the ICE, GN, and BS regions, respectively (Nils Øien, IMR, Norway, unpublished data; Bjarni Mikkelsen, Faroe Marine Research Institute, unpublished data). Sigurjónsson and Víkingsson (1997) also found that most of the migratory mysticetes were abundant for \sim 6 months of the year, except for sei whales that were abundant for only 3 months. Recent telemetry studies of minke, fin, and blue whales demonstrate variable migration timing, but generally support the findings by Sigurjónsson and Víkingsson (1997; see Heide-Jørgensen *et al.*, 2001; Silva *et al.*, 2013; Víkingsson *et al.*, 2014). Furthermore, sightings in Icelandic and Norwegian waters suggest that some of the large whales remain in the study area throughout the winter (Sigurjónsson and Víkingsson, 1997; Magnúsdóttir *et al.*, 2014; Jourdain and Vongraven, 2017). We arbitrarily set the overwintering proportion to 10% of the peak summer abundance (following Sigurjónsson and Víkingsson, 1997). Recent observations have shown large numbers of humpback whales during winter in the ICE and BS regions (Marine and freshwater Research Institute (MFRI), Iceland, unpublished information, Magnúsdóttir *et al.*, 2014; Jourdain and Vongraven, 2017), so the overwintering proportion was set to 20% for this species. Due to the limited information available on timing of migrations, and particularly on overwintering proportions of the migratory species, we included C.Vs. of 0.2 around the number of days in the system and a C.V. of 0.5 for the overwintering proportions in our calculations, following Smith *et al.* (2015). While harp seals pupping in the White Sea in the BS region spend all their non-breeding time in the BS, harp seals pupping off East Greenland perform foraging migrations across the GN, ICE, and BS regions. Telemetry data indicate that 32, 45, and 23% of their time are used in the GN, ICE, and BS, respectively (Folkow *et al.*, 2004, Martin Biuw, IMR Norway, unpublished data). Therefore, we used these proportions to assign consumption by the GN harp seals to the three regions. Finally, telemetry studies also indicate that the BS–GN bowhead whale stock use 50% of their time in the GN; hence, we assigned 50% of the stock to each region (Kit M. Kovacs and Christian Lydersen, NPI, Norway, unpublished data).

Uncertainty estimation of annual consumption

Annual consumption by marine mammal species was estimated using equation (1) to derive daily individual consumption, and this number was scaled up according to the number of individuals and number of days in each region. Furthermore, we ran 1000 Monte Carlo simulations to estimate the uncertainty in annual consumption estimates (in kg) by each marine mammal species in each of the three regions. For each run, we randomly selected among the relevant pairs of the α and β for the consumption model (equation (1), Supplementary Table S2), and randomly selected body weight, abundance, residence times, and overwintering proportions from normal distributions (and log-normal distributions of abundance) defined by the parameter values and associated C.Vs. This bootstrapping procedure resulted in distributions of total annual consumption by each species in each region, reflecting variation in parameterization of equation (1), and uncertainties in parameter values of body weight, abundance, residence times, and overwintering proportions. An overview of mean annual consumption and CI for the marine mammal species is given by regions in Supplementary Table S4.

Marine mammal diets

We reviewed the information available on marine mammal diets within the study area. We compiled the information into a detailed diet matrix with 18 prey species or groups, including three groups of zooplankton (copepods, krill, and amphipods), cephalopods, shrimps, other invertebrates, four species of pelagic fish (blue whiting *Micromesistius poutassou*, herring, capelin, and polar cod *Boreogadus saida*), myctophids, sandeel *Ammodytes* spp, mackerel *Scomber scombrus*, gadoid fish, flatfish, redfish *Sebastes* spp, other fish species, and marine mammals (Supplementary Table S5). For mammalian species for which there was limited diet information from the study region, we included information from neighbouring ecosystems or from ecosystems with similar prey species (e.g. northwest Atlantic, Arctic). Only information sources quantifying prey use were included (e.g. frequency of occurrence, wet weight, and reconstructed weight), except for killer whales, *Lagenorhynchus* dolphins, and bowhead whales where very limited or no quantitative information from the region was available. For killer whales, the literature suggests a dominance of herring in their diet, but that they also feed on flatfish, cephalopods, marine mammals, and other fish (e.g. lumpfish *Cyclopterus lumpus*, Samarra *et al.*, 2018). Also, one study found a large-scale spatial association between killer whales and mackerel in the Norwegian Sea (Nøttestad *et al.*, 2014). We summarized these studies into three dietary categories: (i) 100% herring, (ii) 70% herring, 10% mackerel, and 5% of each of flatfish, cephalopods, other fish, and mammals, and (iii) 50% herring, 30% mackerel, and 5% of each of flatfish, cephalopods, other fish, and mammals. For *Lagenorhynchus* dolphins, several qualitative observations from the study regions suggest diet combinations of blue whiting, haddock, herring, capelin, and polar cod, which differ slightly from the quantitative information available from outside the study region (e.g. more myctophids, less capelin, and polar cod). We therefore included the qualitative diet observations from the study region by assigning equal diet proportions to the observed prey species. For bowhead whales, Christensen *et al.* (1992) and Lowry *et al.* (2004) suggested a dominance of krill, and krill and copepods, with some use of amphipods, which were translated into two diet categories: (i) 90% krill, 5% copepods, and 5% amphipods, and (ii) 47.5% copepods, 47.5% krill, and 5% amphipods. Total annual prey consumption per marine mammal species per region was estimated by randomly selecting among the available diets for each species and multiplying the selected diet with the estimated total consumption of that marine mammal species for each of the 1000 runs in each region.

Assessing variation in annual consumption estimates due to parameter uncertainty

To assess the influence of parameter uncertainties on total variation in annual consumption estimates, we ran the following Generalized Linear Model (GLM) for each marine mammal species and region separately:

$$tC_{ann} = C_{mod} + N + M_{ind} + R + P,$$

where tC_{ann} is the total annual consumption, C_{mod} is the consumption model (Equation 1 above), N is the estimated population size, M_{ind} is the average individual body mass, R is the residence time, and P is the proportion of overwintering population. We used the deviance explained and statistical signif-

icance of each parameter to assess their relative contributions to the total variation, and hence uncertainties, in annual consumption estimates.

Fishery catches

Fisheries catches for the 10-year period 2006–2015 were collected from the databases of the International Council for the Exploration of the Sea (ICES) and used to calculate mean annual removal per species for each region. However, the catch data were only available for large statistical regions that are not an ideal match to the three regions in this study (Figure 1). Thus, we assigned the catches to our regions based on knowledge of species distributions and information from stock assessment reports (for details see the Supplementary Material section).

Marine mammals and fishery interactions

Potential competition between marine mammals and fisheries was explored using three indicators (see Wallace, 1981; Krebs, 2008; Pranovi *et al.*, 2014; Link *et al.*, 2015): (1) TL overlap; (2) Morisita's overlap index; and (3) overlap in the CB–TL relationship. Morisita's overlap index ranges from 0 (no overlap) to 1 (complete overlap). Values >0.6 are generally considered biologically significant amounts of niche overlap (Wallace, 1981). The third index captures variation in biomass across TL. By constructing 95% CIs, which correspond to a two-sided test, we tested if the overlap was statistically significant. The TLs of the prey species are listed in Supplementary Table S6, along with corresponding literature sources.

Results

Abundance and biomass of marine mammals

Among the three regions, the marine mammal species that dominate in terms of abundance and consumption vary substantially. In terms of numbers (Table 2, Supplementary Table S1), harp and hooded seals were most abundant in the ICE, followed by pilot whales, ringed seals, and *Lagenorhynchus* dolphins. In the GN, harp seals were most abundant, followed by ringed seals, hooded seals, and minke whales. In the BS, harp seals were most abundant, followed by ringed seals, *Lagenorhynchus* dolphins, and harbour porpoises. However, in terms of biomass (Figure 2, Supplementary Table S3), the baleen whales dominated in all three regions (i.e. fin and humpback whales in the ICE, fin and minke whales in the GN, and minke and humpback whales in the BS), but pilot whales (ICE) and sperm whales (ICE and GN), as well as harp seals (all three regions) and hooded seals (ICE) also contributed considerably to overall marine mammal biomass. Thus, in terms of taxonomic groups, the mysticetes dominated the biomass in all three regions, followed by odontocetes in the ICE and GN, and pinnipeds in the BS (Figure 2b). Total biomass of marine mammals was three times larger in the ICE (mean 3.56 million tonnes) than the other two regions (GN—mean 1.12 million tonnes and BS—mean 1.15 million tonnes).

