# Consumption by marine mammals on the Northeast U.S. continental shelf

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*Abstract.* The economic and ecological impacts of fish consumption by marine mammals, the associated interactions with commercial fish stocks, and the forage demands of these marine mammal populations are largely unknown. Consumption estimates are often either data deficient or not fully evaluated in a rigorous, quantitative manner. Although consumption estimates exist for the Northeast United States (NEUS) Large Marine Ecosystem, there is considerable uncertainty in those estimates. We examined consumption estimates for 12 marine mammal species inhabiting the regional ecosystem. We used sensitivity analyses to examine metabolically driven daily individual consumption rates, resulting in a suite of feasible parameter-pair ranges for each of three taxonomic groups: mysticetes, odontocetes, and pinnipeds. We expanded daily individual consumption to annual consumption based on abundance estimates of marine mammals found on the NEUS continental shelf coupled with estimates of annual residence time for each species. To examine consumptive removals for specific prey, diet compositions were summarized into major prey categories, and predatory removals by marine mammal species as well as for total marine mammal consumption were estimated for each prey taxa. Bounds on consumption estimates for each marine mammal species were determined using Monte Carlo resampling simulations. Our results suggest that consumption for these 12 marine mammal species combined may be similar in magnitude to commercial fishery landings for small pelagic and groundfish prey groups. Consumption by marine mammals warrants consideration both as a source of mortality in assessments of prey stocks, and to determine marine mammal forage demands in ecosystem assessment models. The approach that we present represents a rigorous, quantitative method to scope the bounds of the biomass that marine mammals are expected to consume, and is appropriate for use in other ecosystems where the interaction between marine mammals and commercial fisheries is thought to be prominent.

*Key words: Atlantic Ocean; commercial fisheries; competition; conservation; consumption estimates; ecosystem modeling; energetics; marine mammal diets; Northeast U.S. shelf; uncertainty estimation.*

## Introduction

Evaluating species interactions is essential to understanding an ecosystem, and in some instances such interactions can have significant social, economic, and cultural impacts. Prominent global examples are the interactions between marine mammals and commercially important fish species (Yodzis 2001, Savenkoff et al. 2008, Gerber et al. 2009). These interactions can have notable effects in one of five ways. First, these interactions can alter the population and community dynamics of fish and other prey that are eaten by marine mammals, particularly if the prey is already depressed into a "predator pit" due to other factors such as overfishing (Savenkoff et al. 2007, Swain and Chouinard 2008, Bundy et al. 2009). Second, the population and community dynamics of marine mammals can be impacted by these interactions if there is insufficient or inadequate quality of food (Kenney et al. 1985, Hlista et al. 2009). Third, these interactions have the potential to establish a competition for forage between marine mammals and those fisheries targeting the same marine mammal prey (Trites et al. 1997). Fourth and related, these interactions can also establish the potential for competition between marine mammals and other upper trophic level predators that may be species of concern or in decline (Mohn and Bowen 1996, Butler et al. 2006, Lindstrom et al. 2009). Finally, alterations in how energy and biomass flow to marine mammals can be symptomatic of ecosystem overfishing (Bundy et al. 2009, Link 2010).

The controversies over trade-offs involving federally protected or endangered marine mammals and socially and economically important commercial fisheries have evoked numerous opinions and proposals. These proposals have ranged from increasing harvest of mammals to ensure adequate food for people (Punt and Butterworth 1995, Butler et al. 2006) to stopping fishing to

ensure adequate forage for mammals (DeMaster et al. 2001, Smith et al. 2011), with several more balanced options (Butler et al. 2008, Bundy et al. 2009, Gerber et al. 2009). Although the focus has been largely on whales (e.g., Hinga 1979, Tamura and Ohsumi 2000, Leaper and Lavigne 2007), concerns about pinniped interactions with fish are also prominent (Trzcinski et al. 2006, Benoît and Swain 2008, Morissette et al. 2009). Reasonable estimates of how much and of which species marine mammals eat would help to address these issues (Link et al. 2006).

There is limited information on the food habits of marine mammals relative to food habits of fish, and the representativeness of the data that does exist is uncertain (e.g., Yodzis 2001, Corkeron 2009, Gerber et al. 2009). Food habits data for marine mammals are largely derived from necropsies on stranded or bycaught cetaceans (Laerm et al. 1997, Craddock and Polloni 2009), pinniped scat samples (Payne and Selzer 1989), limited biochemical analyses from tissue samples, or observations of some smaller odontocetes and pinnipeds from artificial environments such as aquaria (Brodie 1975, Murie 1987), each of which has potential biases. Given these caveats, some estimates of marine mammal feeding have been proposed (e.g., Kenney et al. 1997, Link et al. 2006, Overholtz and Link 2007).

