Fisheries and Oceans Canada | Pêches et Océans Canada
Ecosystems and Oceans Science | Sciences des écosystèmes et des océans

Canadian Science Advisory Secretariat (CSAS)

Research Document 2024/018

Quebec Region

Consumption of Northern Contingent Atlantic Mackerel (*Scomber scombrus*) by Various Predators

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April 2024

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044
ISBN 978-0-660-70559-0 Cat. No. Fs70-5/2024-018E-PDF

Correct citation for this publication:

Van Beveren, E., Smith, B., Smith, L., and Pelletier, D. 2024. Consumption of Northern Contingent Atlantic Mackerel (*Scomber scombrus*) by Various Predators. DFO Can. Sci. Advis. Sec. Res. Doc. 2024/018. v + 41 p.

Aussi disponible en français :

*Van Beveren, E., Smith, B., Smith, L., et Pelletier, D. 2024. Consommation du contingent nord du maquereau bleu (*Scomber scombrus*) par divers prédateurs. Secr. can. des avis sci. du MPO. Doc. de rech. 2024/018. v + 46 p.*

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ABSTRACT

Atlantic mackerel is a forage fish species preyed upon by various predators, including seabirds, pinnipeds, cetaceans, tuna and groundfish. We assessed the potential order of magnitude of total mackerel consumed by each of these groups, and any change therein. This is a first step to incorporate ecosystem considerations within the mackerel stock assessment and inform assumptions on the natural mortality rate. We concluded that an ensemble of predators is likely driving overall natural mortality patterns, with apparent changes in the relative contribution of each predator group over time. The reliability of consumption estimates varied between predators, but there was indication that overall absolute removals might have increased over time, despite possibly large interannual variations. Depending on the functional response between each predator and mackerel density, this increase could translate into a rise in the natural mortality rate, as estimated spawning stock biomass has been below or near the limit reference point since 2011. The likely increase in mackerel consumption is also inverse to changes in fishery landings; during the 10 last years (2012-2021) mackerel consumption by predators became likely at least twice as high as reported Canadian landings (<11 kt).

1. INTRODUCTION

Management of commercial fisheries in Canada is based on information on stock status and fishing pressure, provided by a scientific stock assessment. Such an assessment often involves the use of a model that integrates multiple data sources and relies on several assumptions about the stock and fishery dynamics. One of the most common assumptions is that the instantaneous natural mortality rate (*M*) is constant over time. It is however well-known that this is often untrue, potentially generating significant bias in the science advice (e.g., Deroba and Schueller 2013; Johnson et al. 2015; Forrest et al. 2018; Punt et al. 2021). To address this issue, various research papers aimed at estimating the consumption of a species of interest by one or more of its key predators (e.g., Moustahfid et al. 2009; Benoît et al. 2011; Trijoulet et al. 2018). For the large majority of fish stocks, consumption estimates remain nonetheless elusive as a great deal of data and effort is required to obtain this information. For instance, some knowledge of the predator's abundance, diet composition, energetic needs and spatiotemporal interaction with the prey is required. Estimating prey consumption is especially challenging for highly migratory species, as they might face a variety of predators along their migration path, and predator-prey interactions can vary drastically over time and space.

West-Atlantic mackerel is a highly migratory pelagic species that is also at the centre of the food-web. The northern contingent, which spawns predominantly in the southern Gulf of St.-Lawrence, is currently assessed by Canada as a distinct unit. The assessment relies on a statistical catch-at-age model in which natural mortality rate is constant over time and age (Van Beveren *et al.* 2023a), a common assumption in stock assessment models. The current model framework requires an external estimate of *M*, and there is insufficient information in the data to attempt within-model estimation. Previous attempts at providing more realistic mortality values based on life-history approaches (methods of for instance Alverson, Gislason, Gunderson and Zhang; see Grégoire and McQuinn 2014) provided divergent results and did not improve the model fit (Van Beveren et al. 2020). The constant *M* hypothesis remains however questionable in light of the increases in the stock's putative main predators (northern gannets, Atlantic bluefin tuna and grey seals; Carruthers and Butterworth 2018; Guillemette et al. 2018; Rossi et al. 2021). An increase in mackerel consumption would contrast sharply with the assumed decrease in absolute deaths; under a constant *M*, absolute deaths decrease in parallel with the decrease in estimated Spawning Stock Biomass (SSB).

Here we make a first attempt at assessing potential large-scale changes in mackerel consumption over time based on predator-specific data on their abundance, diet composition and energetic needs. Consumption can rarely be estimated precisely, as analyses are often based on imperfect or fragmentary data that are collated using various assumptions. We therefore present a framework in which all assumptions are made transparent, that can easily be updated to include more recent years or reflect improved knowledge, or extended to include other predators. Future work might focus on the integration of these results into the assessment.

2. METHODS

In order to gain an understanding of the magnitude of collective mackerel consumption and the relative importance of individual species, the first step is to identify potentially important predators (Table 1). For a predator to be important, at least three of the following criteria must be salient: I) its spatio-temporal distribution with mackerel, II) the percentage of mackerel in its diet, III) its population abundance and/or IV) the energetic need of an individual.

Atlantic mackerel start their spring migration around the end of May by moving to warmer surface waters on the Scotian Shelf. The majority of fish then migrate towards their dominant

spawning ground in the southern Gulf, typically around early June. Later in the year, they disperse across the Gulf of St.-Lawrence and Newfoundland for feeding. Finally, they return to deeper waters on the Scotian and US shelf.

Once predators were identified, we compiled the variety of data required to initiate a consumption estimation algorithm.

2.1. IDENTIFICATION OF KEY PREDATORS

2.1.1. Seabirds

Atlantic mackerel are available to seabirds when they are in warm surface waters from late spring to fall. Because northern contingent mackerel are in East Canadian waters during that period, predation by seabirds is therefore only considered within this area.

In Canada, northern gannets are known to predominantly feed on mackerel when available. They have evolved a specific plunge-diving foraging technique adapted to mackerel's high swimming speed (Garthe et al. 2014). Gannets in Canada form large colonies that can remove multiple thousands of tons of mackerel from the ecosystem each year (Cairns et al. 1991; Guillemette et al. 2018). There are six major gannet colonies off East-Canada, and all were included in this research document.

Other seabird species were excluded from consideration as their contribution to total mackerel mortality is expected to be minor. Other abundant piscivorous bird species show foraging behaviors likely less efficient at capturing mackerel. Stomach samples of double-crested cormorant in the southern Gulf, which overlapped with the presence of mackerel in the area, suggested that mackerel represents a very small proportion of their diet (1.1%W, May-Aug 1977-1978; Pilon et al. 1983). Other reports on stomach contents of double-Crested cormorants, focusing again on an area and moment when mackerel is present, do not mention mackerel (see Cairns et al. 1991; Rail and Chapdelaine 1998). Likewise, great cormorants and black guillemots, although abundant, appear to not or only sporadically consume mackerel (Cairns et al. 1991). Further, the overall energetic needs of these seabirds are low compared to other potential predators (e.g., seals, cetaceans, Atlantic tuna) and their spatial overlap with mackerel is mostly limited to coastal waters, supporting the assumption that their annual consumption of mackerel is small compared to other predators.

2.1.2. Pinnipeds

Grey and harbour seal are the two dominant pinniped species in the waters of Atlantic Canada in summer. The grey seal population, with breeding herds in the southern Gulf, on Sable Island (Scotian Shelf) and along the coast of Nova Scotia, has reached record levels (Hammill et al. 2023). Although this triggered conservation concerns for several prey species (e.g., Rossi et al. 2021), the impact of the seal increase on the mackerel stock is unquantified. Although mackerel is acknowledged to be a less common prey, the large numbers of grey seals and their high energy demand could make them a significant contributor to mackerel natural mortality.

The US grey seal colonies were excluded from our analyses as they are at least ten times less abundant than the three Canadian breeding herds combined (Hayes et al. 2022), they prey on northern contingent mackerel only during winter when foraging intensity is less intense (Beck et al. 2003), and when both contingents are mixed in deeper waters. Smith et al. (2015) estimated annual consumption of scombrids (including an important fraction of southern contingent mackerel) by US grey seals to be around 0.6kt (80% CI: 0.2-1 kt).

Harbour seals in Canada are compared to grey seals more stationary and prefer shallow near-shore waters (Lesage et al. 2004), often in regions not regularly or intensively frequented by mackerel, or only so during a relatively short period (e.g., the estuary and northern Gulf). Diet data of harbour seals is rare, but we are not aware of evidence that mackerel is an important prey. Harbour seals are also much less abundant and smaller (lower energetic requirement) than grey seals. They therefore remove less fish biomass from the ecosystem (total fish consumption by the population estimated at around 5 t in 1996; Hammill and Stenson 2000). In US waters, harbour seals consume a mix of southern and northern contingent mackerel. The annual consumption of scombrids by US harbour seals was estimated to be around 1.1 kt (80% CI: 0.18-2.9 kt; Smith et al. 2015).

2.1.3. Cetaceans

Numerous cetacean species feed in the waters of Atlantic Canada during summer. Four of the most prevalent whale species are the harbour porpoise, long-finned pilot whale, common dolphin and white-sided dolphin (Lawson et al. in prep.[1]; Lawson and Gosselin 2009). Because the overlap of their spatial distribution with mackerel is poorly defined, information on their diet is rare, and their abundance estimates are punctual and highly uncertain, estimates of mackerel consumption by these cetacean species would be limited in time and space and highly uncertain. Other species are less abundant and do not or only occasionally feed on mackerel (e.g., minke and humpback whales, e.g. Johnson and Davoren 2021).

Cetaceans also feed on mackerel in winter on the U.S. shelf (Smith et al. 2015). Because of a lack of data, we currently could not integrate Atlantic U.S. cetaceans in our analysis.

2.1.4. Pelagic fish

Atlantic bluefin tuna is the only pelagic fish species with significant spatio-temporal overlap with mackerel, that is abundant and large enough to consume substantial amounts of this prey species. There are two stocks of Atlantic bluefin tuna, associated with either the western or eastern Atlantic. Both stocks are highly migratory, transboundary, and can migrate to and spent time in East Canadian waters in summer and fall. Tagging demonstrated that bluefin tuna could be present in the Gulf of St. Lawrence (GSL) from early June to mid November (Block et al. 2019) and small pelagic fish, including mackerel, are a key component of their diet in the region (see section 3.4.2).

Striped bass was not included because despite its increase in abundance (DFO 2021), its distribution within Canada is limited to coastal waters, mackerel is not an important prey species (e.g., Hanson 2020), and their energetic need is small compared to tuna.

2.1.5. Groundfish

The potential importance of various groundfish predators is in large part driven by the vertical component of their spatial distribution. During roughly the warmest half of the year (late spring to fall), mackerel inhabit surface waters and there is a vertical mismatch with the habitat of the various groundfish species. For instance, around the Magdalen Islands, only about the upper 12 m of the water column is suitable thermal habitat for mackerel (e.g., Galbraith and Grégoire

[1] Lawson, J., Gosselin, J.-F., St.-Pierre, A. In prep. Abundance and distribution of cetaceans during the North Atlantic International Sighting Survey (NAISS) in 2016. DFO Can. Sci. Advis. Sec. Res. Doc.

2015). Large-bodied species such as Atlantic cod, white hake and thorny skate occur in contrast often in deeper off-shore waters, especially during the last two decades (Swain et al. 2015). Dietary studies for larger species typically abundant in bottom trawl surveys covering the Gulf of St.-Lawrence and Atlantic Canada (Swain et al. 2015; Bourdages et al. 2020; DFO 2020) such as Atlantic cod (Kohler and Fitzgerald 1969; Waiwood and Majkowski 1984; Schwalme and Chouinard 1999; Hanson and Chouinard 2002; Hanson 2011), white and silver hake (Waldron, 1992) and pollock (Carruthers et al. 2005) indeed indicate that mackerel is a prey item of low overall importance (often only to some extend to the less abundant largest fish). Further, extensive diet composition data of groundfish in the US collected during fall and spring bottom trawl surveys supports the idea that none of the above mentioned groundfish predators would consume substantial quantities of mackerel during summer.

From late fall to early spring, mackerel from both the southern and northern contingents overwinter in deep shelf waters. Previous U.S. studies indicated that mackerel has some importance in the winter diet of especially spiny dogfish (on average ~10% mass in their diet; Link and Almeida 2000; Smith and Link 2010). Because stomach content and abundance data of groundfish in the area is routinely collected by NOAA through a spring and fall bottom trawl survey (see Link and Almeida 2000; Smith and Link 2010), estimates of time-varying total mackerel consumption can be produced. We included 9 U.S. groundfish predators for which sufficient data is available to estimate consumption, amongst which are the most likely to affect mackerel biomass (e.g., spiny dogfish). Others like fourspot flounder (*Hippoglossina oblonga*) were excluded because mackerel was never found in their diet.

Table 1. List of species included in this study.