Annual consumption

Patterns in annual consumption followed the patterns seen for marine mammal biomass, albeit increasing the importance of harp seals and pilot whales relative to the larger whales (Figure 3a, b, Supplementary Table S4). This is due to the

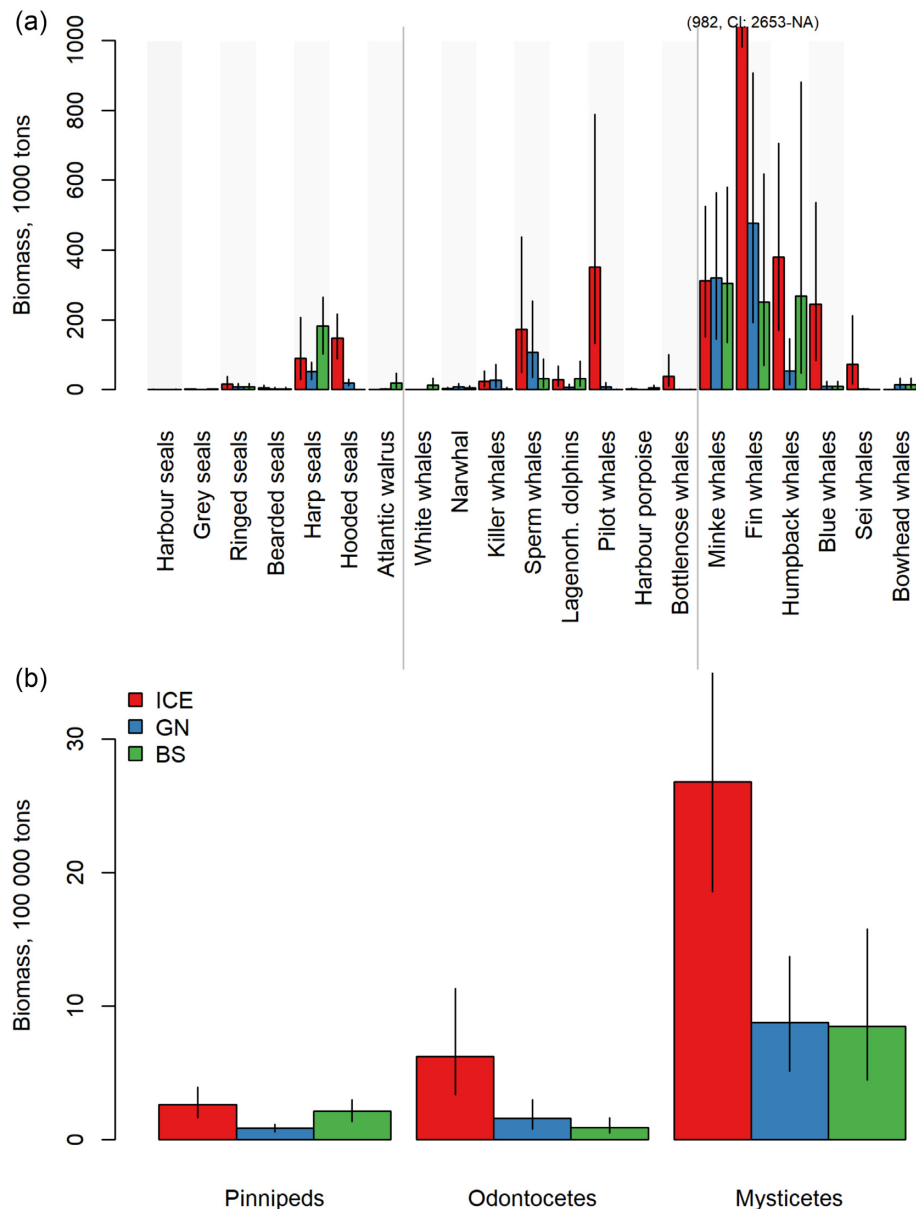


Figure 2. Mean estimated biomass (in 1000 tonnes) of (a) marine mammal species and (b) taxonomic groups in the ICE, GN, and BS regions. Error bars indicate 95% CI. Note that fin whale biomass extends beyond the scale of the Y-axis (in a); therefore, the mean and CI values are provided for this species.

smaller mammal species consuming more, relative to their body mass, compared to the larger whales (Table 3). While the seals were estimated to consume on average 3–8 kg prey day⁻¹, equal to 3–4% of their body mass, the estimated consumption by minke, humpback, and fin whales were on average 179, 495, and 769 kg day⁻¹, equal to 2.8, 1.7, and 1.4% of their body mass, respectively (Table 3). The species consuming most in the ICE were fin whales (mean 4.6 million tonnes of prey year⁻¹, CI: 2.7–7.4), followed by pilot whales (mean 2.6 million tonnes of prey year⁻¹, CI: 0.7–5.6), minke whales (mean 1.7 million tonnes of prey year⁻¹, CI: 0.8–3.0), and humpback whales (mean 1.3 million tonnes of prey year⁻¹, CI: 0.6–2.3). The species estimated to consume most in the GN were minke whales (mean 1.7 million tonnes of prey year⁻¹, CI: 0.8–3.1), followed by fin whales (mean 1.3 million tonnes

year⁻¹, CI: 0.6–2.3) and harp seals (mean 0.2 million tonnes year⁻¹, CI: 0.1–0.4). In the BS, the species with the highest overall consumptions included harp seals (mean 2.5 million tonnes of prey year⁻¹, CI: 1.3–3.9), followed by minke whales (mean 1.7 million tonnes year⁻¹, CI: 0.7–3.1) and humpback whales (mean 1.0 million tonnes year⁻¹, CI: 0.2–2.4). Aggregated by taxonomic groups, mysticetes consumed most in the ICE and GN, followed by odontocetes in the ICE, while pinnipeds and odontocetes consumed similar amounts in the GN (Figure 3b). In the BS, mysticetes consumed slightly more than pinnipeds, and both groups consumed more than odontocetes in this region (Figure 3b). In total, marine mammals in the ICE, GN, and BS consumed on average 13.4 (CI: 5.6–25.0), 4.6 (CI: 1.9–8.6), and 7.1 (CI: 2.8–13.8) million tonnes of prey year⁻¹.

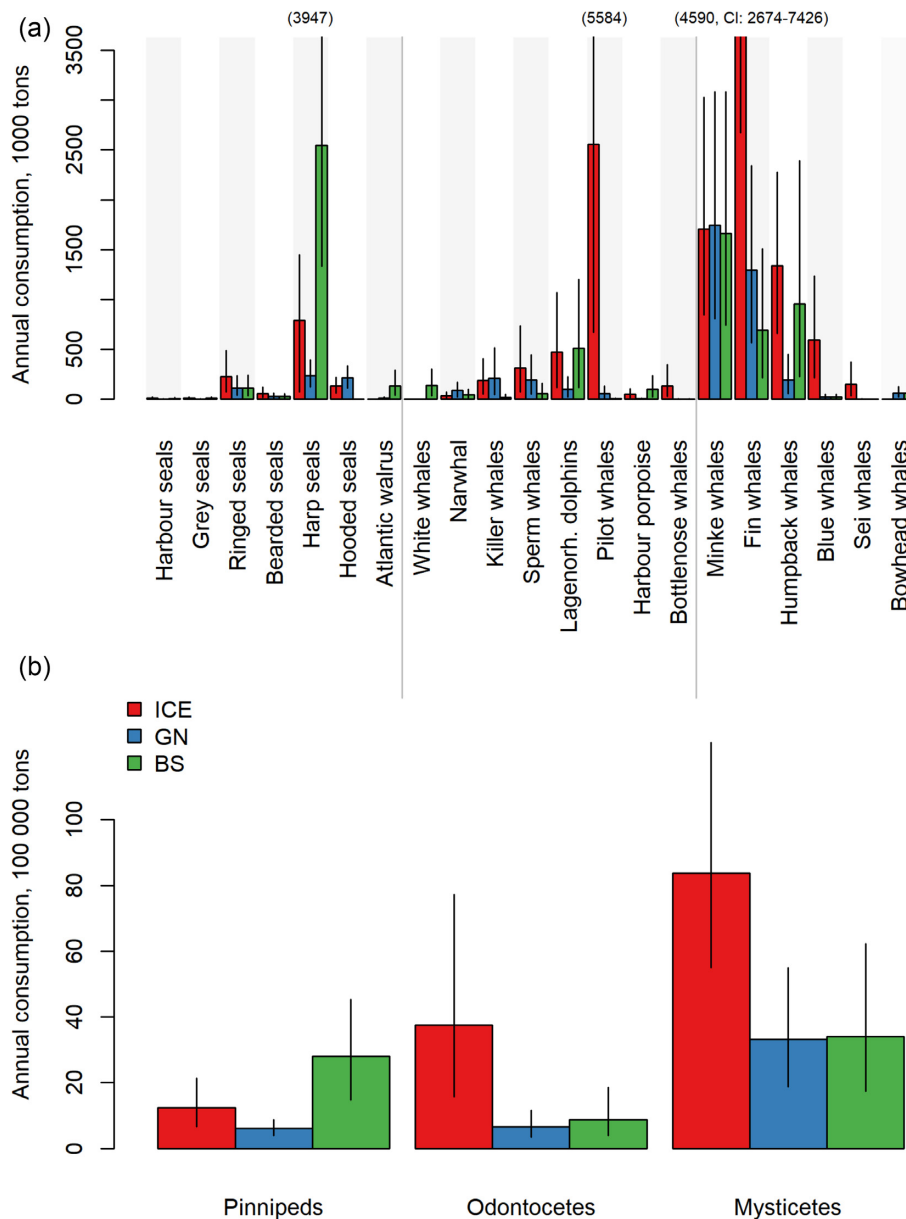


Figure 3. Estimated mean annual consumption (in 1000 tonnes) by (a) marine mammal species and (b) taxonomic groups in the ICE, GN, and BS regions. Error bars indicate 95% CI. Note that mean and upper CI for fin whales, and upper CI for harp seals and pilot whales extends beyond the scale of the Y-axis (in a); therefore, these values are provided in the graph.