The challenges with most estimates of marine mammal feeding are that they rarely provide quantifiable measures of uncertainty, they rarely document statistical biases, they rely on a host of unevaluated assumptions about underlying trophic models, and they do not robustly and rigorously attempt to provide confidence limits. This degree of uncertainty and the ad hoc manner in which variance has been considered for consumption estimates have limited the utility of such information. As some populations of marine mammals increase and potential conflicts between marine mammals and human uses of the ocean continue to increase (Payne and Selzer 1989, Lundström et al. 2010), an approach to quantitatively evaluate marine mammal consumption estimates would be beneficial.

We developed and applied such an approach for the Northeast U.S. (NEUS) continental shelf ecosystem, which could be used as an example for other regions. This ecosystem has a well-documented history of exploited marine resources (Fogarty and Murawski 1998), finfish and invertebrate dynamics (NEFSC 2008*b*, 2011), and associated trophodynamics in this food web (Smith and Link 2010). Although food web and multispecies models have demonstrated that apex predators such as marine mammals do not constitute a major energy pathway in this ecosystem relative to other trophic levels (Read and Brownstein 2003, Link et al. 2006), prey-specific removals by marine mammals can be substantial (Trites et al. 1997, Overholtz and Link 2007, NEFSC 2012). There are estimates for marine mammal consumption in the NEUS region (e.g., Kenney et al. 1997, Link et al. 2006, Overholtz and

Link 2007) and in contiguous northwest Atlantic ecosystems (Hammill and Stenson 2000, Trzcinski et al. 2006, Bundy et al. 2009). However, these estimates span multiple orders of magnitude because of differing methodologies, different time periods, and inconsistent assumptions. To inform marine mammal and fisheries management decisions, a more robust evaluation of such consumption estimates has been developed in this paper.

As marine mammal and fisheries science moves toward ecosystem-based fishery management, there is a growing need for detailed information on marine mammal consumption (Leaper and Lavigne 2007, Link 2010). Such data are essential for improving single-species assessments, informing ecosystem models, and providing accurate evaluations of trade-offs. Thus our objectives were to provide estimates of consumption for 12 species of marine mammal species from the NEUS ecosystem, formally evaluate the uncertainties about those estimates, and place those estimates into a broader fisheries–ecosystem context.

## METHODS

The study area is the NEUS continental shelf waters, as defined by the area within the Northeast Fisheries Science Center (NEFSC) bottom trawl survey strata (Fig. 1). Five mysticete species (fin, humpback, right, sei, and minke whales), five odontocete groups (long- and short-finned pilot whales, bottlenose dolphin, Atlantic white-sided dolphin, common dolphin, and harbor porpoise), and two pinniped species (gray and harbor seals) were included as the marine mammal predators in this study (see Appendix: Table A3). These species were chosen because they feed primarily on the NEUS shelf and met a minimum requirement of having at least nine published sources of diet data available worldwide, if not specifically within the NEUS region. Here we present methods to estimate marine mammal daily per capita consumption, abundances, diet compositions, annual consumption, and total prey-specific removals, as well as sensitivities related to these estimates. We also compared marine mammal consumption to commercial fisheries catches for prey species to provide context for the magnitude of prey consumed by marine mammal species.

### Daily per capita consumption and parameter pair examination

Consumption by marine mammals has been estimated through several methods (Lockyer 1981, Innes et al. 1987*a*, Markussen et al. 1992). However when empirical data are not available, an energetics equation is most commonly used to estimate the energy required to maintain a marine mammal. Consumption is usually derived through the general relationship of ingestion to individual mass (Read and Brownstein 2003):