Group	Common name	Latin name	Region	Subunits
Seabirds	Northern gannet	*Morus bassanus*	Gulf, Newfoundland	6 East-Canadian colonies
Pinnipeds	Grey seal	*Halichoerus grypus*	Gulf, Nova Scotia	Southern Gulf & Nova Scotia (Atlantic coast & Sable Island) herds
Cetaceans	Harbour porpoise	*Phocoena phocoena*	Atlantic Canada	-
	Common dolphin	*Delphinus delphis*		
	White-sided dolphin	*Lagenorhynchus acutus*		
	Long-finned pilot whale	*Globicephala melas*		
Pelagic fish	Atlantic bluefin tuna	*Thunnus thynnus*	Gulf	-
Groundfish	Atlantic cod	*Gadus morhua*	Atlantic U.S.	-
	Bluefish	*Pomatomus saltatrix*		
	Goosefish	*Lophius americanus*		
	Red hake	*Urophycis chuss*		
	Silver hake	*Merluccius bilinearis*		
	Spiny dogfish	*Squalus acanthias*		
	Summer flounder	*Paralichthys dentatus*		
	White hake	*Urophycis tenuis*		
	Winter skate	*Leucoraja ocellata*		

2.2. CALCULATIONS

There are many studies estimating prey consumption, but they are often focused on one or on few predator groups (e.g., Van Beveren et al. 2017; Guillemette et al. 2018; Saraux et al. 2021). Although the overall concept to estimate prey consumption is always alike, there can be variations in the algorithm because of differences in data availability or predator biology. Here we present a stepwise approach aimed at creating a generic and transparent framework that can easily be applied to a suit of predators.

The total annual consumption (C_y, in tonnes) of mackerel by a given predator (population, stock or a specific unit of it) is given by the following general principle;

$C_{y,i} = \sum_{l=1}^{L} N_{y,l,i} * \%W_{y,l,i} * TI_{y,l,i}$,

where $N_{y,l.i}$ is the total abundance (numbers) of the predator by year *y*, level *l* and iteration *i*, $\%W_{y,l,i}$ is the average proportion of mackerel in the diet in terms of weight over a specific period ($DAY_{y,l,i}$, see further) and area during which predator and prey overlap (%g), and $TI_{y,l,i}$ is the average total ingestion rate (t/year) of the predator over this period. The level *l* is predator dependent and can be any combination of different life stages (e.g., age such as for tuna and seals or chick, breeders and non-breeders for seabirds), sex (e.g., seals) and subunits (e.g., herds for seals or colonies for seabirds). For some predators the lack of finer scale data forces us to work with a single level (e.g., cetaceans). Note that in consumption studies both the proportion of the prey in the predator's diet (second component in the equation) and the predator's energetic needs (third component in the equation) are often expressed in units of energy (% kJ and kJ/year, respectively) rather than weight, because different prey species could have a different energy density (kJ per unit of body mass) and a shift in diet might affect the total mass of prey consumed. Because diet composition data is rare and often provided in weight, we applied a less time- and data-intensive weight-based approach.

For the large majority of predators, $TI_{y,l,i}$ is not readily available and is calculated as the product of the daily ingestion rate ($DI_{y,l,i}$, g/day) and the number of days ($DAY_{y,l,i}$, days) during which the predator consumes the prey of interest;

$TI_{y,l,i} = DI_{y,l,i} * DAY_{y,l,i} * 10^{-6}$

Estimates of $DI_{y,l,i}$ can be obtained in various ways. If information derived from experimental studies is unavailable (option 1), $DI_{y,l,i}$ can be estimated by multiplying the predator population's average body mass ($M_{y,l,i}$, g) with a daily ration, expressed as a fraction of body mass ($\%BM_{y,l,i}$, % per day);

$DI_{y,l,i} = M_{y,l,i} * \%BM_{y,l,i}$ (option 2)

Another approach is based on the gastric evacuation rate (Eggers 1977; Elliott and Persson 1978) of the predator, habitually used by NOAA to estimate fish predation pressure on the northeast US continental shelf (e.g., Smith et al. 2016; Smith and Smith 2020). The predator-specific gastric evacuation rate $E_{y,l,i}$ (%/day) is estimated as a function of habitat temperature ($E_{y,l,i} = a * e^{b*T}$, where a and b are evacuation rate parameters) and is subsequently multiplied by the average weight of stomach contents collected over 24 h ($SW_{y,l,i}$), and a 24 h timeframe;

$DI_{y,l,i} = 24 * SW_{y,l,i} * E_{y,l,i}$ (option 3)

Additionally, $DI_{y,l,i}$ can be computed by dividing daily energy expenditure ($DEE_{y,l,i}$, kj/day) by the average energy density of the diet ($ED_{y,l,i}$, kj/g) and the assimilation efficiency ($AE_{y,l,i}$, here defined as the proportion of prey energy not fully ingested because of regurgitation or partial prey consumption);

$DI_{y,l,i} = \frac{DEE_{y,l,i}}{ED_{y,l,i} * AE_{y,l,i}}$ (option 4)

For some predators, estimates of $DEE_{y,l,i}$ can be extracted directly from bio-energetic models. In the absence of such a model, the (modified) Kleiber equation (Kleiber 1975) can be applied;

$$DEE_{y,l,i} = \frac{\alpha * M_{y,l}^{\beta} * AF_i * GP_{l,i}}{ME_{l,i}},$$

where α is the intercept and β is the scaling exponent for the Kleiber equation $\alpha * M_{y,l}^{\beta}$, which determines the allometric relationship between a predators' body mass ($M_{y,l,i}$) and its metabolism. A modification can be made for species which require additional energy during early life growth (in this study seals, see Benoît et al. 2011). If such information is available a growth premium (GP) is added. An activity factor (AF) can be included to correct for increased metabolism due to changes in activity, and a proportion of metabolized energy (ME) can be provided to represent the proportion of energy that is available to maintenance and growth. Both GP and AF are however commonly unaccounted for (or assumed to be one).

US groundfish prey on mackerel from the northern and southern contingents during winter. Estimates of season-specific mackerel consumption are already available online. We assumed that between 15% and 85% of total winter removals (6 month periods) would be mackerel from the northern contingent ($C_{y,i} * \%NC,\ with\ \%NC \sim unif(0.15,0.85)$, based on the large uncertainty in contingent mixing strength and indications of large interannual variability therein (Arai et al. 2021).

All parameters have uncertainty associated with them. Calculations were therefore bootstrapped (n samples *i* per *l* of each parameter) and the median values with their 95%CI across simulations are presented (n = 300 for grey seals with a high number of levels, n = 1000 for all other predators). A range of uncertainty distributions were used (normal, uniform, multivariate normal, pert, gamma), as well as pre-sampled values from a combination of model posterior distributions (e.g., multi-model assessment estimates of $N_{y,l}$).

The total number of simulations used for each predator may differ due to variations in computational costs. To sum consumption estimates for all predators, each characterized by their own uncertainty distribution, estimates were first summed over all levels *l* to obtain predator-specific annual values. These values were if necessary resampled to obtain 1000 simulations for each predator (e.g., seals), before total consumption was calculated for each simulation and the median and 95% CI were determined.

2.3. PARAMETERS

The parameters and assumptions used for each predator are summarized in tables S1-S4 and are detailed below. All input values, code and output are available on github (consumption repository).

2.3.1. Seabirds

All parameters used to estimate predation by gannets are provided in Table S1. Consumption is estimated by life-stage: breeders, non-breeders and chicks (e.g., Guillemette et al. 2018, Saraux et al. 2021). Northern gannets consume mackerel at each stage.

2.3.1.1. Abundance of breeders

The number of breeding birds ($N_{y,c}$) was received from Jean-Francois Rail (pers. comm., Environment and Climate Change Canada, Canadian Wildlife Service) for all 6 Canadian colonies (c; for details on methodology see Chardine et al. 2013; Rail et al. 2013). Time-series are not continuous and years ($y = \{1968, ..., 2021\}$) with no estimates were extrapolated using a colony-specific Generalized Additive Model (gam; $N_y \sim s(y)$, gaussian), with k set to 3 for Anticosti Island, but kept at the default for all other populations (Figure 1). To avoid negative values, abundance estimates at Bird Rock were kept constant for the first 6 extrapolated years.

Estimates of gannet abundance do not have uncertainty associated with them, and none was added as observation error associated with such aerial surveys is considered small (J.-F. Rail, ECCC, pers.comm.).

2.3.1.2. Abundance of non-breeders

The abundance of non-breeders is calculated as the product of the number of adults ($N_{y,c}$) and the fraction of birds that are non-breeders ($\%NB_{y,c}$). Guillemette et al. (2018) assumed that $\%NB_{y,c}$ for the Gulf colonies (Anticosti Island, Bonaventure Island and Bird Rock) is 0.11. However, Montevecchi *et al.* (1988) used a value of 0.25. In our analyses, we sampled values so that $\%NB_{y,c} \sim unif(0.11,0.25)$.

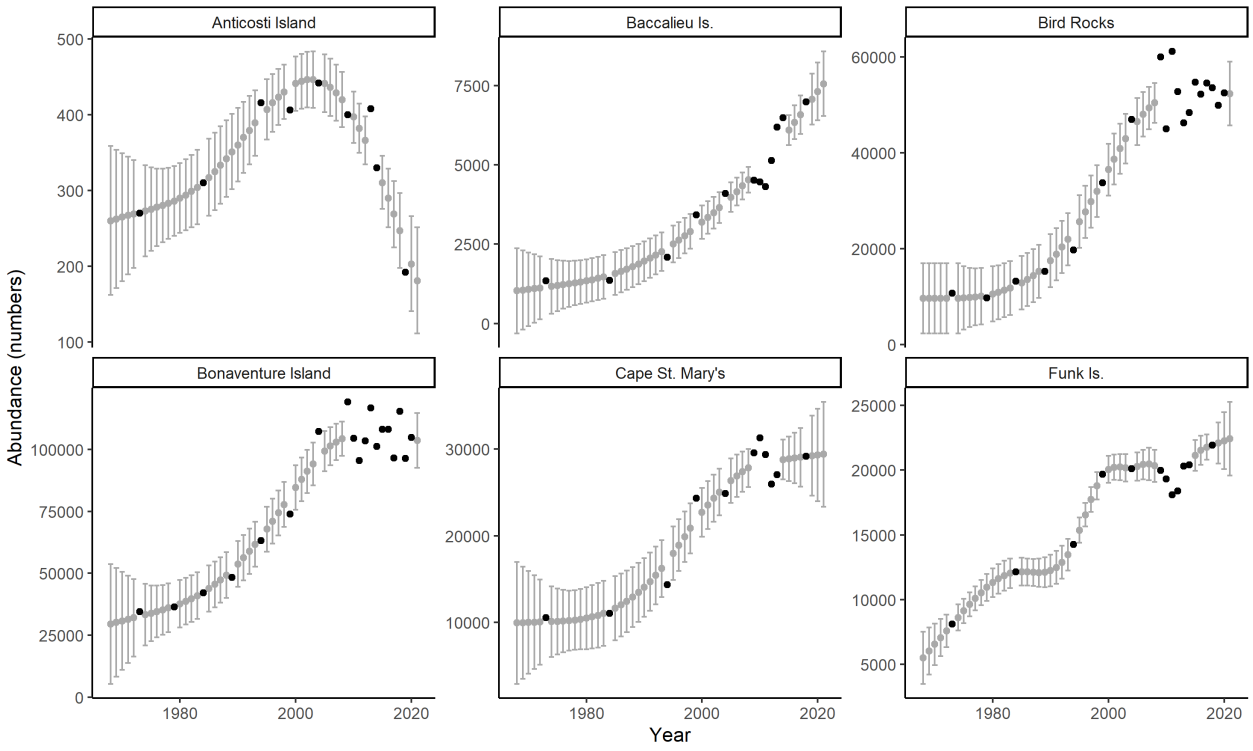

Figure 1. Annual abundance of breeding gannets in colonies in Atlantic Canada (mean + 95% CI). Black values indicate observations, whereas grey dots and bars are interpolations.

2.3.1.3. Abundance of chicks

The abundance of chicks is calculated as the product of the number of breeding pairs ($N_{y,c}/2$) and the breeding success ($B_{y,c}$, number of chicks fledged per active nest). Time-series of breeding success (Figure 2) are collected by the Canadian Wildlife Service and were received from Jean-Francois-Rail (pers. comm., see Rail et al. 2013) and supplemented with data from d'Entremont et al. (2022b) and Pelletier and Guillemette (2022). For Bonaventure Island, we used a gam to predict breeding success for missing years ($B_y \sim s(y)$, gaussian distribution), and average breeding success during the early period (1968-1974) was assumed to be constant and identical to the prediction for the initial year (1976). The observations for Bonaventure Island do not have uncertainty associated with them; we applied the average CV of observations from the St Mary's colony. For St. Mary's, missing values prior to 2009 were replaced with the average (with 95% CI) across the time-series up to and including 2010. For all other colonies (Funk Island, Anticosti Island, Baccalieu Island and Bird Rock), unless estimates were available, we

assumed that the breeding success was within the average (95% CI) observed across all colonies and years. The two estimates available for Bird Rock were assumed to have the same CV as was on average calculated for St. Mary's.