Parameter uncertainties and deviance in marine mammal consumption estimates

GLMs run for each marine mammal species and region demonstrated how estimated or assigned variance in the input parameters, and the different parameterizations of the consumption model (equation (1)), contributed to the overall variance in the consumption estimates (Figure 4). Most of the variance in consumption was associated with variance in abundance estimates and the parameterization of the consumption model. Also, the consumption models contributed relatively more to the variance associated with pinniped and odontocete consumption estimates than those of mysticetes. Finally, the uncertainty bounds assigned to overwintering proportion, residence time, and individual weights contributed relatively little to overall variation in consumption estimates.

Marine mammal prey use and fisheries removals

The number of prey types per marine mammal species ranged from 2 to 12 (Figure 5, Supplementary Table S5). Overall, seals had the broadest diets, including most of the prey species and groups, while bottlenose, pilot, and sperm whales had the most restricted diets, including primarily cephalopods (Figure 5). As seen from Figure 6 (and Supplementary Table S6), marine mammals within the ICE region were estimated to consume mostly euphausiids, followed by cephalopods, herring, capelin, and “other fish”. Furthermore, in the GN, they are estimated to consume mostly euphausiids, followed by herring, capelin, ammodytes, and “other fish”. In the BS, marine mammals are estimated to consume mostly euphausiids, followed by capelin, amphipods, herring, and polar cod.

Fisheries removed on average 1.55, 1.45, and 1.16 million tonnes year⁻¹ from the ICE, GN, and BS, respectively

Table 3. Estimated individual prey consumption day⁻¹ for marine mammal species in the northeast Atlantic (mean and 95% CI, kg day⁻¹ ind⁻¹)

Species	Daily consumption, kg day ⁻¹ ind ⁻¹	Daily consumption, % of body mass
Harbour seal	3.6 (1.8, 5.9)	4.1 (2.1, 6.5)
Grey seal	6.3 (2.8, 9.8)	3.2 (1.4, 4.6)
Ringed seal	3.1 (1.5, 5.2)	4.1 (2.3, 6.9)
Bearded seal	7.6 (3.9, 11.4)	3.1 (1.6, 4.2)
Harp seal	4.4 (2.2, 7.0)	3.6 (1.9, 5.6)
Hooded seal	7.6 (3.9, 11.6)	3.1 (1.6, 4.3)
Walrus	23.6 (10.6, 43.6)	2 (0.9, 3.2)
White whale	37.7 (11.7, 61.0)	2.8 (0.9, 4.2)
Narwhal	37.3 (10.9, 59.9)	2.9 (1, 4.2)
Killer whale	93.1 (27.1, 182.6)	2.2 (0.7, 3.5)
Sperm whale	428.7 (143.5, 709.5)	1.1 (0.4, 1.5)
L. dolphins ^a	9.5 (2.9, 17.1)	4.5 (1.5, 7.7)
Pilot whale	45.1 (13.5, 73.4)	2.7 (0.9, 3.8)
Harbour porpoise	3.1 (1.1, 5.1)	5.6 (2.1, 8.7)
Bottlenose whale	120.1 (34.6, 247.8)	2 (0.7, 3.5)
Minke whale	179.0 (106.5, 278.3)	2.8 (2, 3.8)
Fin whale	769.0 (504.3, 1 086.5)	1.4 (1.1, 1.7)
Humpback whale	494.8 (319.0, 699.9)	1.7 (1.3, 2)
Blue whale	1 204.0 (744.4, 1 766.7)	1.2 (0.9, 1.6)
Sei whale	378.7 (225.5, 704.1)	2.3 (1.6, 3.5)
Bowhead whale	993.3 (659.5, 1 497.5)	1.3 (0.9, 1.6)

^a*Lagenorhynchus* dolphins.

(Figures 6 and 7, Supplementary Table S7). Thus, the estimated removal by marine mammals is on average 8.6 (CI: 3.6–16.1), 3.1 (CI: 1.3–5.9), and 6.1 (CI: 2.4–11.9) times the biomass removed by fisheries in these three regions, respectively. In all three regions, fisheries targeted pelagic fish and gadoids, taking smaller biomasses of flatfish, redfish, cephalopods, “other” invertebrates, marine mammals, and “other” fish. In addition, fisheries targeted shrimps in the ICE and BS, myctophids in the ICE and copepods in the BS (Figure 6). Marine mammals in the ICE are estimated to consume more cephalopods, herring, “other fish”, and capelin than that removed by fisheries, while consuming comparable biomasses of mackerel, flatfish, and gadoids and less blue whiting and redfish than that removed by fisheries (Figure 6). In the GN, mammals removed more capelin and “other fish” than fisheries, less herring, blue whiting, and mackerel and gadoids than fisheries and comparable biomasses for the remaining prey groups. In the BS, mammals were the dominant consumers of almost all prey groups. Gadoids were the exception with fisheries removals being larger than estimated consumption by marine mammals for this fish group. Marine mammal removals of other marine mammals (average 6356, 7319, and 672 tonnes in the ICE, GN, and BS, respectively) were greater than the marine mammal biomasses harvested in the ICE (4300 tonnes) and GN (1375 tonnes), but less than the amount harvested in the BS (1972 tonnes).

When comparing average removals of the 19 prey categories by marine mammal taxonomic groups and fisheries, mysticetes dominated the removals of copepods, euphausiids (in the ICE and BS), and herring, while seals dominated the removals of amphipods (Figure 7). Removals of pelagic fish were dominated by baleen whales in the ICE, fisheries and baleen whales in the GN, and baleen whales and seals in the BS. Cephalopods were predominantly consumed by toothed whales. Exceptions to these overall patterns were a slightly greater fisheries removals of herring in the GN compared to the consumption by all marine mammal groups com-

bined, and substantially greater fisheries removals of gadoids in the BS compared to the consumption by all marine mammal groups combined.

Trophic and dietary overlap between fisheries and marine mammals

Trophic levels of all prey groups are given in Supplementary Table S8. The mean TL of fishery catches ranged from 3.3 in the ICE to ~4.1 in the BS (Figure 8A). The mean overall TL (all groups) of marine mammals in the ICE, GN, and BS was estimated to be 2.7 (CI: 2.5–2.9), 3.0 (CI: 2.7–3.3), and 3.1 (CI: 2.8–3.3), respectively for the different regions. Overall, these numbers indicate that fisheries operate at a significantly higher TL compared to marine mammals. However, among the marine mammals, the highest mean TL was observed in toothed whales (3.1–3.6) followed by seals (2.9–3.2), while baleen whales had the lowest mean TL (2.6–2.9). The overlapping CIs in the ICE and GN indicates potential competition between seals and toothed whales and fisheries. Due to the higher TL of fisheries in the BS compared to the other two regions, there was no evidence of overlap between fisheries and marine mammals in this region, despite the fact that toothed whales in this region showed the highest TLs of all marine mammals in any of the three regions.

The estimated mean overall Morisita’s overlap indexes (Figure 8B) for all marine mammals combined was 0.22 (CI: 0.05–0.41) in the ICE, 0.35 (CI: 0.06–0.89) in the GN, and 0.08 (CI: 0.02–0.16) in the BS. The error bars indicate significant potential for competition between all marine mammal groups and fisheries in the GN (i.e. index > 0.6, Wallace, 1981). This is due in large part to both mammals and fisheries targeting pelagic fish (Figures 5–7). Also, there was an overlap between odontocetes and fisheries in the ICE.