$$Y = \alpha M^\beta \qquad (1)$$

where $Y$ is the daily per capita consumed biomass, $M$ is the body mass of an individual predator, and $\alpha$ and $\beta$ are
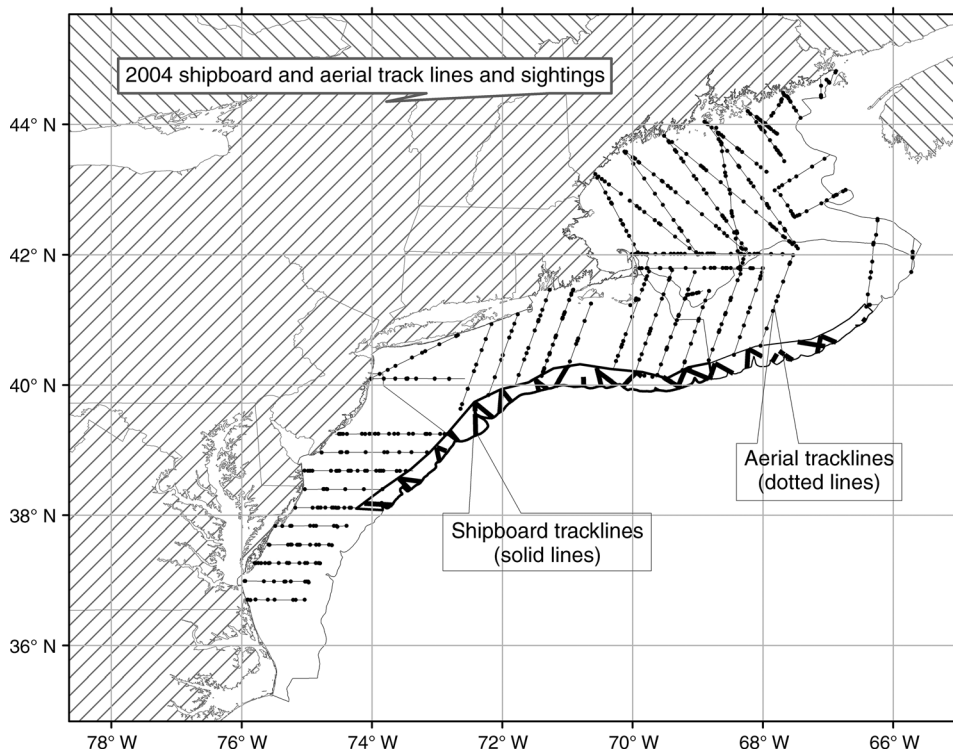
Fig. 1.   Shipboard (23 June–4 August 2004) and aerial track lines and cetacean sightings from the Northeast Fisheries Science Center's (NEFSC) 2004 summer marine mammal survey, including only regions covered by the NEFSC bottom trawl survey on the Northeast U.S. continental shelf.

species-specific consumption parameters. This equation was first introduced by Kleiber (1975) to estimate the basal metabolic rates for a wide range of homeotherms, and has since been used to estimate daily consumption for a range of marine mammals (Hammill and Stenson 2000, Leaper and Lavigne 2007, Stevick et al. 2008). Although more complicated models that include interactions with prey density would add more realism to consumption estimates, we used Eq. 1 because of the lack of detailed information on how diet compositions and prey density estimates have changed over time for most marine mammals considered in this study.

A wide range of α and β parameters for marine mammal consumption has been reported, and we attempted to consider the broadest range of parameters that were used in the literature for each marine mammal species group (Table 1). All estimates were converted to kg/d through methods described in Leaper and Lavigne (2007). To identify outliers, surface plots were then used to explore reasonable bounds for the parameter values (Fig. 2). Consumption parameters were analyzed separately for mysticetes, odontocetes, and pinnipeds. An average individual mass for each marine mammal group was used to visualize daily per capita consumption as a function of α and β parameters. Literature values of α and β parameter pairs were superimposed as boxes within the surface plot of each taxonomic group to which they were applied in the publication (Fig. 2). Parameter pairs

were excluded from further analysis if the resulting consumption estimates were 50% higher or lower than the mean consumption calculated from the remaining parameter pairs. However, if excluding a parameter pair resulted in none of the remaining parameter pairs falling within 50% of the new consumption mean, all parameter pairs were included in further analyses in order to account for the uncertainty of the parameter estimates.