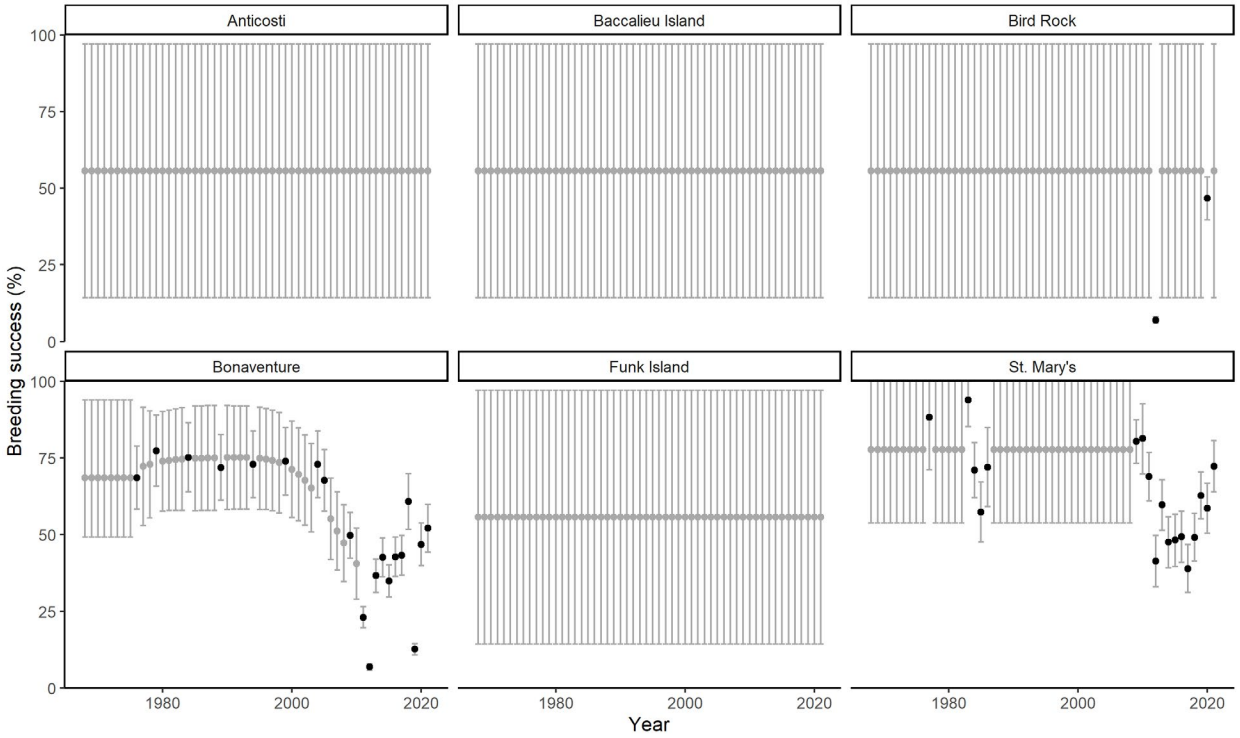

Figure 2. Annual breeding success of gannet colonies in Atlantic Canada (mean + 95% CI). Black values indicate observations, whereas grey dots and bars are interpolations.

2.3.2. Pinnipeds

All parameters used to estimate predation by grey seals are provided in Table S2.

2.3.2.1. Abundance (N)

Estimates of beginning-of-the-year seal abundance by year ($y = \{1960, ..., 2022\}$), sex ($s = \{female, male\}$), herd ($h = \{Scotian\ Shelf, Gulf\}$) and age ($a = \{0, ..., 30+\}$) were obtained from a new integrated Bayesian population model (Rossi et al. 2021) that was used during the 2021 fall seal stock assessment (Hammill et al. 2023). Four model configurations were retained during this process, and we correspondingly work with equally weighted posterior samples ($N_{y,s,h,a}$) from these four models (see Figure 10 in Hammill et al. 2023). Because we directly work with posterior samples, covariance between the different levels (year, sex, herd and age) is included.

Most mackerel consumption by seals presumably takes place in summer. Therefore, model-specific posterior samples of $M_{s,a}$ were used to estimate $N_{y,s,h,a}$ in June ($N_{y,s,h,a}e^{-M*5/12}$) (Figure 3).

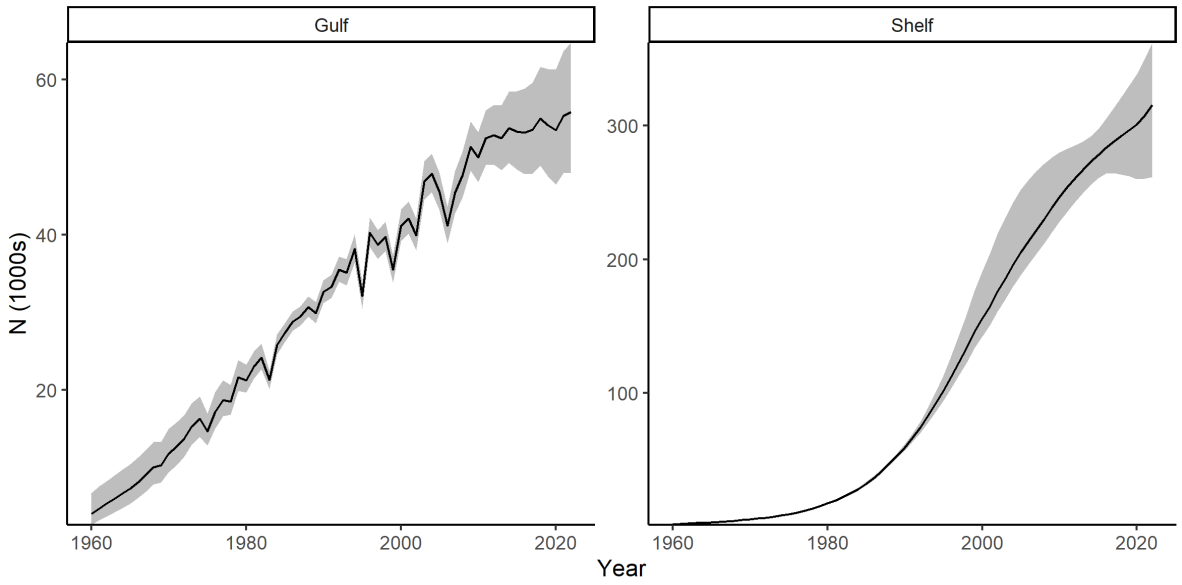

Figure 3. Abundance estimates (thousands) of grey seals (median and 95% CI) for the southern Gulf and Scotian Shelf in June, based on 2000 simulations per level.

2.3.2.2. Average proportion of mackerel in the diet (%W)

Available information on East-Atlantic grey seal diet is summarised in Table S5. Although over the past decades, the diets of at least 3000 seals from Canadian waters have been analysed based on stomach, intestine, faeces or fatty acid analyses, the proportion of mackerel in them remains highly uncertain. All studies agree that mackerel is a minor prey source, of which the relative important varies during and between years (Benoit and Bowen 1990a; Hammill et al. 2007) as well as between regions (although not necessarily sex, e.g., Hammill 2011; Hammill et al. 2014a). To accurately reflect the proportion of mackerel in the diet and total mackerel consumption, samples covering these various levels would be needed and the drawbacks of each sample method should be well understood. Such an effort is unrealistic, and in reality the data are fragmented and prone to several sources of bias. For instance, stomach content and faecal data have known issues with species-specific digestibility of prey. Further, samples are collected from seals hunted on a limited number of beaches, and are therefore often specific of onshore diets with a certain degree of pseudo-replication.

Based on the available information, we assumed that mackerel contributes up to 4% of the average grey seal diet ($\%W_{y,c} \sim unif(0.1\%, 4\%)$). Although some studies provide higher estimates, they are unlikely to be applicable to the entire population, as these values are from very specific periods or regions, or resulted from small sample sizes. Note that more recent unpublished data exist that could, after validation, be used to narrow this range of values.

2.3.2.3. Mass (M)

Sex-specific seal mass-at-age $M_{s,a}$ was estimated using the approach presented by Benoît et al. 2011. Average values were first predicted based on the Gompertz growth model (Mohn and Bowen 1996);

$$M_{s,a} = \gamma_{1s} * exp^{(-\gamma_{2s} * exp^{(-\gamma_{3s} * a)})},$$

where γ_{1s}, γ_{2s} and γ_{3s} are sex-specific stochastic parameters that follow a normal distribution (see Table S6). Seal mass can however change significantly during the year due to breeding,

lactation and moulting (see Beck et al. 2003) and therefore Benoît et al. 2011 applied a seasonal correction to produce monthly estimates ($M_{s,a,m}$, see Figure 4). The same correction was applied here and a monthly seal mass-at-age was randomly sampled from the values from June to October ($M_{s,a} = \{M_{s,a,m=6}, \dots, M_{s,a,m=10}\}$) to estimate the energetic needs of seals, as this is presumably when the seal-mackerel interaction is strongest. Specifically, grey seals inhabit and feed predominantly in the southern Gulf and the Scotian Shelf (Hammill and Stenson 2000), where mackerel fishing is most intense around spring (mid-May to June on the Scotian Shelf and June in the southern Gulf; Van Beveren et al. 2023b) and when seals forage intensively (April-June: Beck et al. 2003).

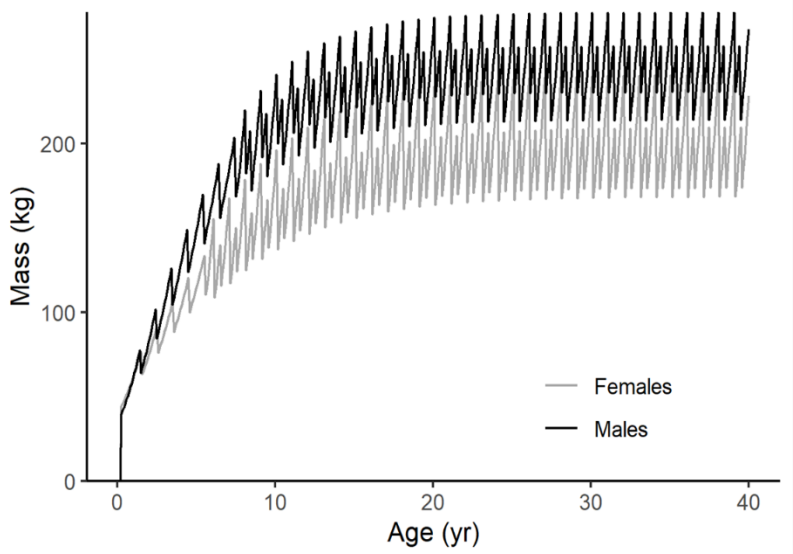

Figure 4. Interannual growth curve of female and male grey seals (redrawn from Benoît et al., 2011; Benoît and Rail, 2016).

2.3.2.4. Prey energy density (ED)

The average energy density (kj/g) of the prey was estimated as the unweighted average of the summer energy density of a range of prey species (see Beck et al. 2007; Table S7). Energy densities per prey species were not weighted by their relative contribution to the diet, as this is highly variable over time (annual and seasonal) and space (Gulf of St.-Lawrence and Scotian Shelf) and there should be no significant bias in doing so, as key prey species (e.g., sand lance: ~5.5 kj/g, Bowen et al. 1993; Hammill and Stenson 2000) have energy densities near the overall average (5.6 kj/g). We also compared the dataset of prey energy density compiled by Beck et al. (2007; focussed on the Scotian Shelf, summer values) with the one from Hammill et al. (2007; focussed on the Gulf of St.-Lawrence, not season-specific) to validate that the selection of prey species and their caloric values does not meaningfully impact results (Figure S1).

2.3.3. Cetaceans

All parameters used to estimate predation by whales and dolphins are provided in Table S3.

2.3.3.1. Abundance (N)

There have only been two aerial surveys aimed at quantifying cetaceans across most of the Gulf of St.-Lawrence and the Canadian Atlantic Shelf: the Trans North Atlantic Sightings Survey (TNASS) in 2007 and the Northwest Atlantic International Sightings Survey (NAISS) in 2016. Spatial coverage of previous surveys was too narrow to be useful in the estimation of total

mackerel consumption. Abundance estimates of the four cetaceans of interest in the Canadian northwest Atlantic were received from Jean-François Gosselin (Fisheries and Oceans Canada, Maurice Lamontagne Institute, Lawson *et al.*, in prep.[1]). The abundance estimates of cetaceans have several important uncertainties associated with them for which we cannot account. For example, marine mammal surveys provide a summer snapshot (August-September) whereas these are highly migratory species that inhabit large areas, so that migration from, to and across the survey area is expected. A part of the surveyed area is also not typically a part of mackerel's spatial distribution (i.e., the Labrador shelf). We did not make the effort to estimate cetacean abundance excluding this area, as these individuals might still have been present more to the South earlier in the year. The spatiotemporal overlap of the four cetaceans with mackerel's abundance likely varies significantly over time, but there is insufficient knowledge about marine mammal migration to attempt any correction or finer-scale analysis. Further, the abundance estimates are in themself highly imprecise in part because of corrections for perception and availability bias. Bias correction factors can indeed have a great effect on the estimates and were here considered conservative (see Lawson *et al.*, in prep.[1] for details). There are also relatively high numbers of unidentified dolphins that were excluded from consideration. Despite the highlighted drawbacks, the provided numbers (Figure 5) can still help provide an idea on the order of magnitude of mackerel that these predators consume.

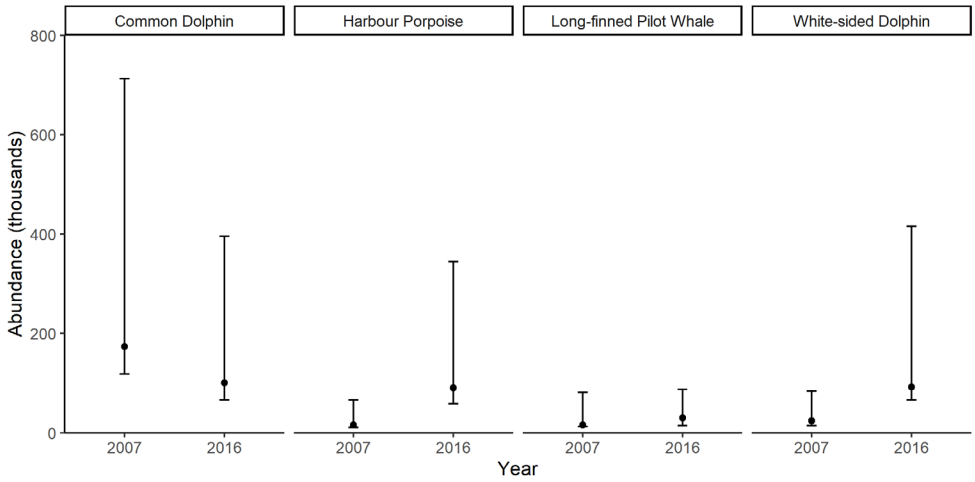

Figure 5. Abundance estimates (August-September) of harbour porpoise, common dolphin, white-sided dolphin and long-finned pilot whale in eastern Canadian waters (Gulf of St.-Lawrence, Scotian Shelf, Newfoundland and Labrador) in 2007 and 2016.