The third measure of potential competition, the overlap in the CB–TL relationship is plotted in Figure 9. The marine mammal CB–TL profile differed from the fishery profile, particularly in the ICE and BS. Marine mammals in the ICE target lower-intermediate TLs (2.2–3.2), with exploitation peaks or TL-inflection points around 2.2 and 3.3. In contrast, the fishery CB–TL profile comprised two TL-inflection points at 3.3 and 4.2. Thus, fisheries remove proportionally less at lower TLs and more at higher TLs than the marine mammals. The marine mammal CB–TL envelope in the GN partially overlapped the fishery profile and the main fishery TL-inflection point (TL = 3.3) overlapped the second marine mammal TL-inflection point. In the BS, the fishery CB–TL profile remained significantly above the marine mammal CB–TL envelope throughout all TLs. Fisheries in the BS displayed a much higher (TL = 4.1) TL-inflection point than marine mammals, which displayed no clear TL-inflection point, but rather displayed a gradual increase in the CB–TL relationship. The CB–TL envelopes for marine mammals showed a gradual rightwards shift, indicating an increasing contribution of higher TL prey, from the ICE via GN to BS (Figure 9). Fisheries displayed a similar pattern, but it was much more pronounced than for the marine mammals.

Discussion

Results of this study suggest that (1) baleen whales consume the largest prey biomass in all three regions, followed by toothed whales in the ICE, toothed whales and seals in

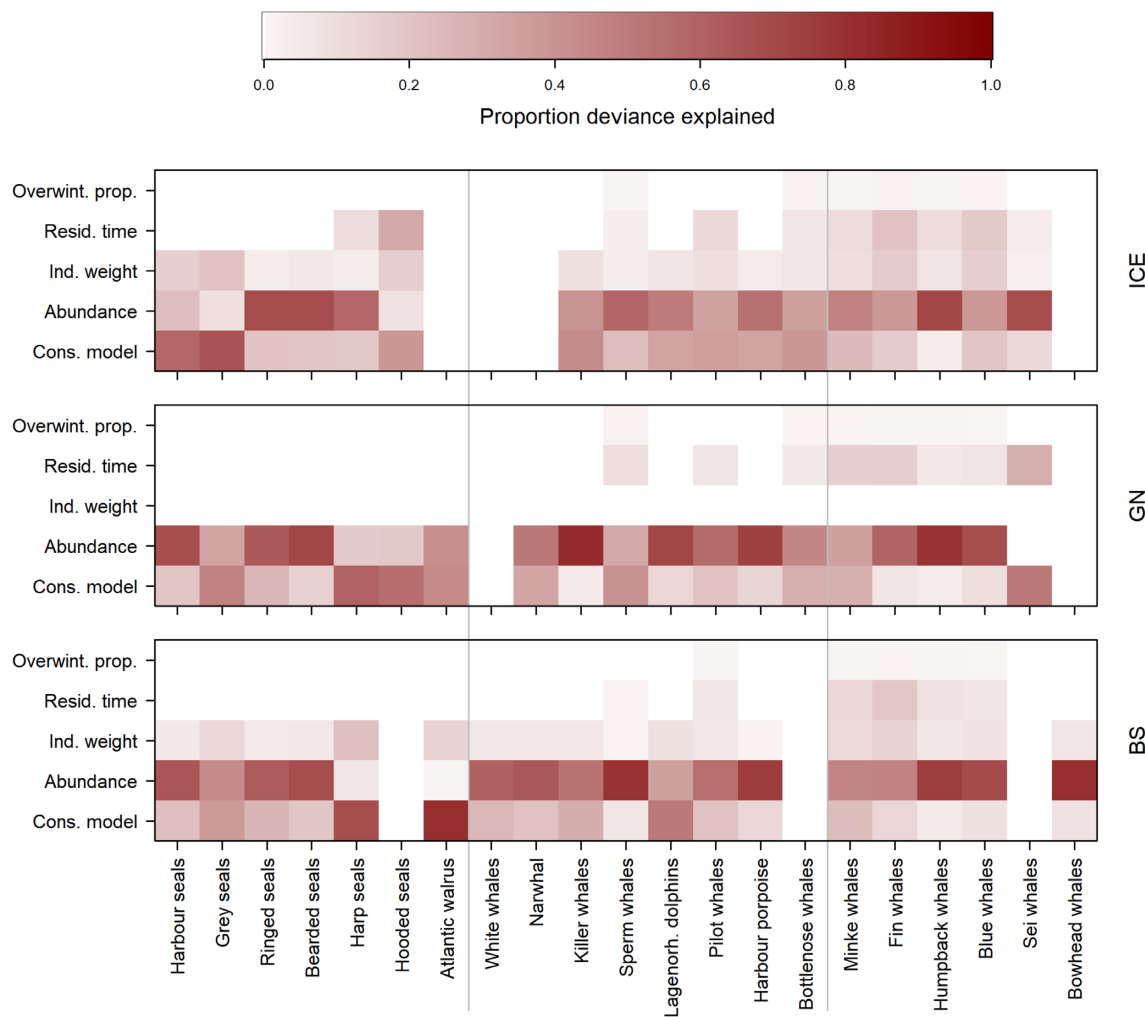


Figure 4. Analyses of deviance associated marine mammal species consumption estimates, in the ICE (upper panel), GN (middle panel), and BS (lower panel) regions. The Y-axis shows the variables included in the GLMs of consumption, and coloured squares indicate the proportion of deviance that is explained by the variable, for each of the marine mammal species (X-axis).

the GN, and pinnipeds in the BS; (2) fin whales consume the largest prey biomass, followed by minke and humpback whales among the baleen whales, whereas pilot whales and harp seals are the largest consumers among toothed whale and pinniped species; (3) marine mammals remove roughly nine, three, and six times the biomass harvested by fisheries in the ICE, GN, and BS regions; and (4) there are substantial regional variations in the degree of niche overlap and potential competition both among marine mammal species and between marine mammals and fisheries, with highest potential levels of competition in the GN region.

Total consumption by marine mammals

Estimated annual consumption generally reflected the species biomass patterns, with baleen whales being by far the greatest consumers overall in the northeast Atlantic. Smaller species, such as the various pinnipeds, have higher per capita prey consumption rates as a result of their higher mass-specific metabolic demands and the fact that most individuals remain within the northeast Atlantic year-round. Marine mammal prey removals were on average 8.6, 3.1, and 6.1 times the biomass removed by fisheries in the ICE, GN and BS, respectively.

Consumption estimates generated in this study were more constrained than those of Smith *et al.* (2015), because we removed allometric models that generated unrealistic low or high consumption estimates (i.e. consumption estimates below or very close to basal metabolic demands and consumption estimates $> 10 \times$ BMR). This also resulted in lower (ca. 20%) individual daily consumption estimates for some large whale species. Species-specific consumption estimates in this study generally agree with estimates from previous studies (Sigurjónsson and Víkingsson, 1997; Bogstad *et al.*, 2000; Skjoldal *et al.*, 2004), although there are some notable differences. Our estimates for fin, humpback, and pilot whale consumption in the ICE were 1.97, 1.12, and 1.10 million tonnes greater, respectively, than those estimated by Sigurjónsson and Víkingsson (1997), primarily due to higher abundances (29400 vs. 17400 for fin whales, 12500 vs. 1800 for humpback whales, and 210000 vs. 53000 for pilot whales). Higher abundance estimates in our study are explained by marked fin and humpback whale population increases in the region, due to both recovery from overharvesting in the late 1800s and early 1900s, and northward shifts in distribution of these species (Víkingsson *et al.*, 2015; Pike *et al.*, 2019; Leonard and Øien, 2020a, b). Rather than reflecting changes in abundance, the larger