*Marine mammal abundance*

Marine mammal abundance estimates were derived from NEFSC surveys (Appendix: Tables A1–3; Waring et al. 2011), where only survey track lines that were on the NEUS shelf were included (methods from Link et al. 2006; see Fig. 1 and Appendix). Annual residence ratios, based on the proportion of the stock found in the study area by season (Appendix: Table A2), were used to scale the abundance estimates to average annual abundance estimates (Appendix: Table A3). This annual residence ratio (Res) was calculated as the abundance-weighted proportion of the stock found in the study area, averaged over four seasons ($s$) and the four eco-regions ($r$) that make up the NEUS shelf study area (Table A1):

$$\text{Res} = \sum_r \left[ \sum_s \frac{P_{sr}}{4} \times \frac{S_r}{\sum_r S_r} \right] \quad (2)$$

TABLE 1. Daily per capita consumption parameters from literature for marine mammals grouped by taxa.

| Taxa | Consumption type | kJ/d | kcal/d | Watts | α | β | Source(s) |
|---|---|---|---|---|---|---|---|
| **A) Odontocetes** | | | | | | | |
| Odontoceti juvenile | biomass for maintenance | | | | **0.178** | **0.760** | 4 |
| Odontoceti adult | biomass for maintenance | | | | **0.313** | **0.660** | 4 |
| Odontoceti all | biomass for maintenance | | | | **0.258** | **0.690** | 4 |
| Cetaceans | daily prey consumed | | | | (0.042) | (0.670) | 4, 15, 19 |
| All marine mammals | BMR | 293.1 | | | (0.060) | (0.750) | 2, 9, 18, 19 |
| All marine mammals | BMR | | | 70 | (0.060) | (0.750) | 5, 6, 10 |
| All marine mammals | daily consumption | | | | **0.035** | **1.000** | 1, 13, 17 |
| Phocid and Odontoceti | biomass for maintenance | | | | **0.123** | **0.800** | 4, 14, 16 |
| **B) Mysticetes** | | | | | | | |
| Baleen whales | daily requirement | 863.6 | | | (0.177) | (0.783) | 11, 19 |
| Baleen whales | FMR | | | 80 | *0.068* | *1.000* | 7, 19 |
| Baleen whales | BMR | | | 70.5 | (0.060) | (0.733) | 3 |
| Baleen whales | high daily consumption | | | | (1.660) | (0.559) | 17 |
| Cetaceans | daily prey consumed | | | | (0.042) | (0.670) | 4, 15, 19 |
| All marine mammals | BMR | 293.1 | | | (0.060) | (0.750) | 2, 9, 18, 19 |
| All marine mammals | BMR | | | 70 | (0.060) | (0.750) | 5, 6, 10 |
| All marine mammals | daily consumption | | | | *0.035* | *1.000* | 1, 13, 17 |
| Phocid and Odontoceti | biomass for maintenance | | | | (0.123) | (0.800) | 4, 14, 16 |
| **C) Pinnipeds** | | | | | | | |
| Juvenile phocid seals | energy for growth | | | 40.2 | **0.710** | **0.430** | 4 |
| Juvenile phocid seals | energy for growth | | | 24.1 | **0.426** | **0.570** | 4 |
| Juvenile pinnipeds | energy for growth | | | 26.8 | **0.474** | **0.340** | 4 |
| Juvenile pinnipeds | energy for growth | | | 28.9 | **0.511** | **0.520** | 4 |
| Adult phocid seals | energy for growth | | | 6.19 | **0.109** | **0.800** | 4 |
| Juvenile Otariididae | energy for growth | | | 9.64 | *0.170* | *0.870* | 4 |
| Juvenile phocid seals | energy for maintenance | | | 17.5 | **0.309** | **0.570** | 4 |
| Juvenile phocid seals | energy for maintenance | | | | **0.086** | **0.860** | 4 |
| Juvenile phocid seals | energy for maintenance | | | | **0.092** | **0.840** | 4 |
| Juvenile phocid seals | energy for maintenance | | | | **0.032** | **1.000** | 4 |
| Juvenile phocid seals | energy for maintenance | | | 9.35 | **0.165** | **0.740** | 4 |
| Juvenile phocid seals | energy for maintenance | | | 9.93 | **0.175** | **0.720** | 4 |
| Adult phocid seals | energy for maintenance | | | | **0.055** | **0.840** | 4 |
| Adult phocid seals | energy for maintenance | | | | **0.079** | **0.710** | 4 |
| Adult phocid seals | energy for maintenance | | | | **0.057** | **0.830** | 4 |
| Adult phocid seals | energy for maintenance | | | 7.5 | **0.133** | **0.710** | 4 |
| Adult phocid seals | energy for maintenance | | | 3.75 | **0.066** | **0.870** | 4 |
| Adult phocid seals | energy for maintenance | | | 7.1 | **0.125** | **0.720** | 4 |
| All phocid seals | energy for maintenance | | | | **0.068** | **0.780** | 4, 15 |
| Adult pinnipeds | energy for maintenance | | | 27.8 | **0.491** | **0.440** | 4 |
| Phocid seals | BMR | 0.0034 | | | *0.695* | *0.750* | 8 |
| Adult phocid pooled | ingested energy | | | 5.07 | **0.090** | **0.800** | 4 |
| Phocid seals | daily prey consumed | | | | **0.100** | **0.800** | 12, 19 |
| Phocid seals | daily energy intake | | 125 | | **0.107** | **0.750** | 5 |