2.3.3.2. Average proportion of mackerel in the diet (%W)

Diet data for most cetaceans is extremely limited in space (generally focussed on US waters) and time (only specific months and years), as well as having often important bias or uncertainty (Table S8). The number of stomachs analysed for diet composition is often low and obtained from incidental catch of the commercial fishery, therefore likely showing a bias toward commercially exploited fish species (e.g., Overholtz and Waring 1991). Also, the analyses are sometimes limited to intact prey items (see Gannon et al. 1997a).

For all four cetacean species included in this study, an arbitrary uniform distribution on %W was therefore used. For harbour porpoises, we assumed that %W ranged from 0.1% to 7% in accordance with the range of observed values (see Table S8).

The diet of both white-sided and common dolphin has only rarely been studied in northwest Atlantic waters (Table S8). When studies with a very large positive bias were excluded (Waring

et al. 1990; Overholtz and Waring 1991), the evidence points towards a diet that is dominated by squid and/or includes other schooling fish. Therefore, mackerel might overall be of relatively minor importance to both dolphin species (between 0.1% and 5%, Table S8). Higher proportions of mackerel in the diet of common dolphins have been observed (e.g., Wenzel and Reulbach unpub.), but we assumed that these are unlikely to be representative of the average diet of the surveyed dolphin abundance, given that their distribution overlaps only partially with that of mackerel.

Pilot whales likewise favour squid in combination with other schooling fish, as mackerel dominated stomachs have only been observed in whales directly competing with the US mackerel fishing fleet (%W assumed to be between 1% and 10%).

The selected ranges for all four cetaceans are smaller than the ones assumed by Smith et al. (2015) who analysed US cetacean predation on a broader variety of prey including mackerel, and who worked with a wide and unselective range of literature values of %W. The presented ranges were nonetheless considered cautionary as the spatial match between mackerel and cetaceans in Canada is only partial (e.g., cetaceans are present around Newfoundland and at higher latitudes earlier in summer, whereas mackerel is usually not) and this is not reflected in most literature-derived values of %W.

2.3.4. Pelagic fish

All parameters used to estimate predation by Atlantic bluefin tuna are provided in Table S4.

2.3.4.1. Abundance (N)

The estimation of tuna abundance in Canada is challenging as individuals of the East- and West-Atlantic tuna stock are present in the GSL and both components are transboundary and highly migratory. Further, only a relative index of catch per unit of effort is available. Previous efforts to approximate regional tuna population sizes, aimed at assessing herring consumption, were based on either a combination of model estimated overall population abundances (virtual population analysis) and assumptions of regional proportional availability (Overholtz 2006; Turcotte et al. 2021), or a combination of landings data and assumptions of natural and fishing mortality (Benoît and Rail 2016). Here, we directly extracted GSL abundance estimates from the recently developed spatial Management Strategy Evaluation (MSE), which has a framework consisting of 33 operating models (OMs) that describe the dynamics of the East- and West-Atlantic stock across seven discrete areas and with trimestral intervals. For each OM, we selected the abundance-at-age of tuna in the GSL during the third trimester, when tuna is most abundant in the region.

An examination of these OM-derived abundance estimates showed that many OMs reflect a situation in which small tuna (ages < 7) are largely dominant. We considered this to be a red flag because the GSL is a feeding area for larger (ages > 7) tuna rather than a spawning or nursery ground. Indeed, the GSL temperature is only suitable for small tuna during a limited period (Druon et al. 2016), tagging confirmed that small fish prefer warmer waters (Marcek et al. 2016) and they are rarely captured or observed by harvesters (Hanke 2021). We therefore only retained estimates from the 8 OMs assuming the number of young tuna (age 1 to 6) to be on average less than 1/3th of the total regional abundance, across all years. The annual log-transformed abundances across the OMs were averaged (with standard deviation) to estimate mackerel consumption by tuna (Figure 6). Similar results were obtained when the total abundances of ages 6+ tuna across all OMs were used.

Note that the abundances are specific to the GSL and do not include the east-coast of Newfoundland or the Scotian Shelf, were tuna can also be present. Although this might lead to

underestimation of mackerel consumption, the effect is expected to be small. Tuna are present in larger numbers on the Scotian shelf only after the bulk of mackerel already migrated to the GSL, and tuna only became more prevalent in East Newfoundland waters since around 2012. The predation pressure of tuna on mackerel in East Newfoundland should also be lower because the temporal overlap between both species is shorter.

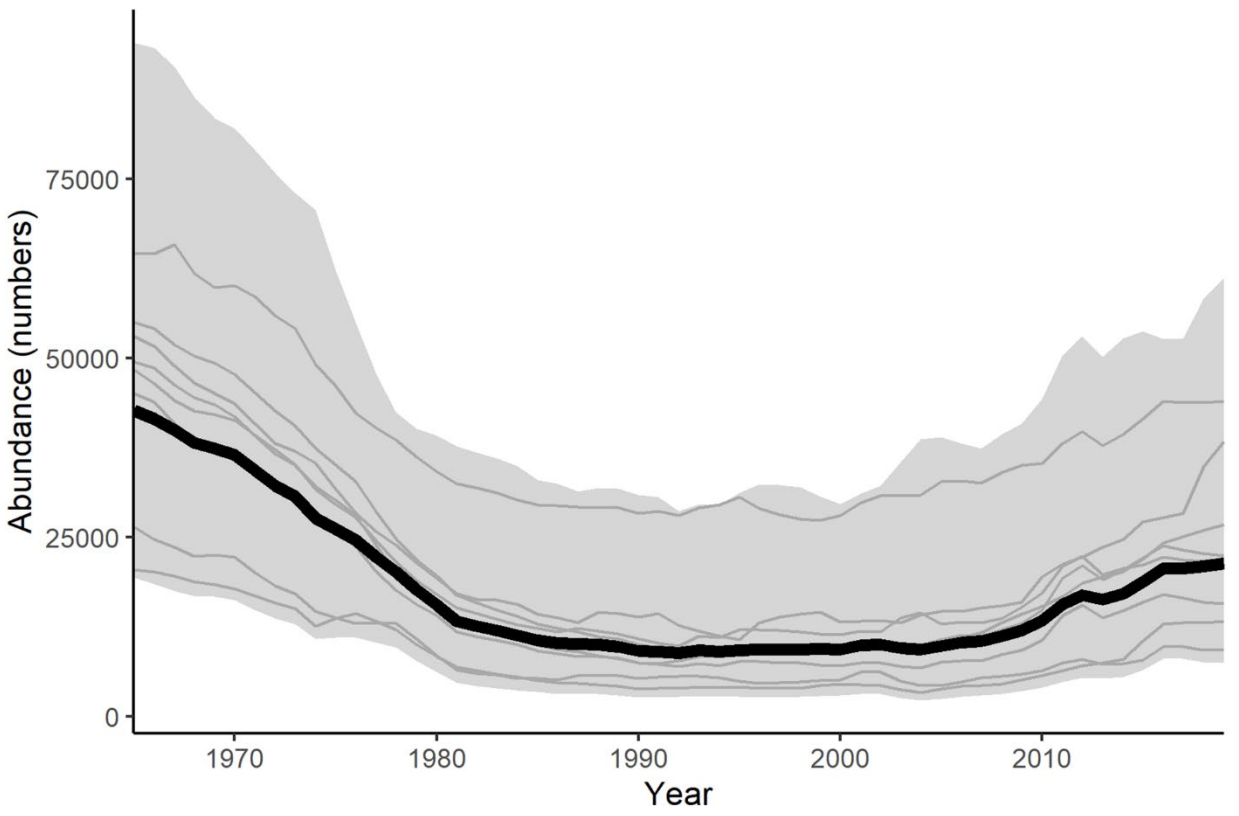

Figure 6. Abundance estimates of Atlantic bluefin tuna in the Gulf of St.-Lawrence. The ribbon represents the 95%CI and individual lines show the estimates of individual operating models.

2.3.4.2. Average proportion of mackerel in the diet (%W)

There have been several studies on bluefin tuna diet, from the West Atlantic (e.g., Eggleston and Bochenek 1990; Butler et al. 2010; Logan et al. 2011) and especially the East Atlantic (e.g., Sorell et al. 2017; van Beveren et al. 2017; Jansen et al. 2021). There is thus ample evidence that Atlantic bluefin tuna are opportunistic predators that can feed primarily on schooling pelagic fish such as herring, mackerel and sand lance. Within Canadian waters, the relative importance of mackerel in the diet of tuna (%W) can vary markedly between years (e.g., Varela et al. 2020a) and remains very uncertain. There were only three published diet studies focussing on tuna diet within Canadian or northern Atlantic US waters (Table S9, excluding early literature with little informative value). Based on this knowledge, we assumed %W for each year to be between 10% and 75% (uniform distribution).

2.3.4.3. Mass (M)

The 8 OMs used to determine tuna abundance also served to estimate the average weight of tuna in the GSL. The numbers- and weights-at-age from each operating model were used to determine annual weight ($W_y = \sum_{a=1}^{A}(W_{y,a}/N_{y,a})/\sum_{a=1}^{A} N_{y,a}$), and values from each OM were subsequently averaged so that tuna weights could be sampled from a normal distribution. Note

that the average weight used here is for most years considerably smaller than the median weight of tuna in landings from the GSL (between about 200 and 300 kg in 2003-2021) because of the estimated fishery selectivity and local age composition (Figure 7.).

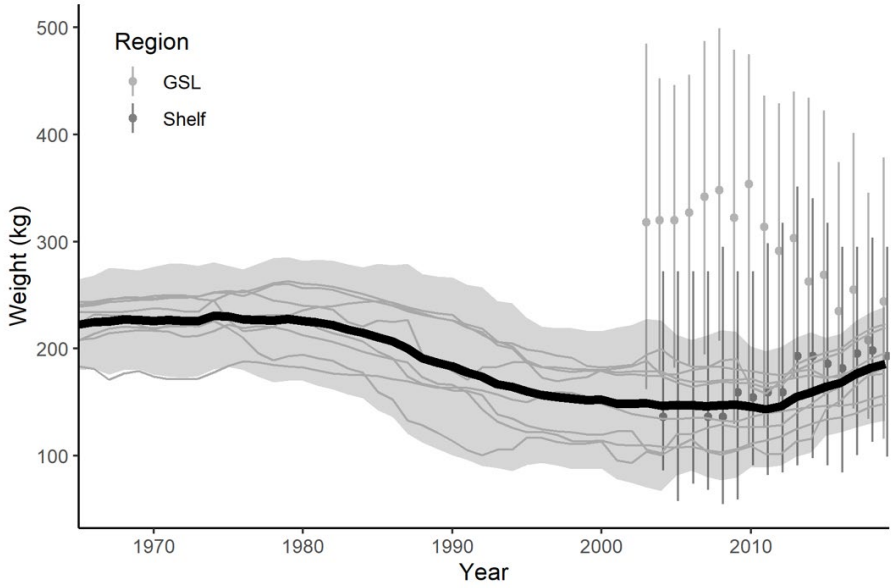

Figure 7. Average weight of Atlantic bluefin tuna in the Gulf of St.-Lawrence (GSL). The black line and ribbon are the average tuna weight with 95% CI derived from the MSE. Individual lines show operating model specific values. Dots and bars (median and 95%) show the distribution of tuna weights landed in the GSL and from the Scotian Shelf.

2.3.4.4. Daily ration (%BM)

The daily food consumption of tuna is typically determined as a percentage of its biomass (Table S10) (Overholtz 2006; Benoît and Rail 2016; Turcotte et al. 2021). Previous consumption studies have applied the Kleiber equation (linking mass to energetic requirements, see section 2.2) to estimate %BM, using parameters attributed to homeothermic marine mammals (e.g., Overholtz 2006). Because these parameters and subsequent results are largely dependent on the marine mammals considered (e.g., seals versus whales), we only worked with the available tuna-specific statistics. We assumed that %BM follows a pert distribution ($\sim pert(0.5, 1.5, 4)$), with the most likely value (1.5%) matching the results of the most pertinent study (Varela *et al.* 2020b). Bounds were set to reflect other plausible values, estimated by other authors. Some studies included younger tuna and estimated that %BM could be above 4%, but because tuna in the GSL are mostly large adult individuals, they likely require less energy relative to their body mass.

2.3.5. Groundfish

The US Northeast Fisheries Science Center (NEFSC) has two annual long-standing and shelf-wide bottom trawl surveys (spring and fall) which both include an intensive fish diet sampling program. Only spring predator data was used to estimate northern contingent mackerel consumption, as the survey is performed when mackerel are still in deeper waters and the northern contingent has presumably not yet left the US shelf. Consumption estimates of the top-nine US groundfish predators (spanning 95% of all mackerel occurrences as prey) were based on spring estimates of 1) swept-area population abundance (Figure 8), 2) annual proportions of mackerel consumed (Figure S2) and 3) daily ingestion rates based on the evacuation rate

method. The number of days of mackerel consumption is set equal to 182.5 (half a year). Because consumption estimates for 2020 were missing, we made a simplistic extrapolation based on the neighbouring years. NOAA is actively working on consumption estimates for a variety of prey, and they provided us with the mackerel-specific results.