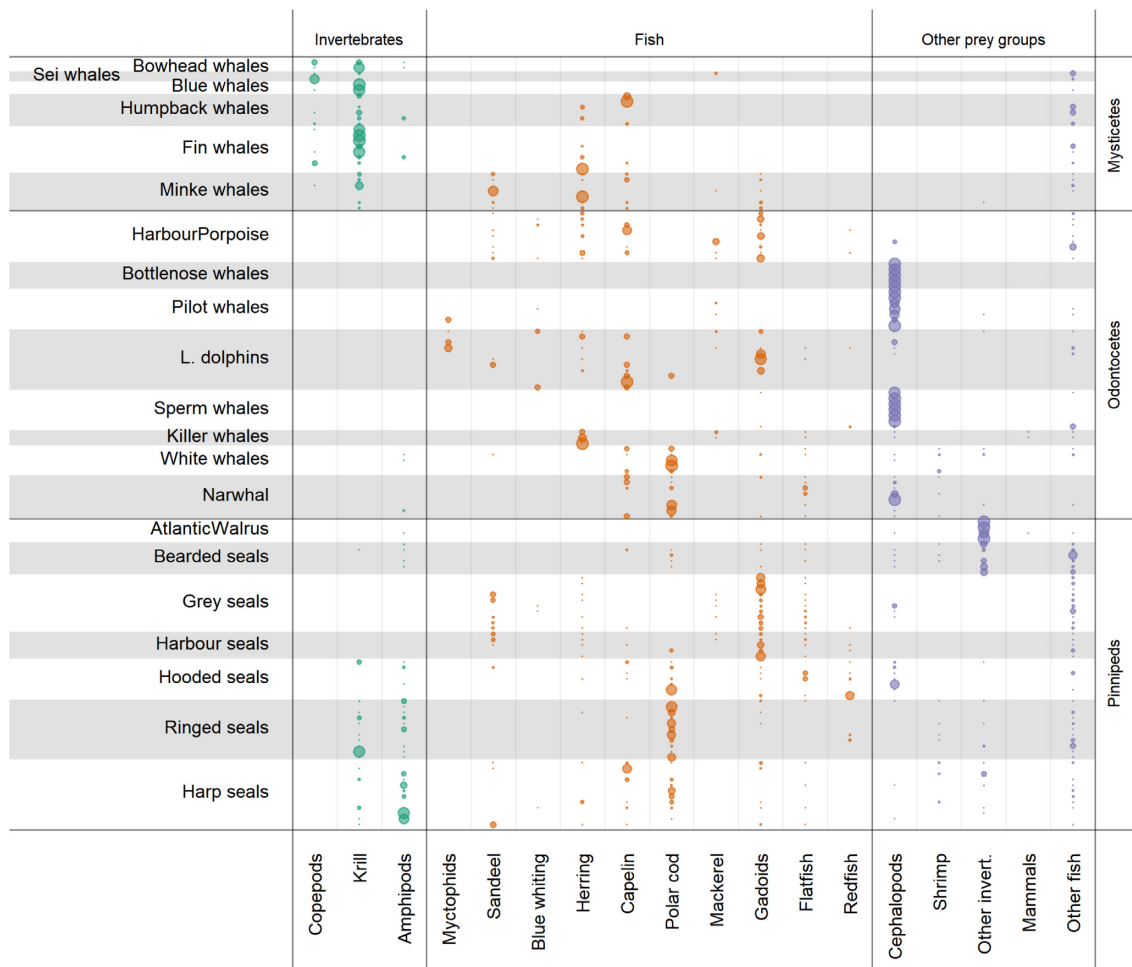


Figure 5. Diets (prey species/categories along the X-axis) of marine mammal species (Y-axis) used in estimation of prey consumption. Each horizontal line shows one observed diet of the taxon. Dot sizes reflect proportional use (range 0–1). Details are provided in Supplementary Table S5.

numbers of pilot whales within the three regions compared to earlier estimates likely reflects changes in distribution, associated with large-scale variations in the subpolar gyre and bottom-up driven impacts on prey availability (Skjoldal *et al.*, 2004; Hátún *et al.*, 2009; Pike *et al.*, 2019).

Bogstad *et al.* (2000) estimated consumption of harp seals to be around 3.4 million tonnes in the BS, compared to an average of 2.5 million tonnes in this study. Harp seal abundance estimates used in Bogstad *et al.* (2000) were higher (2.2 million seals) than those herein (1.5 million seals). This reduction is due to decreased pup production and a decline in harp seal abundance that has been ongoing since the early 1980s (ICES, 2019a; Stenson *et al.*, 2020), possibly associated with climate-related changes in the sea ice habitat used for pupping and prey availability in BS (Øigård and Smout., 2013). Overall, these comparisons clearly demonstrate that over decadal scales, marine mammal abundance is dynamic in these regions, significantly influencing the flow of biomass through the food webs.

Our consumption estimates are associated with considerable uncertainties, resulting from both “guesstimates” for population abundances and associated non-quantified uncertainties for a number of input parameters, as well as quantified uncertainties related to abundance estimates. Among more abundant marine mammals, estimates were lacking for

some Arctic seal species, pilot whales in the GN, and white whales in the Russian sector of the BS (Vacquie-Garcia *et al.*, 2020). Species with abundance estimates based on best guesses contributed 3.1, 1.7, and 3.4% of the total consumption estimates for the ICE, GN, and BS, respectively. Therefore, uncertainties associated with these estimates are likely to have limited impacts on the overall consumption estimates for these regions. Regressions of species-specific consumption demonstrated that the main source of variation in consumption estimates—within the bounds of set or estimated parameter uncertainties used in our calculations—was uncertainties associated with abundances and choice of consumption models. These results indicate that refining the total consumption estimates primarily requires more precise estimates of abundance and better estimates for marine mammal energetic requirements.

The study regions are covered by large scale cetacean surveys at 5–10 year intervals (e.g. Skaug *et al.*, 2004; Hansen *et al.*, 2018; Pike *et al.*, 2019, 2020a, b; Leonard and Øien, 2020a, b). While all cetaceans are reported, these surveys are designed to optimize abundance estimation of specific target species (common minke whales, fin whales, and long-finned pilot whales); other species are likely underestimated to an unknown degree, in particular smaller (e.g. dolphins, porpoises) and deep-diving (sperm whales, bottlenose whales, and other

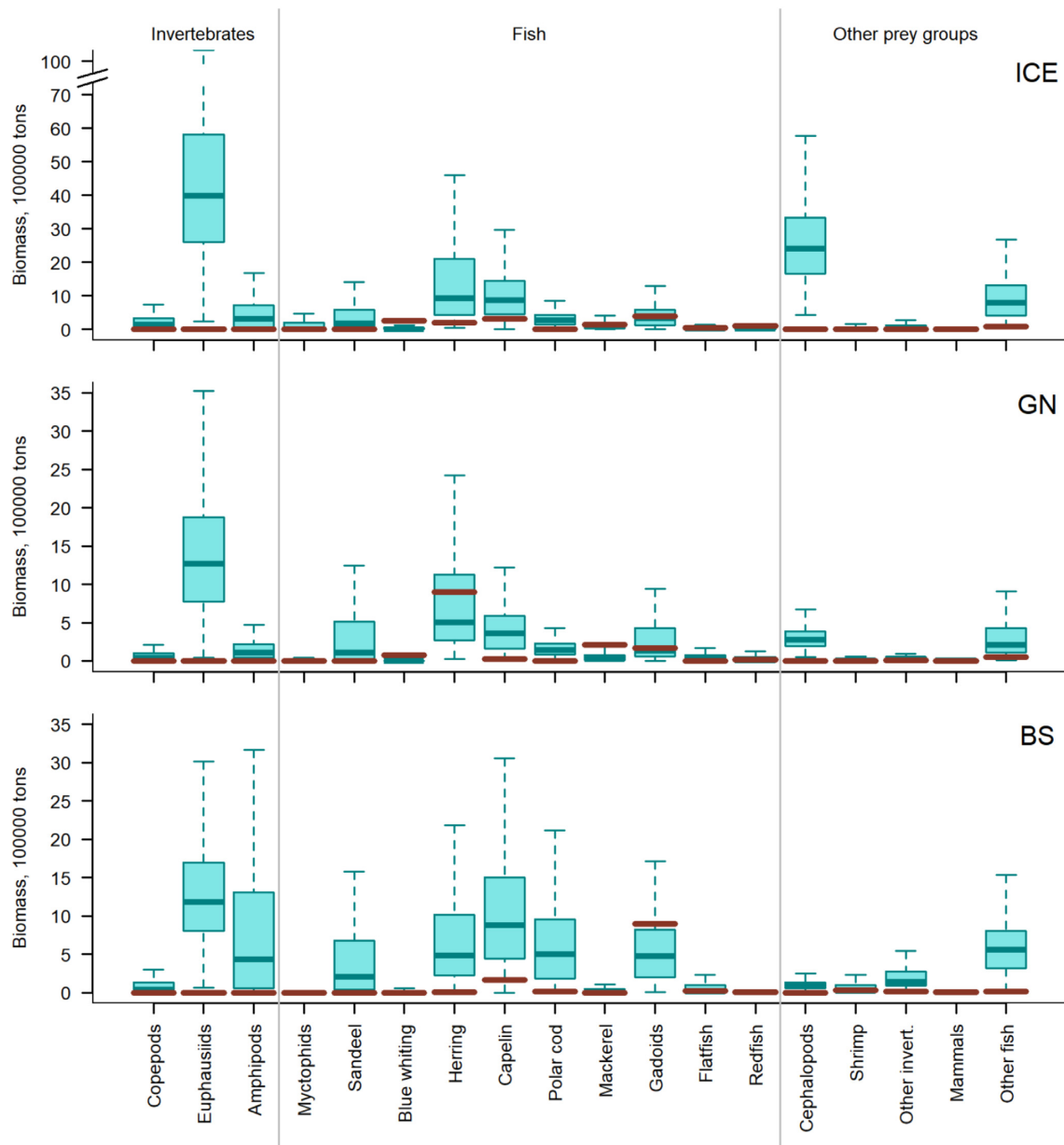


Figure 6. Estimated marine mammal prey consumption. Boxplots [the box indicates the median (line) and the 25th and 75th quartiles], whiskers reflecting minimum ($Q_{25}-1.5*(Q_{75}-25)$) and maximum $Q_{75} + 1.5*(Q_{75}-25)$ values. Red lines indicate mean annual fisheries removals.