*Notes:* Values that were reported as energy consumption were converted to kg/d (see *Methods: Daily per capita consumption and parameter pair examination*). Italicized values of α and β indicate parameters that produced daily per capita consumption estimates 50% higher than the average for the taxa group; α and β values in parentheses produced estimates 50% lower than the average. Boldface α and β values indicate parameters selected from the literature to be used in consumption analyses for each taxonomic group, as discussed in *Methods*. Some sources included parameters from multiple published and unpublished data sets or were used for multiple taxonomic groups. Literature sources are: 1, Klumov (1963); 2, Kleiber (1975); 3, Lockyer (1981); 4, Innes et al. (1987b); 5, Murie (1987); 6, Hain et al. (1992); 7, Blix and Folkow (1995); 8, Hammill et al. (1995); 9, Lavigne (1996); 10, Kenney et al. (1997); 11, Sigurjónsson and Víkingsson (1997); 12, Trites et al. (1997); 13, Tamura and Ohsumi (2000); 14, Read and Brownstein (2003); 15, Link et al. (2006); 16, Overholtz (2006); 17, Leaper and Lavigne (2007); 18, Stevick et al. (2008); 19, Tamura et al. (2009).

where $P_{sr}$ is the proportion of the summer population estimate in a given eco-region for each season (Appendix: Table A2) and $S_r$ is the summer abundance estimate by eco-region.

Humpback and right whales greatly reduce feeding during migration to and from tropical breeding grounds during the spring and fall, and while occupying these breeding grounds during the winter. The annual residence ratios for these species were thus multiplied by the percentage of animals that do not migrate long distances per year ($n$), and this was added to the percentage of animals that do migrate ($m$) multiplied by the percentage of annual feeding that occurs on the NEUS for these individuals ($f$):