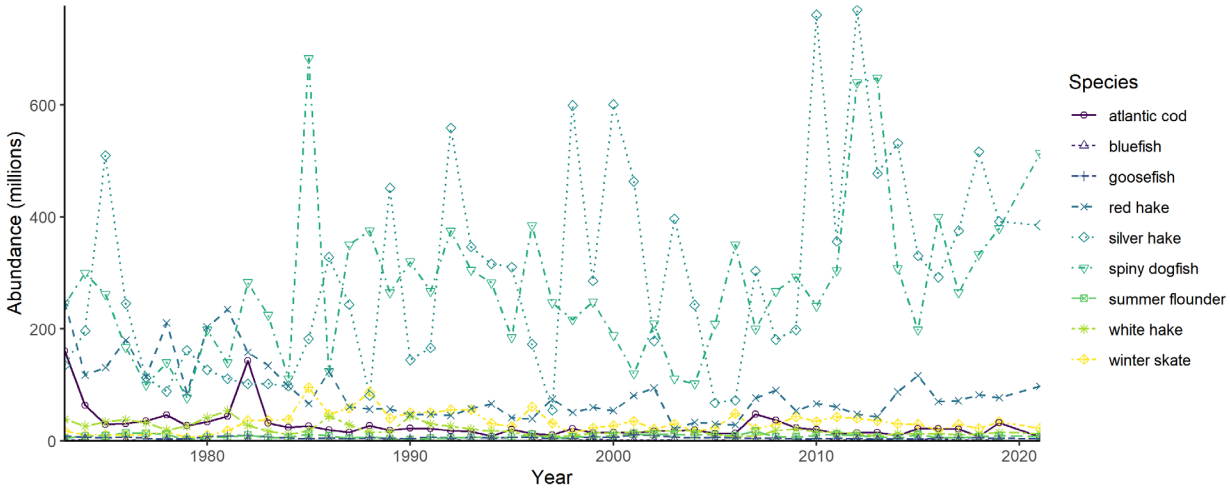

Figure 8. Swept-area abundance estimates (spring bottom trawl survey) of US groundfish from 1973 to 2021.

3. RESULTS

3.1. SEABIRDS

Over the last five decades, the northern gannet abundance of all Canadian colonies at least tripled, with the exception of a decrease observed in the smallest colony on Anticosti Island (Figure 1). In the simulations, the proportion of mackerel in the gannet diet (%W), the energetic need of the predator, and the duration of predation were assumed to be constant. Therefore, the increase in overall gannet population abundance resulted in an estimated increase in total mackerel consumption by northern gannets (Figure 9). It is likely that gannet predation pressure on mackerel indeed increased meaningfully over time, as the upper bounds of the early year consumption estimates are still below the lower bound of the consumption estimates of the more recent period. Further, there is no evidence for a clear and consistent change in the proportion of mackerel in the diet of gannets over time (Guillemette et al. 2018). For example, %W in 2014 was slightly larger than in 2004 when the mackerel stock was still outside the Critical zone.

Bonaventure Island is the largest colony and was after 2010 estimated to consume roughly between 4 kt and 12 kt of mackerel annually (Figure S3). The colony on Bird rock likely consumes about half as much mackerel (2 kt to 6 kt), and the other colonies are of relatively minor importance. The biomass of mackerel removed by northern gannets is evidently more uncertain for the Newfoundland colonies, for which %W can vary more drastically over time (see Montevecchi et al. 1988) and for which less data was available. In all colonies, breeding gannets rather than chicks and non-breeders were by far the largest consumers of mackerel (Figure S3). Over the last 10 years, northern gannets in Canadian waters would have consumed between 11 kt and 23 kt of mackerel per year (95% CI).

3.2. PINNIPEDS

Changes in grey seal mackerel consumption estimates (Figure 9) were driven by the exponential increase in predator abundance (Figure 3). At the start of the time-series (1968-1977), grey seals mackerel consumption was likely less than 1000 t annually. By the end of the time-series (2020-2021), consumption estimates varied between 7 kt and 13 kt (95% CI), with much of the uncertainty being associated with the percentage of mackerel in the diet (%W). Nonetheless, even if mackerel could represent only 0.1%W of the grey seal diet, the increase in the seal population was of such magnitude that the resulting increase in mackerel consumption would likely have become a substantial component of mackerel's overall predator-induced mortality.

3.3. CETACEANS

Annual mackerel consumption by common and white-sided dolphins, harbour porpoise and pilot whales over the last two decades was likely in the range of 2 to 30 kt. These consumption estimates are highly uncertain (Figure 9, Figure S4) as abundance estimates were only available for 2 years (2007 and 2016) and had a wide uncertainty range. All other parameters necessary to estimate consumption were likewise imprecise (e.g., average predator weight to deduce energetic needs, the proportion of mackerel in their diet). Because these are long-lived species, abundance should however vary slowly between years and the two years of data would therefore be a reasonable approximation of abundance over the last two decades.

3.4. PELAGIC FISH

Estimates of mackerel consumption by Atlantic bluefin tuna in Canadian waters decreased between 1968 and 1985 (median declining from 8 kt and 2 kt). Consumption remained low until 2010 (median < 2 kt), after which it somewhat increased again (median of 4 kt in 2020; Figure 9). This pattern was again driven by changes in tuna abundance, as %W was assumed to be constant because of a lack of data. Major uncertainties in the estimation of tuna consumption of mackerel include absolute predator abundances (see Figure 6), average tuna weight, and the proportion of mackerel in their diet. Within the estimated consumption bounds, true mackerel removals by tuna might fluctuate heavily between years (Figure 9), because of the likely high interannual variability of mackerel in their diet (see table S9).

3.5. GROUNDFISH

Northern contingent mackerel removals by US groundfish were largely dominated by spiny dogfish. Median consumption estimates by spiny dogfish were above 7 kt during 50% of the years with sufficient data, in sharp contrast with the consumption by other groundfish species, which rarely exceeded 1 t. Abundance of these other groundfish species was, with the exception of silver hake, at least an order of magnitude lower than spiny dogfish (Figure 8). They are often also smaller bodied and mackerel was generally of lesser importance in their diet.

Consumption estimates of groundfish were more variable than for other predators because of the unique availability of annual diet data in combination with relatively noisy swept-area abundance estimates. High frequency fluctuations in estimated consumption are thus a product of both data-availability and true ecological changes. Mackerel consumption by spiny dogfish was highest between 1980 and 2007, during a period when mackerel was more prominent in their diet (Figure S2). There was however great interannual variability, as the proportion of mackerel in spiny dogfish stomachs could vary by one order of magnitude (4% to 49%) between years, based on analyses of over 100 stomachs annually. The variability in northern contingent

mackerel consumption might nonetheless be overestimated, given that swept-area abundance estimates were not smoothed. Underestimation of total consumption is also possible, as a reasonable amount of fish in the spiny dogfish diet was unidentified, and a gut evacuation rate model with conservative parameter values was used.

Overall, spiny dogfish in particular was estimated to substantially contribute to mackerel predator-induced mortality in many years.

3.6. TOTAL CONSUMPTION

Total mackerel consumption (excluding cetaceans) was estimated to have increased over time. Between1968 to1983, median consumption was generally between 10 kt and 17 kt (2.5% quantile or likely minimum between 6 kt and 8 kt). Atlantic bluefin tuna and northern gannets were identified as the dominant predators during that period. A potential shift in the main consumers occurred around 1984, when predation by spiny dogfish might have increased (driven by an increase in %W), pressure from northern gannets continued to rise (driven by an increase in abundance) and tuna became a less important predator (driven by a decline in abundance). From 1984 onwards, median values generally fluctuated between 18 kt and 45 kt. A part of this potential shift could however be the result of data-availability; stomach sampling of spiny dogfish only started in 1977, and we assumed that the period from 1968 to 1976 was in terms of %W similar to the years after (1977-1981), when mostly no or small amounts of mackerel were found in the stomachs.

The lower confidence interval (2.5% quantile) indicates that no less than 12 kt of mackerel might have been removed annually since 1984. Predation pressure might have continued to increase over time; northern gannet and grey seal abundance have both reached historic highs, compensating for the estimated decrease in mackerel consumption by spiny dogfish. In the last decade (2012-2021), minimum mackerel removals (2.5% quantile) were estimated to be between 21 kt and 29 kt, whereas median values were between 28 kt and 44 kt.

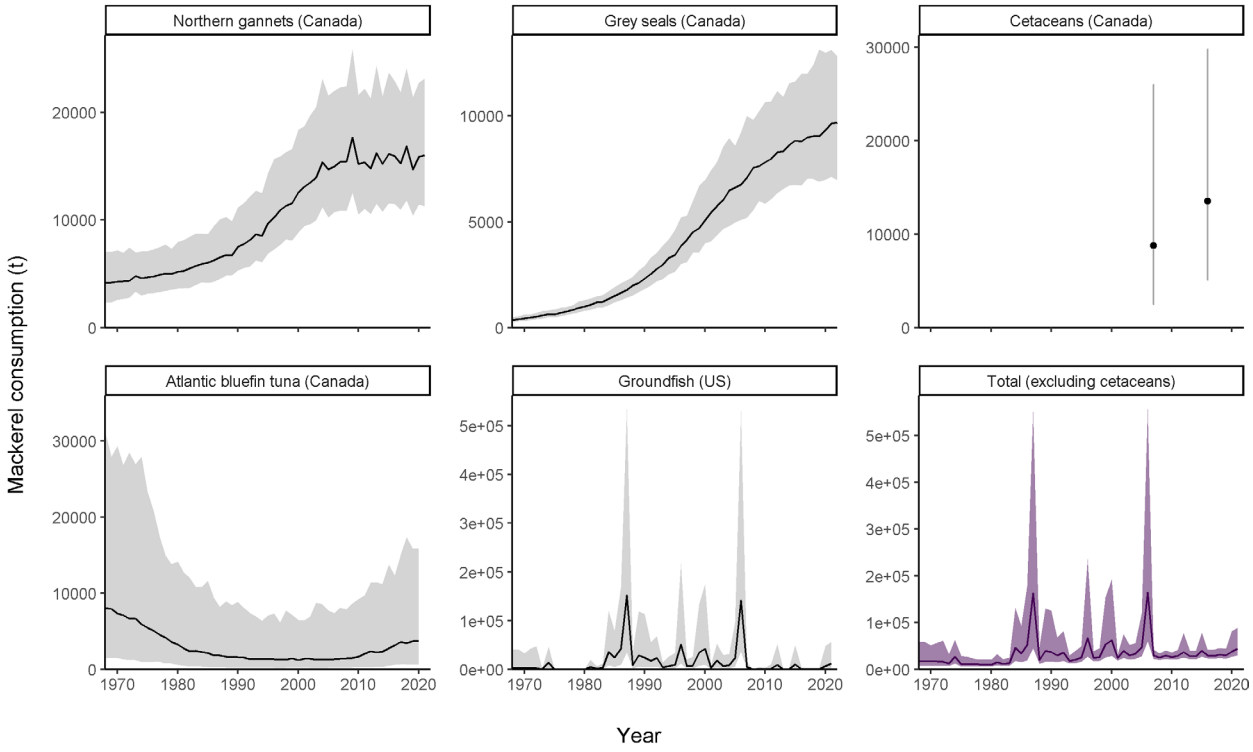

Figure 9. Mackerel consumption estimates (t) by predator group (median and 95% confidence interval).

4. DISCUSSION

The estimation of mackerel consumption by various predators performed in this study showed that an ensemble of predators is likely driving changes in total natural mortality of northern contingent mackerel. The relative importance of each predator varied over time and we could not identify a single dominant predator species. Despite the often large uncertainty associated with input data and parameters used in the estimation process, our results showed that total consumption of mackerel likely increased over time, despite potentially large interannual variability. The amount of mackerel consumed by all predators included in this study was during the last 10 years (2012-2021) likely at least two times greater than reported Canadian commercial fishery landings (< 11 kt).

Our results are difficult to compare with mackerel consumption estimates from other studies. For instance, Hammill and Stenson (2000) provided estimates of mackerel consumption by four seal species in Atlantic Canada (harp, hooded, grey and harbor seals), based on grey seal abundance estimates that differ substantially from the more recent ones applied here. Cairns et al. (1991) estimated mackerel consumption by a diversity of seabirds, again using input data and methods that have considerably evolved since. Savenkoff et al. (2005) applied a mass-balance model to determine mackerel mortality by several predator groups, but did so only for the Gulf of St.-Lawrence and under a set of specific assumptions. More recent predation studies were used as baseline material for our analyses (e.g., Guillemette et al. 2018 for northern gannets) and unsurprisingly have very consistent results.

Consumption estimates for most marine predators inevitably have a high degree of uncertainty associated with them, not all of which is quantifiable and can be integrated within the computations. Absolute abundance estimates that underpin consumption analyses are often obtained from stock assessment models (e.g., here used for seals and tuna), of which the output depends on some subjective assumptions (e.g., the natural mortality rate) as well as data quality- and quantity. Although the use of an ensemble of models might buffer against bias (as done for both seals and tuna), it is not a bullet-proof approach. For other predators, indices of absolute abundance are used directly (e.g., spiny dogfish, gannets and cetaceans), despite potentially imperfect survey catchability (i.e., not equal to one) and an often larger level of noisiness (e.g., swept-area abundance of US groundfish). Further, the contribution of mackerel to any predator's diet can vary significantly over the season, locally, across years and with the predator's life stage (see %W for all species), but available data is rarely comprehensive enough to account for this. Although with the exception of spiny dogfish we used wide uniform distributions to reflect diet uncertainty, these bounds are somewhat subjective as true uncertainty can generally not be computed. All methods to gain diet composition information also have important sources of bias (e.g., prey digestibility), of which in-depth discussion is out of the scope of this research document. Additionally, our list of predators is incomplete, and for instance cetaceans have the potential to considerably alter the estimated collective consumption pattern, scale and uncertainty. Other authors indeed already indicated the potentially large role of cetaceans in West-Atlantic mackerel mortality (Savenkoff et al. 2005; Smith et al. 2015). Nonetheless, analyses of prey consumption are, especially in the absence of specific data to estimate natural mortality (e.g., tagging, model-based approaches), highly valuable to inform annual natural mortality rates.