beaked whales) cetaceans (see Pike *et al.*, 2019, 2020a, b; Gilles *et al.*, 2020; Leonard and Øien, 2020a, b). Among the pinnipeds, harp seals and hooded seals are surveyed every 5 years (Stenson *et al.*, 2020), walrus are surveyed approximately every 6 years (Kovacs *et al.*, 2014), and coastal seals every 5–6 years (Hauksson, 2010; Nilssen *et al.*, 2010; Øigård and Hammill, 2012). The remaining marine mammal populations are assessed only opportunistically. We do not expect an increase in survey frequencies or coverage that would significantly reduce uncertainties in abundance estimates in the foreseeable future, unless monitoring costs are reduced by the use of new technologies (e.g. satellite images, use of drones, video, and acoustic techniques, Williamson *et al.*, 2016; Aniceto *et al.*, 2018; Cubaynes *et al.*, 2018; Bamford *et al.*, 2020). Also, inclusion of environmental covariates to model variation in spatial densities, and more use of information on ma-

rine mammal distributions and habitats in survey stratification, could further reduce abundance estimate uncertainties (e.g. Hedley and Buckland, 2004; Franchini *et al.*, 2020). Furthermore, such modelling refinements could also provide explanations for yet unexplained changes in whale distributions over time, movements of baleen whales between the Nordic Sea basins, for example (e.g. Víkingsson *et al.*, 2015; Storrie *et al.*, 2018; Leonard and Øien, 2020a, b), substantially impacting consumption estimates.

Uncertainties in consumption models reflect the limited data available on marine mammal energetic requirements (Leaper and Lavigne, 2007). While the requirements of smaller mammals can be measured in captivity and using field methods (e.g. Lavigne *et al.*, 1986; Lydersen and Kovacs, 1999), consumption models for large whales are predominantly based on indirect observations of feeding rates

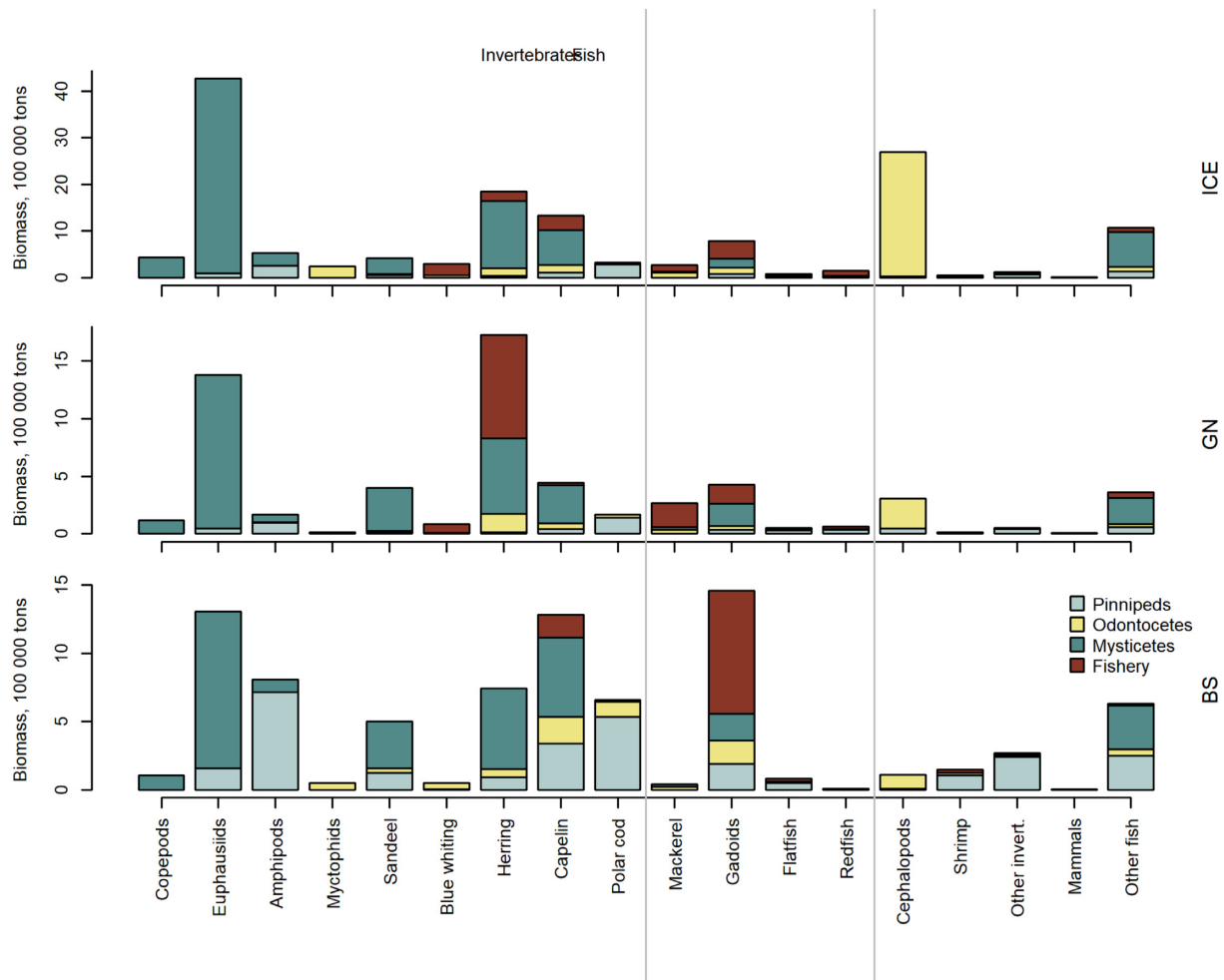


Figure 7. Mean annual removal of prey specie/group by marine mammal taxonomic groups and fisheries. Bar colours indicate proportions removed by pinnipeds, odontocetes, mysticetes, and fisheries.

(Baumgartner and Mate, 2003), stomach contents (Vikingson, 1997), respiration rates (Lockyer, 1981), seasonal variation in energy storage in tissues of harvested or stranded animals (Folkow *et al.*, 2000), and by extrapolation of models developed for smaller mammals (Leaper and Lavigne, 2007). More recently, sophisticated methods using high-resolution, multi-sensor, animal-borne instruments and *in-situ* hydroacoustics have allowed substantial improvements in estimates of energy requirements and consumption rates for several marine mammal species (Friedlaender *et al.*, 2015; e.g. Hazen *et al.*, 2015; Nowacek *et al.*, 2016; Goldbogen *et al.*, 2019). While such process studies are usually limited to a small number of individuals, they nevertheless have the potential to provide more accurate estimates of energy requirements and consumption rates, thereby reducing the uncertainty in population-wide assessments of prey consumption, ecosystem interactions, and marine mammal/fisheries interactions. Also, renewed interest in Dynamic Energy Budget (DEB) modelling within the context of marine mammal population responses to disturbance (Harwood *et al.*, 2020; Silva *et al.*, 2020), coupled with the ongoing improvements in methods for estimating energy requirements (Nowacek *et al.*, 2016), points to research that will reduce uncertainty associated with consumption models.

There is no routine monitoring of marine mammal feeding patterns in any of the areas considered in this study. Assessing detailed diet information is therefore a challenge, and analyses requiring such information are often based on opportunistic sampling that does not capture seasonal or geographic diet variation, or samples obtained from time periods with different prey availability from the current situation. In our study, we have included diet observations from the 1990s, both due to the limited number of observations and to capture more of the variability in the diet, specifically for the *euryphagous* species, such as minke whales and harp seals. However, shortage of diet data from the relevant ecosystems and recent time periods is likely to cause bias and undoubtedly increase uncertainties of consumption of the different prey groups beyond the estimated uncertainties in the current study. Indeed, uncertainties related to diet can exceed uncertainties related to abundance when estimating consumption of specific prey species (Shelton *et al.*, 1997). Hence, obtaining more spatially and temporally representative observations of prey use should be a research priority, especially for abundant *euryphagous* species. Indirect methods such as tracking marine mammal positions in food webs, using for example non-invasive sampling techniques for stable isotopes (Haug *et al.*, 2017a), might be useful to at least track major changes in prey use.