$$\text{Res}_{adj} = (\text{Res} \times n) + (m \times f). \qquad (3)$$

For humpback and right whales, we used approximations of $n = 5\%$, $m = 95\%$ (D. Palka, *personal observation*), and $f = 83\%$ (Lockyer 1981). For species that do not migrate, $n = 100\%$ and $m = 0\%$.
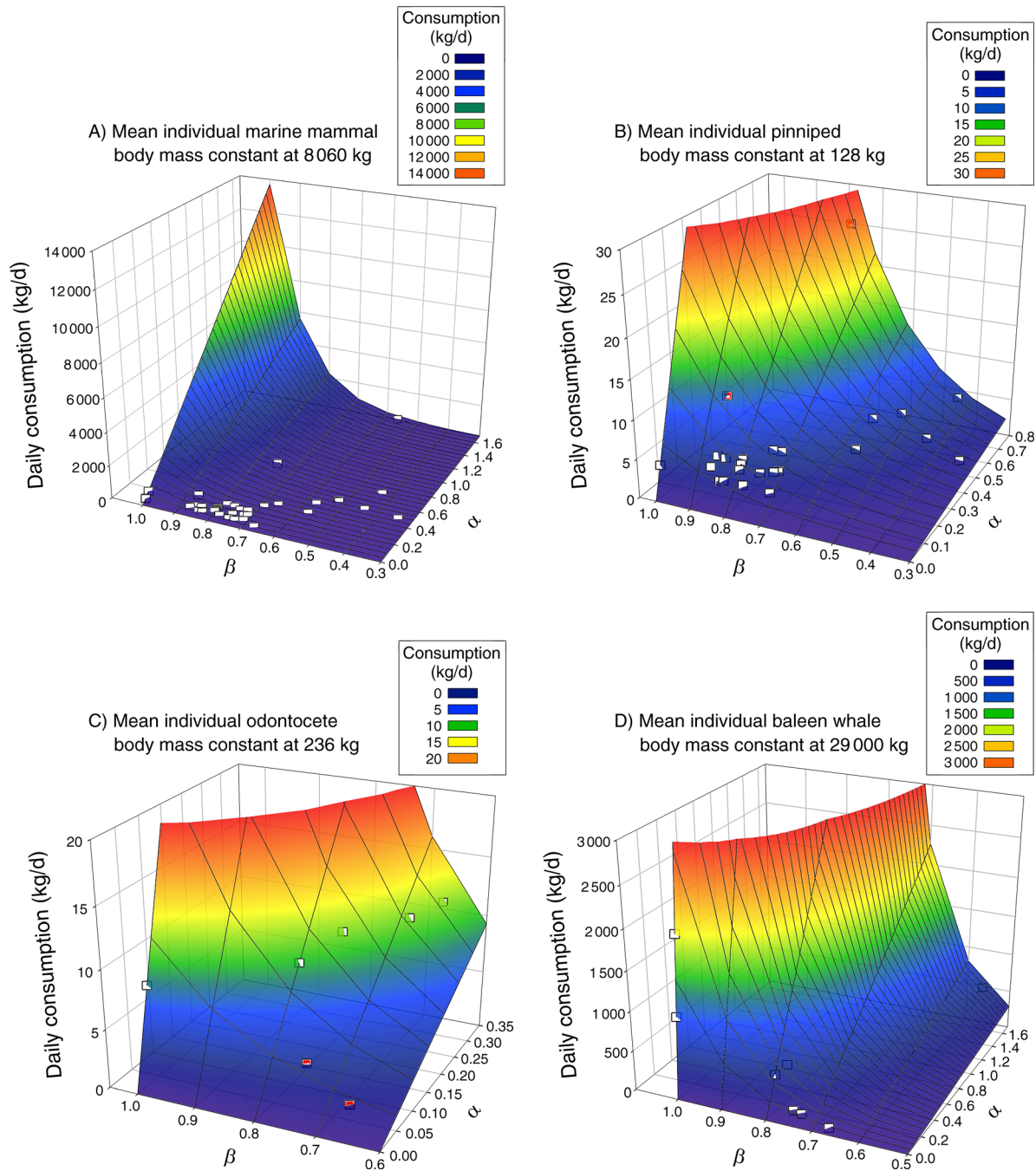
Fig. 2. Daily per capita consumption with varying α and β parameters based on the average body mass for each marine mammal group for (A) all 12 marine mammals, (B) pinnipeds, (C) odontocetes, and (D) mysticetes. Here, α and β are paired, species-specific consumption parameters from the equation $Y = \alpha M^\beta$, relating daily per capita consumption ($Y$) to body mass of a predator ($M$). Literature values of α and β are superimposed, where white squares were included and red squares were excluded from analyses.

### Diet compositions

Scat and stomach analyses from bycaught and stranded animals are the most common methods of determining marine mammal diet compositions, but these may include biases. Specifically, stomachs of stranded and bycaught animals may not be representa-tive of the entire population, and diet compositions obtained from stomachs or scats may be biased toward prey with hard parts that have slower rates of digestion. Some species of marine mammals have little published information on diet composition from animals that resided in the study area. To mitigate these problems

and potential biases, we based daily consumption on energetics equations instead of stomach volume, augmented local diet compositions with data from foreign sources where necessary, and when possible selected diet compositions based on expansion of hard parts to live mass of prey with corrections for erosion. Ideally we would only include diet data from the NEUS area, but when data was sparse and it was necessary to augment with foreign diet data, prey species that were not found in the NEUS were allocated to prey groups based on size, taxonomy, and depth preferences.

Marine mammal diet compositions were allocated to 12 standard prey groups of similar taxonomy that were of either commercial or ecological importance (Appendix: Table A4). The names given to most prey groups (e.g., scombrids) also includes prey species that are from similar taxonomic or trophic level groups (e.g., jacks and scads) to simplify naming convention and groupings. Literature sources of marine mammal diet compositions that did not give quantitative measures of the diet composition were assumed to be equally distributed between prey components unless qualitative distinctions were given. Prey components that were not mentioned in a literature source were assigned a zero percentage composition, except for studies that focused on specific prey (e.g., Overholtz and Waring 1991) or studies that grouped prey into broad categories (e.g., Kenney et al. 1985). In the latter cases, the remaining prey groups were left blank for that source.