There are several important conclusions in the presented information. For example, we provided insight into the relative importance of each predator over time. Grey seals, which have been hypothesized to exert a much greater pressure on mackerel since their upsurge in abundance, have indeed become a more important constituent of natural mortality during the last two decades, but their impact is likely still smaller or at most comparable to northern gannets. Despite all uncertainties, the minimum bounds of estimated consumption should also hold true,

given that many predators as well as other sources of *M* are still excluded. These minimum values by itself should help to inform model scaling. Future work might focus on integrating the presented knowledge within the assessment, improving consumption estimates (e.g., through improved predator diet information such as from Turcotte et al. 2023), and concentrate on the size or age selectivity of the various predators.

5. ACKNOWLEDGMENTS

We would like to thank Jean-François Rail for providing data and expertise on gannets, as well as everyone involved in gannet monitoring: Laboratoire d'ornithologie marine de Rimouski (LOMR) at Université du Québec à Rimouski, Cégep de Rimouski and Parc national de l'Île-Bonaventure-et-du-Rocher-Percé. We are also grateful for the data, code or knowledge shared by several seal (Steven Rossi, Hugues Benoît and Xavier Bordeleau), tuna (Alex Hanke, Tom Carruthers and François Turcotte) and cetacean experts (Jean-François Gosselin and Anne Provencher St-Pierre).

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SUPPLEMENTARY INFORMATION

TABLE S1. SEABIRD PARAMETERS

Table S1. Consumption parameters for northern gannets (Morus bassanus). (*) indicates when the same information applies. All parameters follow standard distributions: uniform(min, max), normal(mean, sd). (GSL = Gulf of St.-Lawrence, NL = Newfoundland, Is. = island, N = abundance, %W = proportion of prey in diet in terms of weight, TI = total ingestion, DI = daily ingestion, DEE = daily energy expenditure, α and β are the Kleiber equation parameters, M = body mass, AF = activity factor, GP = growth premium, ED = energy density, AE = assimilation efficiency)

	Species	Region	Pop.	Life stage	N (numbers)	%W (%)	TI (t/year)			
							DI (g/day)			DAY (days)
							DEE (kj/day)	ED (kj/g)	AE (prop.)	
SEABIRDS	Northern gannet	GSL	Bird Rocks	Breeders	See 2.3.1.1	$\sim unif(54{,}100)$ Guillemette et al. 2018 (longer term monitoring program, summer, Bonaventure Is.) (*)	$\sim N(4865{,}450)$ Birt-Friesen et al. 1989. Uncertainty encompasses values for Cape gannets (Adams et al. 1991). Value might be overestimated due to the methodology and life-stage evaluated (chick-rearing).	$\sim N(7.5{,}1.5)$ Spitz and Jouma'a 2013 (energy density of summer mackerel, which are typically dominating the diet). Uncertainty encompasses values estimated by other authors (Steimle Jr. and Terranova 1985)	$\sim N(0.7519{,}0.0340)$ Cooper 1978 Uncertainty encompasses values estimated for a variety of seabirds (e.g. Dunn 1975; Saraux et al. 2021)	$\sim$N(100 12) See Guillemette et al. 2018 Standard deviation estimated based on the variability in the end of the fishing season (southern Gulf, 19185-2015), a proxy for mackerel presence (Van Beveren et al. 2023b). (***)
			Bonaventure Is.							
			Anticosti							
		NL	Baccalieu Is.			$\sim unif(10\ 100)$ (Montevecchi et al. 1988; Montevecchi 2007) (**)				$\sim N(71{,}29)$ Because fishing is a reasonable proxy for mackerel presence (Van Beveren et al. 2023b), the duration and the variability of the fishing season (95% of landings) in NL was used (1985-2015). This corresponds with the period over which mackerel are observed in NL gannet stomachs (Montevecchi et al. 1988) and the period over which gannets perform V-dives (d'Entremont et al. 2022a) (****)
			Cape St. Mary's							
			Funk Is.							
		GSL	Bird Rocks	Non-breeders	See 2.3.1.2	$\sim unif(54{,}100)$ (*)				$\sim N(100{,}15)$ (***)
			Bonaventure Is.							
			Anticosti							
		NL	Baccalieu Is.			$\sim unif(10{,}100)$ (**)				$\sim N(71{,}29)$ (****)
			Cape St. Mary's							
			Funk Is.							
		GSL	Bird Rocks	Chicks	See 2.3.1.3	$\sim unif(54{,}100)$ (*)	$\sim N(24174{,}0)$ Montevecchi et al. 1984			
			Bonaventure Is.							
			Anticosti							
		NL	Baccalieu Is.			$\sim unif(10{,}100)$ (**)				
			Cape St. Mary's							
			Funk Is.							

TABLE S2 PINNIPED PARAMETERS

Table S2. Consumption parameters for grey seals (Halichoerus grypus). All parameters follow standard distributions: uniform(min, max), normal(mean, sd), pert(min, most likely, max), multivariate normal(mean vector, covariance matrix). (GSL = Gulf of St.-Lawrence, N = abundance, %W = proportion of prey in diet in terms of weight, TI = total ingestion, DI = daily ingestion, DEE = daily energy expenditure, α and β are the Kleiber equation parameters, M = body mass, AF = activity factor, GP = growth premium, ME = metabolic efficiency, ED = energy density, AE = assimilation efficiency)

	Species	Region	Population	Life stage	N (numbers)	%W (%)	TI (t/year)							
							DI (g/day)							DAY (days)
							DEE (kj/day)					ED (kj/g)	AE (prop.)	
							α, β	M (kg)	AF	GP	ME			
PINNIPEDS	Grey seals	4T & 4VWX	Southern GSL & Nova Scotia (Atlantic coast+Sable Island)	Age 0-30+	See 2.3.2.1	See 2.3.2.2	$\sim MVN(\begin{bmatrix}\alpha = 293.75\\ \beta = 0.75\end{bmatrix}, \begin{bmatrix}5393.1 & -12.393\\ -12.393 & 3.035\end{bmatrix})$ Hammill and Stenson 2000; Benoît et al. 2011	See 2.3.2.3	$\sim pert(1.7,2,3)$ Benoît et al. 2011	$GP_{a=0} \sim unif(1.80,2.00)$ $GP_{a=1} \sim unif(1.50,1.70)$ $GP_{a=2} \sim unif(1.25,1.45)$ $GP_{a=3} \sim unif(1.10,1.30)$ $GP_{a=4} \sim unif(1..05,1.20)$ $GP_{a=5} \sim unif(1.03,1.13)$ $GP_{a=6+} \sim unif(1.00,1.00)$ Benoît *et al.*, 2011	$\sim N(0.827, 0.048)$ Benoît et al. 2011	$\sim pert(3, 5.6,7.5)$ See 2.3.2.4	$\sim unif(0.77, 1)$ Benoît et al. 2011 (somewhat arbitrary value used to address observations of seals only partially consuming prey, including mackerel).	$\sim unif(152,182)$ Because fishing is a reasonable proxy for the presence of mackerel in surface waters (Van Beveren et al. 2023b), we assumed that the duration of potential seal predation ranges from 5 months (June 1st to October 31st; fishing season southern Gulf) to 6 months (mid-May to mid-November; fishing season all regions). Although mackerel have been found in seal stomachs outside this period, we assume that such occurrences are rare (see section 2.3.2.2).

TABLE S3. CETACEAN PARAMETERS

Table S3. Consumption parameters for harbour porpoise (Phocoena phocoena), common dolphin (Delphinus delphis), white-sided dolphin (Lagenorhynchus acutus) and long-finned pilot whale (Globicephala melas). (*) indicates when the same information applies. All parameters follow standard distributions: uniform(min, max), normal(mean, sd), pert(min, most likely, max), multivariate normal(mean vector, covariance matrix). (GSL = Gulf of St.-Lawrence, SS = Scotian-Shelf, N = abundance, %W = proportion of prey in diet in terms of weight, TI = total ingestion, DI = daily ingestion, DEE = daily energy expenditure, α and β are the Kleiber equation parameters, M = body mass, AF = activity factor, GP = growth premium, ME = metabolic efficiency, ED = energy density, AE = assimilation efficiency)

	Species	Region	Population	Life stage	N (numbers)	%W (%)	TI (t/year)							
							DI (g/day)							DAY (days)
							DEE (kj/day)					ED (kj/g)	AE (prop.)	
							α, β	M (kg)	AF	GP	ME			
CETACEANS	Harbour Porpoise	CA	Canada-wide	adults	See 2.3.3.1	$\sim unif(0.1,7)$ See 2.3.3.2	$\sim MVN(\begin{bmatrix}\alpha = 0.313\\ \beta = 0.66\end{bmatrix}, \begin{bmatrix}0.0040 & -0.0021\\ -0.0021 & 0.0012\end{bmatrix})$ Innes et al. 1987 (adult Odontoceti, covariance matrix extracted from Figure 3). DEE in kg/day instead of kj/day (ED set to 10^3).	$\sim N(31,6.2)$ Smith et al. 2015 Uncertainty encompasses values cited elsewhere (Kenney et al. 1997; Richardson et al. 2003)	1	1	1	10^3 (see α, β)	1	$\sim unif(152,182)$ Because fishing is a reasonable proxy for the presence of mackerel in surface waters (Van Beveren et al. 2023b), we assumed that the duration of potential marine mammal predation ranges from 5 months (June 1st to October 31st; period of higher landings) to 6 months (mid-May to mid-November; overall fishing season). Outside this period, the spatiotemporal overlap between marine mammals and mackerel in Canada is assumed to be too small for mackerel consumption to be impactful.
	Common Dolphin	CA	Canada-wide	adults		$\sim unif(0.1,5)$ See 2.3.3.2		$\sim N(80,16)$ Smith et al. 2015 Uncertainty encompasses values cited elsewhere (Kenney et al. 1997) (*)						
	White-sided Dolphin	CA	GSL/SS	adults		$\sim unif(0.1,5)$ See 2.3.3.2		$\sim N(92,18.4)$ Smith et al. 2015 (*)						
	Long-finned Pilot Whale	CA	Canada-wide	adults		$\sim unif(0.1,10)$ See 2.3.3.2		$\sim N(850,170)$ Smith et al. 2015 (*)						

TABLE S4. PELAGIC FISH PARAMETERS

Table S4 Consumption parameters for Atlantic bluefin tuna (Thunnus thynnus). All parameters follow standard distributions: uniform(min, max), normal(mean, sd), pert(min, most likely, max). (%W = proportion of prey in diet in terms of weight, TI = total ingestion, DI = daily ingestion, M = body mass, %BM = daily ration in function of body mass)

	Species	Region	Population	Life stage	N (numbers)	%W (%)	TI (t/year)		
							DI(g/day)		DAY (days)
							M (kg)	%BM	
Fish	Tuna	CA	West-Atlantic (Canadian migrants)	Age 1-36	See 2.3.4.1	$\sim unif(10,75)$ See 2.3.4.2	See 2.3.4.3	$\sim pert(0.5,1.5,4)$ See 2.3.4.4	$\sim unif(122,168)$ The minimum number of days is based on the duration of the main directed tuna fishery (4 months) and the maximum duration on the time period over which acoustically tracked tuna have been observed in the GSL (first entry on June 4th and last departure November 19th; Block et al. 2019)

TABLE S5. GREY SEALS - %W

Table S5. Summary of published data on grey seal diet in the West-Atlantic. (N = number of individuals in the study, including those with empty stomachs, %W = % wet weight in diet, SS = Scotian Shelf, GSL = Gulf of St.-Lawrence, NL = Newfoundland, Is.= Island).