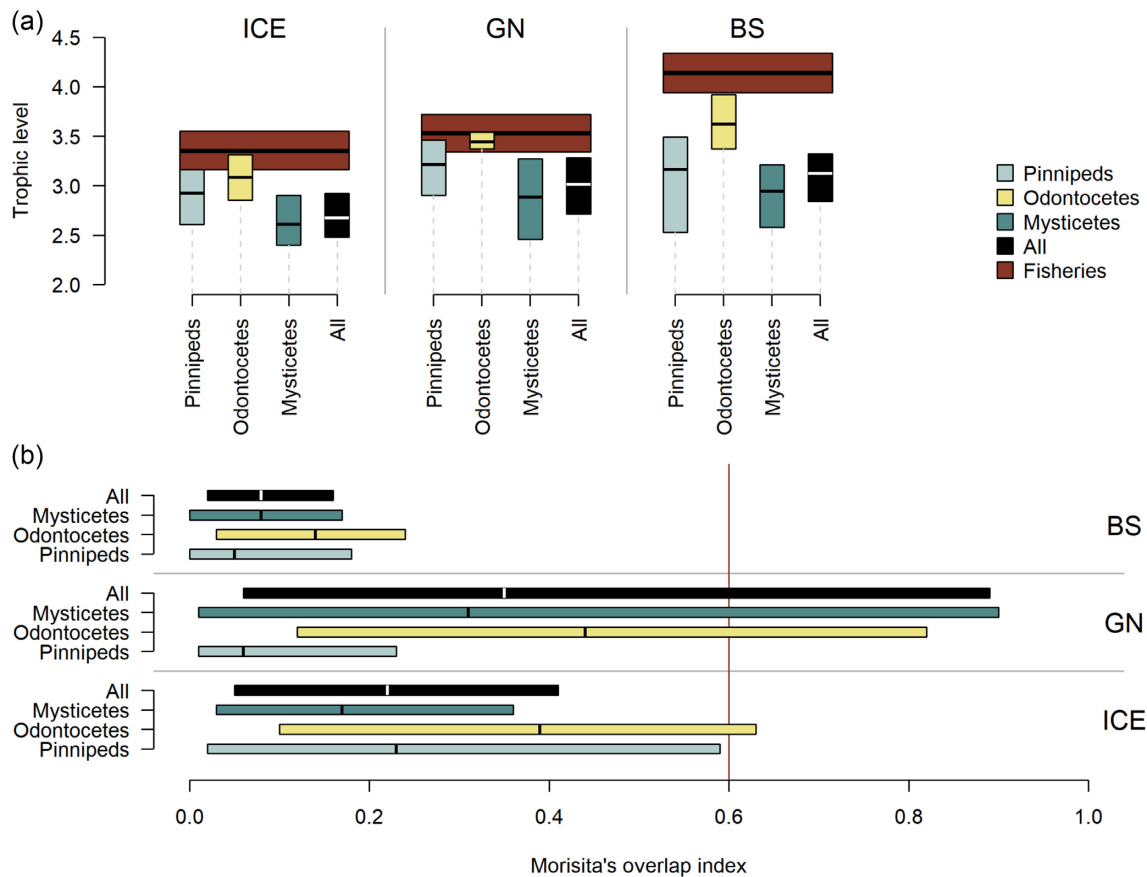


Figure 8. Indicators of potential competition between marine mammal groups (Pinnipeds, Odontocetes, Mysticetes, ALL taxonomic groups combined) and fisheries (red) in the ICE, GN, and BS regions. (a) TL overlap (red boxes mark the level of fisheries) and (b) Morisita's overlap index. Overlap estimates crossing 0.6 (indicated by red line) indicate statistically significant overlaps between mammal groups and fisheries.

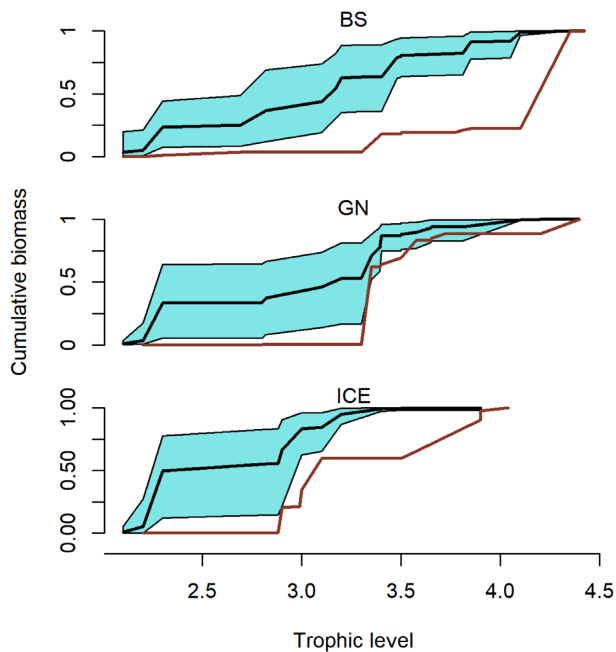


Figure 9. The relationship between TL and CB removal by fisheries (red line) and marine mammals in the ICE, GN, and BS regions. The blue shaded area corresponds to the 95% confidence envelope.

The ecological role of marine mammals and potential interactions with fisheries

Prey composition of marine mammals differed between the three regions. In the ICE, overall biomass consumed was highest for krill, followed by cephalopods, “other fish”, herring, and capelin. In the GN, consumption was dominated by krill, followed by herring, capelin, cephalopods, and “other fish”. In the BS, marine mammals consume mostly krill, followed by capelin, amphipods, herring, and polar cod. Dominant seal species are closely linked to the Arctic food webs, where amphipods and polar cod are key prey species. Although baleen whales occupy both boreal and Arctic habitats (Vacquié-Garcia *et al.*, 2017b; Moore *et al.*, 2019), they are batch feeders more tightly linked to boreal prey species that occur in dense aggregations, such as krill, herring, and capelin. Toothed whales consume mostly squid and fish, captured either by following individual prey or by collaborative herding of schooling species into tight aggregations (e.g. Similä and Ugarte, 1993). Furthermore, many toothed whale species, including sperm whales, use deep-water habitats and, therefore, are more significant consumers in the ICE and GN than in the shallow BS food webs, feeding on, e.g. myctophids, red-fish, Greenland halibut, lumpsucker, mackerel, blue whiting, herring, capelin, and cephalopods. Marine mammals consume similar or greater amounts of some commercially important stocks compared to fisheries in some regions. The three indi-

cators used to assess potential competition suggest that overlap between fisheries and marine mammals is greatest in the GN region. However, while foraging on similar pelagic fish age and size classes as targeted by fisheries, marine mammals may feed on younger and smaller individuals of e.g. gadoids, that may reduce direct competition (Fontaine *et al.*, 1994; Jansen *et al.*, 2010). Nevertheless, our results suggest that marine mammals play an important role as consumers in the ecosystems examined in this study.

DeMaster *et al.* (2001) argued that strong, direct competition between fisheries and marine mammals has primarily involved three types of interactions: (1) cases where a fishery has overharvested and severely depleted the target species, and where numerous and generalist marine mammal species prey on the same species (e.g. grey seal-cod interactions in north-west Atlantic, Benoit *et al.*, 2011); (2) cases where fisheries cause local depletions of key prey species utilized both by marine mammals and a fishery, causing declines in spatially constrained marine mammal populations (e.g. Steller sea lion and demersal fisheries in North Pacific, DeMaster *et al.*, 2001); and (3) cases involving general overharvesting of a target species that is also targeted by a specialist marine mammal predator, where a decline in the target species contributes to a decline in the marine mammal population (e.g. Hawaiian monk seals and bottom fish in the Pacific, Weijerman *et al.*, 2017).

While we cannot draw any firm conclusions regarding potential direct competitive interactions between fisheries and marine mammals in the northeast Atlantic and the Barents Sea, most marine mammal species in the ICE, GN, and BS are generalist predators, and those that have narrow dietary niches tend to prey on zooplankton (e.g. bowhead and blue whales) or cephalopods (e.g. sperm, pilot, and bottlenose whales), which are not subject to substantial exploitation by fisheries. Some marine mammal populations are quite mobile during the months when they forage most heavily. For example, while seals are restricted to specific locations during moulting and breeding, they generally perform long-ranging feeding migrations covering large portions of the study regions throughout the rest of the year (e.g. Folkow *et al.*, 2004; Nordøy *et al.*, 2008; Vacquié-Garcia *et al.*, 2017a). Notable exceptions are coastal seals (such as grey and harbour seals), which use land-based haul-out sites year-round. From a basin-scale ecosystem perspective, these coastal species occur at low numbers and contribute little to the overall consumption by marine mammals in the study area. Also on more local scales, scientific studies indicate that consumption by these species is generally negligible relative to fisheries removals, except in close vicinities to local seal colonies (Bjørge *et al.*, 2002; Nilssen *et al.*, 2019; Sørlie *et al.*, 2020). Yet, their influence on prey availability leads to controversies regarding the potential role of coastal marine mammals in the decline of coastal fish populations. Finally, few of the commercial fish species in the study region are suffering from current or past overfishing, although golden redfish (*Sebastes norvegicus*) in the BS and GN is at a critically low level and suffering from ongoing overfishing (ICES, 2020). Redfish is targeted by both hooded seals (Haug *et al.*, 2007) and odontocetes such as sperm whales (e.g. Martin and Clarke, 1986). The removals of this species in the GN and BS by mammals is comparable to that by fisheries. However, these redfish numbers also include the abundant beaked redfish (*Sebastes mentella*), with a stock biomass of 1.4 million tonnes, which is harvested at sustainable levels (ICES, 2020). Hence, the types of strong direct interactions identified

by DeMaster *et al.* (2001) may not occur within the study region, meaning that reducing fish removals by one “predator” may not directly benefit the other.