A mean diet composition was then calculated across all literature sources for each prey group and marine mammal species, and was scaled to sum to 100% for the total diet composition for each marine mammal species. Minimum and maximum diet compositions were determined from literature values, where the minimum was the average of the zeros and the lowest nonzero value. The exception to this was when there was only one instance of the consumption of a prey group, in which case the minimum for that group was defined as zero. This approach insured that the minimum diet composition was lower than the mean. An example of a diet composition constructed from literature sources is given for humpback whales; the Appendix includes literature values (Table A5) and mean diet composition for humpback whales (Table A6).

### Annual consumption

Mean annual consumption estimates ($C$, in metric tons) for each marine mammal species within the NEUS shelf study area were calculated as:

$$C = Y \times 365 \times \text{Res}_{adj} \times \text{Abundance} \qquad (4)$$

where abundance is the annual abundance of a marine mammal species on the NEUS shelf (Appendix). Consumption was then allocated to prey groups ($i$) based on mean diet compositions ($D_i$):

$$C_i = C \times D_i. \qquad (5)$$

### Uncertainty and sensitivity analyses

Consumption distributions for each prey group by each marine mammal species as well as total consumption of each prey group for all marine mammal species combined were estimated with 10 000 Monte Carlo simulations, using the @RISK 5.7 software package (Palisade 2011). Uncertainty analyses were also performed in @RISK based on multivariate stepwise regressions relating input parameters to either consumption by marine mammal species or to total consumption by prey species, in which regression coefficients indicated the influence of parameters on the consumption estimates.

To develop these consumption distributions, ranges were determined for each input parameter. For abundance estimates, coefficients of variation (CVs) of survey estimates were used to calculate one standard deviation from the mean on-shelf summer abundance estimate. There is no CV associated with right whale survey estimates, so a CV of 20% was included to account for sampling error, as informed from the number of individuals that are typically missed in a given survey year (D. Palka, *personal communication*). Due to the uncertainty of the proportion of the year that many of the species spend in the study area and the interannual variability in the proportion, a 50% CV of mean residence ratios was assumed, with a maximum residence ratio of 1. This CV on residence is intentionally large to acknowledge the fact that there are no published values for residence rates of these species within the NEUS region, and that they are therefore based on expert opinion (D. Palka, *personal communication*). Mean individual body masses (Link et al. 2006) were assumed to have a 20% CV to approximate typical size ranges for adults. Minimum and maximum observed percentages of diet compositions per prey group were used to bound the mean diet (Appendix: Table A6). For daily per capita consumption parameters, the pairs of $\alpha$ and $\beta$ parameters specific to the three taxonomic groups (pinnipeds, odontocetes, and mysticetes; Table 1) were randomly sampled in the sensitivity analysis to provide a range of daily per capita consumption parameters.

To run Monte Carlo simulations in @RISK, distributions were selected for each parameter using the ranges just described. For abundance, individual body mass, and residency ratio, a pert distribution (Program Evaluation and Review Technique, @RISK; Palisade 2011) was used because distributions could be determined based on minimum, best estimate, and maximum values. Pert distributions are related to beta distributions, and have been used in similar studies to characterize uncertainty in predator consumption (Overholtz 2006, Overholtz and Link 2007). For diet compositions, a Johnson Moments distribution was determined for each prey group (@RISK; Palisade

TABLE 2. Marine mammal mean individual daily consumption estimates and consumption as percentage of body mass.

| | Individual daily consumption (kg) | | Daily consumption as percentage body mass | |
|---|---|---|---|---|
| Species | Mean | 80% CI | Mean | 80% CI |
| Fin whale | 981 | (57.5, 3600) | 0.020 | (0.001, 0.072) |
| Humpback whale | 621 | (41.8, 2110) | 0.020 | (0.001, 0.069) |
| Right whale | 502 | (35.1, 1620) | 0.021 | (0.002, 0.069) |
| Sei whale | 367 | (27.1, 1200) | 0.022 | (0.002, 0.071) |
| Minke whale | 165 | (14.6, 468) | 0.025 | (0.002, 0.071) |
| Pilot whale | 28 | (21.1, 35.9) | 0.033 | (0.025, 0.042) |
| Bottlenose dolphin | 8.7 | (5.5, 11.5) | 0.046 | (0.029, 0.061) |
| Atlantic white-sided dolphin | 5.1 | (2.8, 7.0) | 0.055 | (0.030, 0.076) |
| Common dolphin | 4.6 | (2.4, 6.3) | 0.058 | (0.030, 0.079) |
| Harbor porpoise | 2.2 | (0.94, 3.3) | 0.071 | (0.030, 0.106) |
| Gray seal | 6.0 | (3.4, 8.6) | 0.033 | (0.019, 0.048) |
| Harbor seal | 3.0 | (1.6, 4.8) | 0.040 | (0.021, 0.064) |

*Note:* The 80% confidence intervals are included from Monte Carlo simulations, and are expected to be large due to the uncertainty of the input parameters.