Reference	Years	Period	Region	N	Source	%W	Notes
(Mansfield and Beck 1977)	NA	NA	Eastern Canada	446	Stomachs	-	5% of all prey species (% occurrence) Period unknown but includes summer
(Benoit and Bowen, 1990a)	1982-1987	July-Aug	Anticosti	744	Stomachs	5.3%	Mackerel lengths: 25.0-47.9cm
(Benoit and Bowen, 1990b)	1950-1987	Most months	Estuary + GSL + SS (including Grand Manan, Sable Is.)	1878	Stomachs	-	8.1% occurrence across all prey species (nGSL: 5.1%, sGSL: 1.1%, Coastal SS: 17.4%, Sable Is.: 21%). Original + unpublished and published data (including data from Mansfield and Beck, 1977; Benoit and Bowen 1990a)
(Bowen et al, 1993)	1988-1990	Most months	Canadian east coast (Grand Manan Is., SS shore, Sable Is.)	528	Stomachs	6.7±2.7%	Based on only 2 mackerel otoliths (majority of stomachs being empty or dominated by sand lance).
(Murie and Lavigne 1992)	1983	July-Dec	Northwest GSL (Estuary, Anticosti)	82	Stomachs	0%	-
(Bowen and Harrison 1994)	1991-1993	8 months	Sable Is.	393	Faeces	0%	-
(Mohn and Bowen 1994)	1988-1993	All months	SS	NA	Faeces, stomachs	Jan: 0.1% March: 47.4% May: 9.9% Other months: 0%	Original + published data (including Murie and Lavigne 1992; Bowen et al. 1993). Large overlap with Mohn and Bowen 1996 (therefore excluded).
(Hammill and Stenson 2000)	1990-1996	Most months	nGSL (4RS), SS (4VsW), sGSL (4T)	NA	Faeces, stomachs	4VsW summer: 0.1% 4VsW winter: 7.9% 4RS: 5.7% 4T: 4.3%	Published data (Benoit and Bowen 1990a; Murie and Lavigne 1992; Bowen et al. 1993; Bowen and Harrison 1994; Proust 1996)
(Hammill et al. 2007)	1985-2004	Most months	Anticosti, sGSL, around NL	1118	Stomachs, intestine	Anticosti May-July: 13.8±5.1% Anticosti Aug-Sep: 11.5±3.7% sGSL May-July: 0.6±0.2% sGSL August-Sept: 0.7±0.4% sGSL Nov-Dec: 1.4±0.5% eNL ~Aug-Oct: 0% sNL ~Aug-Oct: 0% wNL ~Aug-Oct: 4.5±3.4%	Mackerel lengths: 8.3-45.0cm (mean = 20.3cm, based on 807 otoliths)
(Beck et al. 2007)	1993-2001	May, June, Sept, Oct, Dec, Jan	Sable Is.	587	Fatty acid signatures	<1%	-
(Bowen and Harrison 2007)	1991-1998	All months	Sable Is.	1245	Faeces	<0.1%	Original + published data (1991-1993 data from Bowen and Harrison 1994)

Reference	Years	Period	Region	N	Source	%W	Notes
(Ampela 2009)	1998-2008	Most months	USA: New England, mid-Atlantic Bight	301	Faeces (252), stomachs (49)	<1%	
(Hammill 2011)	1994-2008	June-Nov	sGSL	470	Stomachs, intestine	Stomachs: 0.9±0.4% Intestine: 2.0±0.7%	-
(Hammill et al. 2014b)	1996-2011	April-Jan	Cape Breton (CB), Cabot Strait (CS)	271	Stomachs, intestine	CB stomachs M: 0% CB stomachs F: 1.1% (0-1.6) CB intestine M: 6.2% (3.5-8.2) CB intestine F: 0.7% (0-1.5) CS stomachs M: 1.7% (0.6-2.6) CS stomachs F: 2.7% (0.8-4.6) CS intestine M: 0.4% (0.1-0.5) CS intestine F: 0.4% (0-1.2)	Original + published data (Hammill et al. 2007)

TABLE S6. GREY SEALS – GOMPERTZ GROWTH CURVE

Table S6. Gompertz growth curve parameters for grey seals.

Parameter	Females (f)	Males (m)
$\boldsymbol{\gamma_{1s}}$	$\gamma_{1f} \sim N(183.70, 3.57)$	$\gamma_{1m} \sim N(230.60, 6.93)$
$\boldsymbol{\gamma_{2s}}$	$\gamma_{2f} \sim N(1.242, 0.048)$	$\gamma_{2m} \sim N(1.521, 0.074)$
$\boldsymbol{\gamma_{3s}}$	$\gamma_{3f} \sim N(0.190, 0.014)$	$\gamma_{3m} \sim N(0.250, 0.022)$

TABLE S7. GREY SEALS – PREY ENERGY DENSITY

Table S7. Energy density (kj/g) of prey items from Hammill et al. 2007[1] and Beck et al. 2007[2]. When different values for the same species were given (length classes, regions) these were averaged.

Scientific name	Common name	[1]	[2] (spring)	[2] (summer)	[2] (fall)
Alosa pseudoharengus	Alewife	NA	7.33	7.36	7.39
Amblyraja radiata	Thorny Skate	NA	4.83	4.94	4.89
Ammodytes sp.	Sand lance	5.5	5.645	6.37	5.955
Anarhichas lupus	Wolffish	3.59	NA	NA	NA
Clupea harengus	Atlantic herring	5.61	5.72	6.56	8.075
Cottidae	Sculpin	5.4	NA	NA	NA
Cryptacanthodes maculatus	Wrymouth	4.2	NA	NA	NA
Cyclopterus lumpus	Lumpfish	1.88	7.48	7.74	9.23
Enchelyopus cimbrius	Fourbeard rockling	4.2	NA	NA	NA
Eumesogrammus praecisus	Fourline snakeblenny	4.64	NA	NA	NA
Gadus morhua	Atlantic cod	4.81	4.41	4.515	4.585
Glyptocephalus cynoglossus	Witch Flounder	NA	5.19	5.19	5.19
Hemitripterus americanus	Sea raven	5.4	NA	NA	NA
Hippoglossoides platessoides	American plaice	5.1	4.685	4.675	4.58
Hippoglossus hippoglossus	Atlantic Halibut	NA	5.34	5.49	5.4
Homarus americanus	Lobster	NA	5.06	4.92	5.06
Illex sp.	Squid	NA	6.28	6.28	6.28
Leucoraja ocellata	Winter Skate	NA	4.62	4.57	4.59
Limanda ferruginea	Yellowtail flounder	4.43	5.38	5.25	5.37
Lumpenus maculatus & sp.	Daubed shanny	4.51	NA	NA	NA
Lumpenus lumpretaeformis	Snake blenny	5.57	4.68	4.68	4.68
Lycodes vahlii	Eelpout	6.32	NA	NA	NA
Macrozoarces americanus	Ocean Pout	4.43	4.39	4.55	4.68
Mallotus villosus	Capelin	7.505	6.055	6.765	7.745
Melanogrammus aeglefinus	Haddock	5.3	4.225	4.195	3.45
Merluccius bilinearis	Silver Hake	NA	1.95	2.46	1.98
Myoxocephalus octodecemspinosus	Longhorn sculpin	5.4	4.335	5.195	4.65
Myoxocephalus scorpius	Shorthorn sculpin	5.4	NA	NA	NA
Myoxocephalus sp.	Horned sculpins	4.43	NA	NA	NA
Osmerus mordax	Smelt	4.2	NA	NA	NA
Pandalus borealis	Shrimp	NA	5.66	5.63	5.7
Peprilus triacanthus	Butterfish	4.5	7.86	7.69	7.69
Pleuronectidae sp.	Pleuronectidae sp.	4.2	NA	NA	NA
Pollachius pollachius	Pollock	NA	5.65	5.65	5.65
Pseudopleuronectes americanus	Winter flounder	3.6	5.11	5.25	5.04
Reinhardtius hippoglossoides	Greenland Halibut	NA	5.04	5.04	6.57
Scomber scombrus	Atlantic mackerel	4.85	5.41	9.44	9.44
Scophthalmus aquosus	Windowpane	3.52	NA	NA	NA
Sebastes sp.	Redfish	5.37	5.435	6.37	5.89
Tautogolabrus adspersus	Cunner	6.6	NA	NA	NA
Triglops murray	Moustache sculpin	3.99	NA	NA	NA
Urophycis chuss	Red Hake	NA	4.93	4.93	4.93
Urophysis tenuis	White hake	6.3	4.85	4.91	4.86

TABLE S8. CETACEANS – %W

*Table S8. Summary of published information on the diet of harbour porpoise (*Phocoena phocoena*), common dolphin (*Delphinus delphis), *white-sided dolphin (*Lagenorhynchus acutus*) and long-finned pilot whale (*Globicephala melas*) in the West-Atlantic. (N = number of individuals in the study, including those with empty stomachs, %W = % wet weight in diet, US = United States, NL = Newfoundland, GSL = Gulf of St.-Lawrence).*

Species	Reference	Years	Period	Region	N	Source	%W	Notes
Common dolphin	(Overholtz and Waring 1991)	1989	March-April	US	4	Incidental	100%	Incidental catch from the mackerel trawl fishery Mackerel weights: 249.4 g [113-403.3 g]
	(Waring et al. 1990)	1986-1988	Midwinter-late spring	US	33	Incidental	NA	9 stomachs contained only mackerel (but from mackerel fishery) Other stomachs contained mixed prey and/or squid
Harbour porpoise	(Fontaine et al. 1994)	1989	May-August	Estuary, GSL	138	Incidental	7%	Mackerel weights: 573.4±83.1 g
	(Gannon et al. 1998)	1989-1994	Sept-Dec	US	95	Incidental	<1%	Mackerel lengths: 224±53 cm
	(Orphanides et al. 2020)	1994-2017	Mostly Jan-May	US	50	Incidental	6.3%	Mackerel lengths: 25.9cm [19.3-39.9 cm]
	(Recchia and Read 1989)	1985-1987	June-Sept	Bay of Fundy	127	Incidental	1.5%	Mackerel lengths: 296±14.4 cm
	(Smith and Gaskin 1974)	1969-1972	May-Sept	East coast NS, Bay of Fundy	81	Hunted, floating, incidental	NA	8.6% of otoliths removed from mackerel
Long-finned pilot whale	(Gannon et al. 1997a)	1989-1991	Feb-May	US	30	Incidental	17.2%	Incidental catch from the mackerel trawl fishery Mackerel lengths: 349.2±30 cm [265-375 cm]
	(Gannon et al. 1997b)	1973-1993	March-Sept	US	8	Stranded	4.6%	-
	(Overholtz and Waring 1991)	1989	March-April	US	5	Incidental	71.4%	Incidental catch from the mackerel trawl fishery Mackerel lengths: 363.2 cm [354.8-460.0 cm]
	(Waring et al. 1990)	1986-1988	Midwinter-late spring	US	169	Incidental	NA	2 stomachs taken contained only mackerel (but from mackerel fishery). All other stomachs contained mixed prey and/or squid.
White-sided dolphin	(Craddock et al. 2009)	1991-2006	Winter, summer	US	62	Incidental, stranded	<1%	-
	(Katona et al. 1978)	1976	July	US	1	Floating	NA	Herring, squid, silver hake
	(Schevill 1956)	NA	NA	US	1	Hunted	NA	Herring and squid
	(Sergeant and Fisher 1957)	1954	July	NL (Trinity Bay)	1	Hunted	NA	Herring and squid

TABLE S9. PELAGIC FISH – %W

Table S9. Summary of published data on Atlantic bluefin tuna diet in the Northwest-Atlantic (North of Cape Hatteras, mackerel's southern limit). (N = number of individuals in the study, including those with empty stomachs, %W = % wet weight in diet, eNS = eastern Nova Scotia, sGSL = southern Gulf of St.-Lawrence).

Reference	Years	Period	Region	N	Source	%W	Notes
(Pleizier et al. 2012)	2010	Sept 27-Nov 20	Port Hood (sGSL)	35	Commercial fishery	12.1%	-
		Sept 15-Nov 20	Canso (eNS)	33	-	13.2%	
(Chase, 2002)	1988-1992	July-Oct	New England (5 distinct areas)	819	Commercial & sport fishery	3.3% [0.6-56.2%]	Range of %W spanning the values of each of the 5 sampling locations. Mackerel lengths: 10-36cm (mean = 15.9cm, n = 150)
(Varela et al. 2020b)	2015	Oct	Port Hood (sGSL)	28	Commercial fishery	75.75%	-
	2016	-	-	76	-	21.06%	
	2017	-	-	57	-	26.76%	

TABLE S10. PELAGIC FISH – %BM

Table S10. Summary of published data on the daily ration or percentage of body mass consumed daily (%BM) for bluefin tuna. If within one paper values are provided for various age/length classes, information on the larger individuals was extracted. (ABT = Atlantic bluefin tuna, SBT = southern bluefin tuna)

Reference	Method	Stock	Region	Period	Size/weight	%BM
(Chase 2002)	Ratio stomach content to fish weight	ABT (west)	Gulf of Main	July-Oct.	120- 149 cm	1%
					>230 cm	0.5%
(Van Beveren et al. 2017)	Dynamic Energy Budget model	ABT (east)	East-Atlantic, Mediterranean	N/A	>100 kg or >160 cm	≤0.8%
(Tiews 1978)	Ratio (anecdotal)	ABT (east)	North Sea	NA	250 kg	≤4%
(Young et al. 1997)	Ratio stomach content to fish weight	SBT	Tasmania	May-July	≤125 cm (inshore)	2.69%
					<140 cm (offshore)	1.01%
					≥140 cm (offshore)	0.89%
(Butler et al. 2010)	Feeding rate based	ABT (west)	North Carolina	Nov-Jun	>185 cm	2.03±0.59%
(Varela et al. 2020b)	Feeding rate based	ABT (west)	Gulf of St.-Lawrence	Fall	198-299 cm or 122-457 kg	1.02-1.73% (year-dep.)
(Varela et al. 2020a)	Feeding rate based	ABT (east)	Strait of Gibraltar	All seasons	109-208 cm	11.75±6.85%
(Sorell et al. 2017)	Feeding rate based	ABT (east)	Strait of Gibraltar	Aug-Dec	77-212 cm	2.52-5.84% (year-dep.)