Nevertheless, marine mammals are significant determinants of energy flow through food webs in these regions. At the same time, fisheries also target species with food web connections. Mammal–fisheries interactions will thus depend on a combination of direct and indirect, food web mediated effects, with many trophic links and possible pathways through which responses can occur. One consequence of such complex food web mediated mammal–fisheries interactions is that the outcome is hard to predict and can even be counterintuitive, e.g. marine mammals can, in some cases benefit commercial species and their fisheries (Lindstrøm *et al.*, 2009; Morissette *et al.*, 2012). The trophic overlap between mammals and fisheries is greater in the GN than in the ICE and BS, and the fact that this is (i) a simpler system with fewer interactions and (ii) that both fisheries and mammals likely target overlapping size ranges of the small pelagic fish, such as herring, suggest that interactions between mammals and fisheries are stronger in the GN than in the ICE and BS. Also, these interactions may be strengthened by the unique wintering behaviour of this herring stock. In recent years, the herring population in the northeast Atlantic, which has a current spawning stock biomass of 3 million tonnes, has overwintered in dense aggregations inside narrow fjords in northern Norway, making them highly susceptible to predation by overwintering killer whales, humpback whales and to a lesser degree fin whales (e.g. Jourdain and Vongraven, 2017, Mul *et al.*, 2020, Vogel *et al.*, 2021). This may be a fourth type of strong, direct mammal–fisheries interaction to be added to DeMaster *et al.* (2001)’s list—one in which the targeted prey population is both concentrated and spatially constrained. Indeed, spatial distributions are also key to understanding more complex food web interactions between marine mammals and fisheries. Indices of relative overlap with fisheries for pooled groups of species (mysticetes/odontocetes) on large oceanic scales are not necessarily indicative of competition at smaller geographical or taxonomical scales. For example, in the ICE region, the large fin whale population feeds primarily on euphausiids in the open ocean, while the more piscivorous whale species (minke whales, humpback whales, and smaller odontocetes) are mostly confined to the shelf area where fisheries are also concentrated (Vikingsson *et al.*, 2015). Thus, analysis restricted to the Icelandic continental shelf ecosystem would undoubtedly give higher potential for competition than for the entire ICE region.

Marine mammals are harvested in all three regions: the ICE, GN, and BS in the study area (e.g. Haug *et al.*, 2017b; Moore *et al.*, 2019; Stenson *et al.*, 2020). In general, these harvests have been well below issued quotas in recent years, averaging 4.3, 1.4, and 2.0 thousand tonnes of mammals in the ICE, GN, and BS, respectively, corresponding to 0.12, 0.13, and 0.17% of the total biomass of all mammals in these regions. Such removals are unlikely to have detectable impacts on marine mammal prey consumption or on interactions with fisheries, as the numbers/biomasses taken are well within the uncertainty bounds of the total biomass estimates.

Implications for management

Marine mammals are significant components of the food webs in the study region and hence must be included in fish-

eries management strategies in a multispecies, ecosystem context. Extended single species assessment models (ESAMs) have been developed for some species to account for multispecies interactions (Skern-Mauritzen *et al.*, 2016; ICES, 2018). For example, the capelin consumption by NEA cod is included in the BS capelin assessment (Gjøsæter *et al.*, 2002). A similar system is in use for capelin management in the ICE where predation by NEA cod, haddock, and saithe is taken into account (MFRI, 2021). This approach might be particularly relevant for the herring fisheries, due to the potentially high predation mortality on over-wintering herring. An ESAM model exist for Norwegian spring spawning herring, in which predation by minke whales is included (Tjelmeland and Lindstrøm, 2005), but it was never made operational.

Accounting for multispecies interactions in ESAM demands regular, preferably annual, monitoring of predator diets to obtain sufficiently precise consumption estimates. The monitoring intensity of marine mammal prey use is not likely to be achieved within the near future, due to both sampling challenges and for many species the conservation status of these wide-ranging animals. However, some of the novel methods described above, and improved logistics for marine mammal monitoring that makes use of ongoing fisheries research activities, should be explored as approaches to improve our ability to address specific questions regarding predator/prey and marine mammal–fisheries interactions, as well as complement less frequent, dedicated marine mammal surveys.

While the ESAM models can be used operationally for annual quota advice, more complex multispecies and ecosystem models should be used more strategically to test the wider implications of different harvesting strategies. For instance, to assess whether reference points such as maximum sustainable yield (MSY) and fish stock biomass at MSY (BMSY) in fisheries harvest control rules are robust in allowing for current and future increases in marine mammal consumption and associated uncertainties.

Including biological interactions in ecosystem models often leads to decreased MSY and increased BMSY estimates, resulting in reduced harvest quotas for commercial fish stocks (e.g. Hollowed *et al.*, 2000; Link *et al.*, 2015). Yet, in our study regions synergistic interactions may, under specific circumstances, also support increased harvesting levels. Climate warming has already caused profound changes in these high-latitude systems, including warmer waters, increased primary and secondary production, reduced sea ice cover, and large-scale reorganization of food webs due to changes in species abundances and distributions, at all TLs from plankton through fish to marine mammals (Øigård and Smout, 2013; Dalpadado *et al.*, 2014; Víkingsson *et al.*, 2014, 2015; Fosshem *et al.*, 2015; Moore *et al.*, 2019; Stenson *et al.*, 2020). In both the ICE and the BS, there are indications of negative impacts on marine mammals due to abundant mackerel and NEA cod stocks, which are currently favoured by the warmer conditions (Bogstad *et al.*, 2015; Víkingsson *et al.*, 2015). However, there is little or no tradition, experience or agreement on how to manage very abundant fish stocks that have unwanted effects on populations of other species (e.g. Skern-Mauritzen *et al.*, 2016).

The implementation of the new Harvest Control Rule (HCR) for NEA cod in 2016, which allows for increased fishing mortality at high cod abundances, represents a novel management approach (Sparholt *et al.*, 2021). However, while wider ecosystem effects of high cod abundances were part

of the rationale for implementing the HCR, this new management approach was, in fact, not tested in multispecies or ecosystem models prior to implementation. Hence, its effectiveness in alleviating climate change related stress on the BS food web, including marine mammals, is yet to be assessed. While our study shows that models including a wider range of species from the marine mammal community are clearly warranted to capture the biomass flow through these food-webs, similarities in both distributions and diets allow for lumping mammals into larger functional groups. However, to enable any firm conclusions to be drawn on potential competition between marine mammals and fisheries on a more local scale, model inputs can differ widely between areas, in particular for the generalist species (e.g. diet and residence time of predators), and should preferably originate from that particular ecosystem.

Our estimates, combined with previous studies, demonstrate that shifting marine mammal abundances and distributions alter the consumption by mammals over decadal and possibly shorter time scales. The rates of such changes are likely to increase with continued climate change, due to changes in abundance and distribution of key prey species in response to changes in habitat (e.g. distribution of sea ice and open water habitats). For instance, Arctic amphipods and polar cod, which are key prey species for many seals in Arctic food webs (see Bengtsson *et al.*, 2020; Stenson *et al.*, 2020), are currently declining and retreating northward (Huserbråten *et al.*, 2019; ICES, 2019b; Stige *et al.*, 2019) possibly forcing Arctic seals into more boreal food webs with stronger interactions with both boreal marine mammals and fisheries. Additionally, there is established harvest at lower TLs in the northeast Atlantic (see <https://calanus.no/resource/>). These fisheries may increase overlap with marine mammal prey requirements and thus, increase the potential for competition and interaction between marine mammals and fisheries. However, EBFM considerations should also include the wider role of marine mammals in marine ecosystems. For instance, as food web connectors connecting separate energy pathways, marine mammals may enhance foodweb robustness to perturbations, a property becoming increasingly important with climate change (Blanchet *et al.*, 2019; Cooley *et al.* in press).

Although much uncertainty remains, our work demonstrates that over the last decades we have improved information on marine mammal abundances, distributions and diets, as well as improved our understanding of energy needs and species interactions. This supports the implementation of the EBFM approach in these high-latitude systems. To enact such a framework, regular marine mammal abundance and distribution monitoring are crucial, but we also recognize the need for more targeted studies of prey use and direct interactions between marine mammals and other ecosystem components, including fisheries.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability statement

All data are incorporated into the article and its online supplementary material.

Author contributions

MS-M led the work, including performing most of the calculations and the writing of the manuscript. UL was responsible for indicator analyses. All authors helped identifying relevant data and references, and assisted in the writing of all sections.

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