FIGURE S1. GREY SEALS – COMPARISON OF PREY ENERGY DENSITY DATASETS

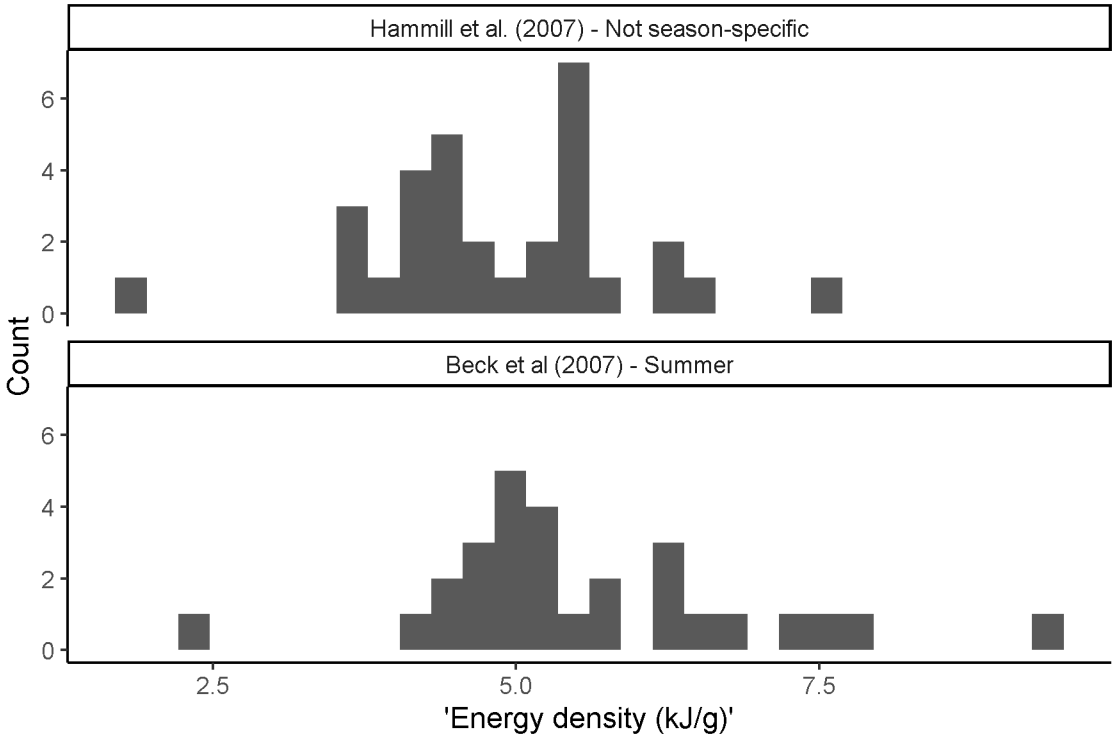

Figure S1. Comparison of energy densities of a variety of grey seal prey (kJ/g) from two different datasets (Beck et al. 2007; Hammill et al. 2007).

FIGURE S2. US GROUNDFISH – %W

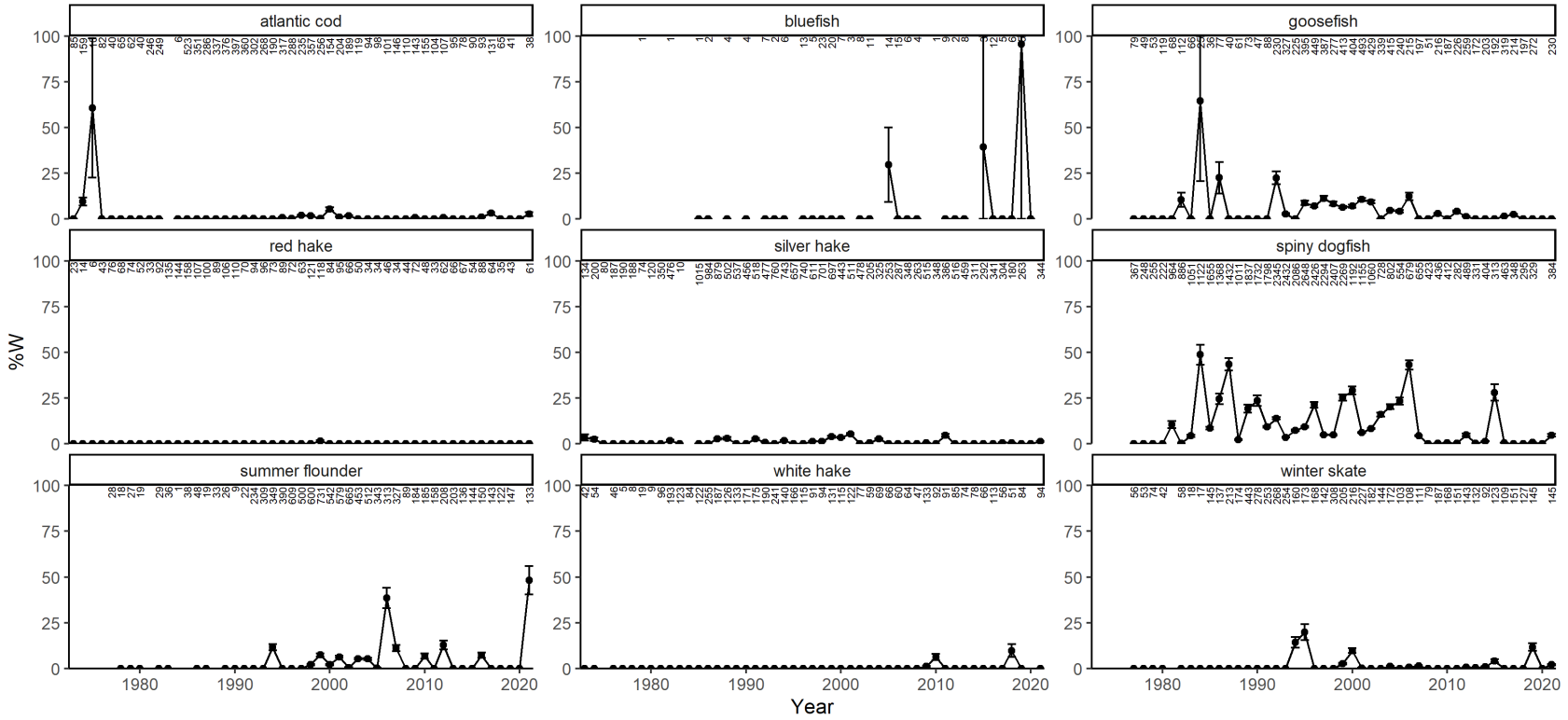

Figure S2. Annual percentage of mackerel in stomachs of US groundfish, in terms of weight (%W, mean with 95%CI). The number of stomachs is indicated on top.

FIGURE S3. GANNETS – MACKEREL CONSUMPTION BY COLONY

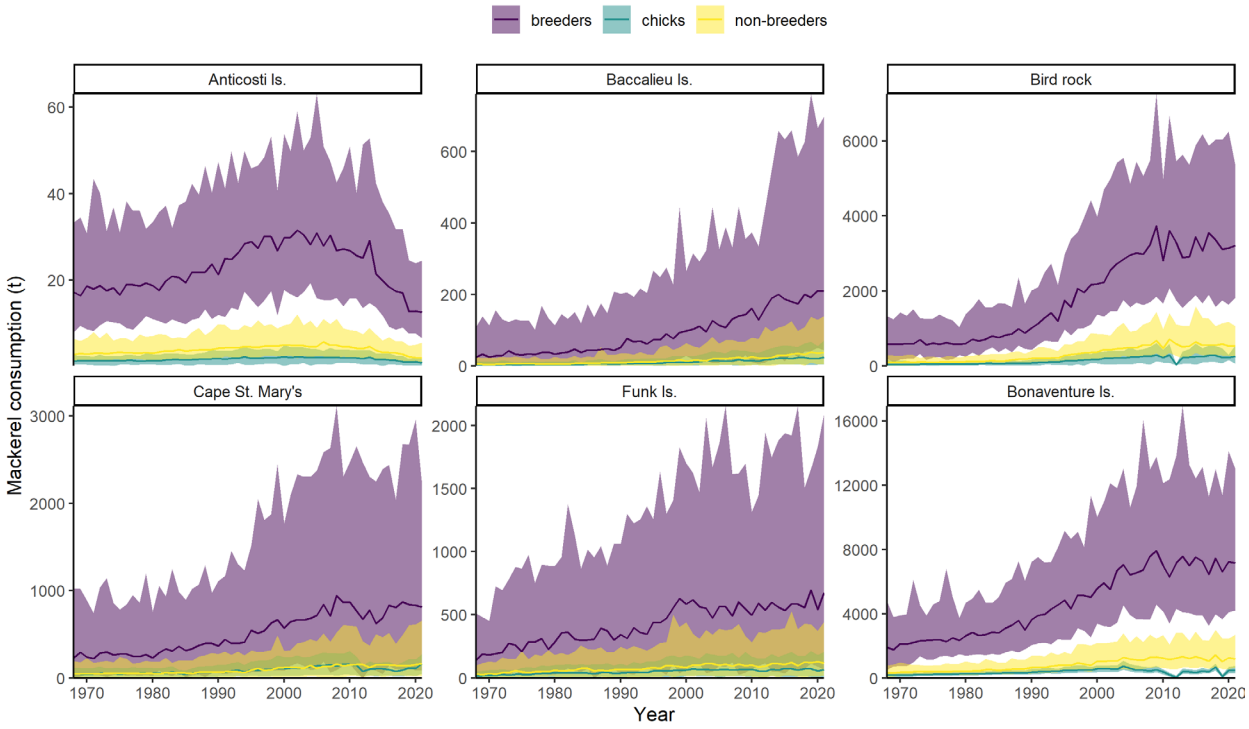

Figure S3. Mackerel consumption estimates for northern gannets in Canada, by colony and life stage.

FIGURE S4. CETACEANS – MACKEREL CONSUMPTION BY SPECIES

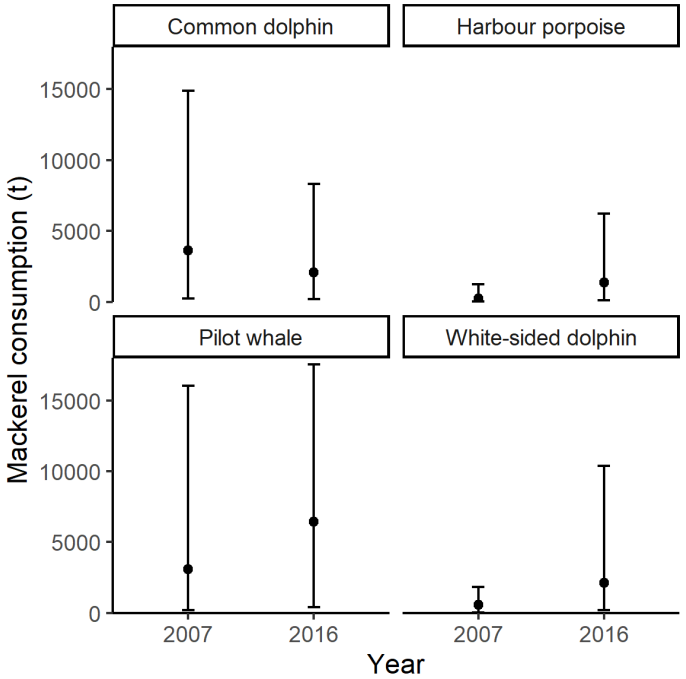

Figure S4. Mackerel consumption estimates for all four cetacean species included in this study.

FIGURE S5. TOTAL CONSUMPTION – RELATIVE IMPORTANCE OF EACH PREDATOR GROUP

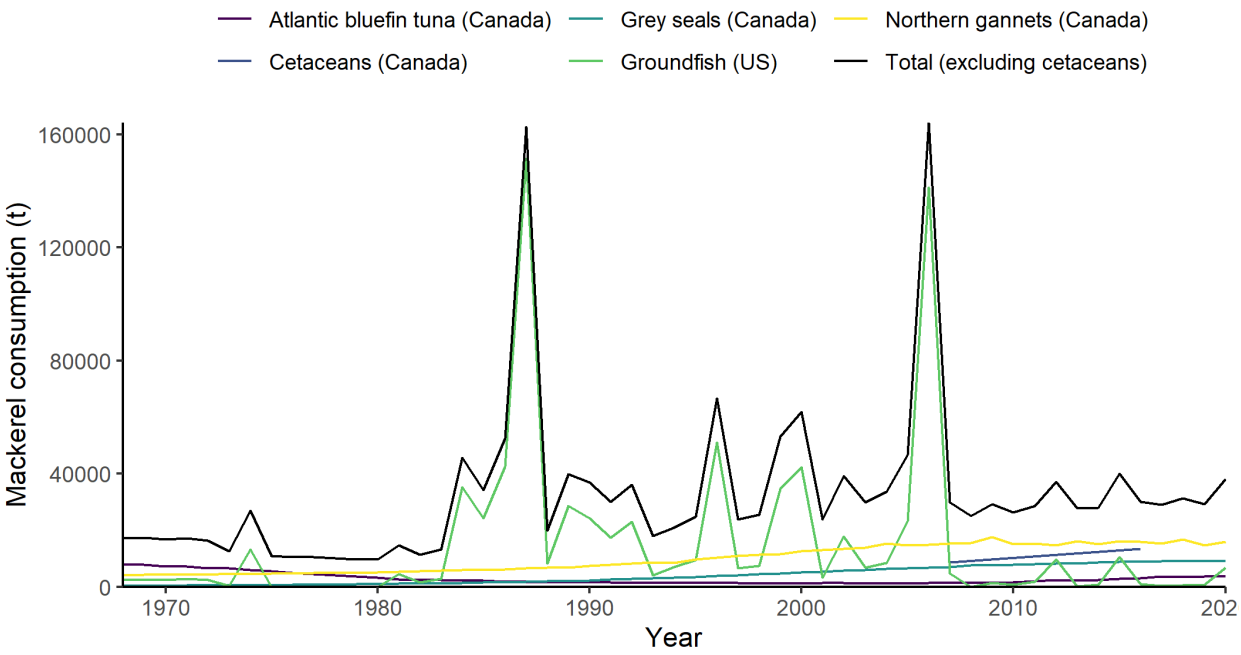

Figure S5. Mackerel consumption estimates (t) by predator group.