2011), which determines the distribution by fitting to the mean, standard deviation, skew, and kurtosis of the data. For each prey group, these parameters were approximated by comparing the distribution to the mean, minimum, and maximum diet compositions from the literature. A number of the marine mammal species consume a broad range of prey groups, and the ability to control the skew is particularly important because the distributions of the prevalence of most individual prey groups within a diet composition are heavily left-skewed. Confidence intervals (CIs) of 80% from Monte Carlo simulations were reported for annual population consumption as well as for consumption by prey group. This was chosen over 95% CIs as to not give a false sense of precision.

### Commercial fisheries catches of prey species

In order to provide context for the magnitude of prey consumed by marine mammals, marine mammal consumption was compared to commercial fisheries catches for prey species. We included the most recent 10 years available of commercial fishery catches from Northeast Fisheries Science Center's stock assessment reports for each commercially important marine mammal prey species (NEFSC 2006, 2008a, b, 2010, 2011). The catches were taken from within the study area and were used to calculate means and CVs. For marine mammal prey groups that included multiple commercial species, catches were summed across species to compare to the marine mammal prey groups: large gadids, small gadids, flatfish, clupeids, scombrids, and squid (Appendix: Table A4). Catches were then compared to mean total marine mammal consumption by prey group.

These comparisons should be considered as an order-of-magnitude approximation because marine mammals consume a wider variety of species than are targeted by commercial fisheries (e.g., spotted hake and rocklings included as small gadid prey are not commercially fished). Many studies report diet as taxonomic groups of

prey species instead of commercially vs. ecologically important species, so it is not possible at this time to provide direct comparisons between marine mammal predation and commercial catch.

### RESULTS

#### Daily per capita consumption, parameter pair examination, and outlier analysis

Examining the surface plot of pinniped daily per capita consumption in relation to consumption parameters, a broad range of $\alpha$ and $\beta$ values can be combined to produce similar daily consumption estimates of 1.9–7.6 kg/d, as seen in the dark blue band of Fig. 2B (Table 1). These estimates include $\alpha$ values ranging from 0.03 to 0.7, and $\beta$ values from 0.3 to 1.0. The only two published combinations that produced daily per capita consumption estimates outside of the 50% margin were $\alpha = 0.695$ combined with $\beta = 0.750$ (Hammill et al. 1995), and $\alpha = 0.170$ combined with $\beta = 0.870$ (Innes et al. 1987b), which produced estimates that were 1.5 and 4.8 times the average of the remaining estimates, respectively (Fig. 2B). These parameter pairs were excluded from subsequent analyses for pinnipeds. The remaining values correspond to daily per capita consumption estimates between 2% and 8% of body size (Table 2).

An average odontocete was estimated to consume between 8.2 kg/d and 11.5 kg/d (green band in Fig. 2C). For the five species of odontocetes included in this study, this results in mean daily per capita consumption of 2.2–28 kg/d (Table 2). Again, these estimates were produced by a broad range of parameter values: $\alpha$ values between 0.035 and 0.31, and $\beta$ values between 0.66 and 1.0. Within these ranges, there were two of the published parameter pairs that were below the 50% margin of the mean estimate and were thus removed from subsequent odontocete analyses (Fig. 2C): $\alpha = 0.06$ with $\beta = 0.75$ (e.g., Kleiber 1975), and $\alpha = 0.04$ with $\beta = 0.67$ (e.g., Innes et al. 1987b). The remaining range of daily per

TABLE 3. Mean annual consumption of prey groups by marine mammal species with upper and lower 80% CI (in parentheses).

| Predator species | Prey consumption, by group (thousands of metric tons/yr) | | | | | |
|---|---|---|---|---|---|---|
| | Large gadids | Small gadids | Flatfish | Clupeids | Scombrids | Sandlance |
| Fin whale | 1.2 (0.06, 2.9) | 1.0 (0.04, 2.4) | | 27.7 (0.8, 71.0) | 12.8 (0.3, 32.6) | 16.5 (0.6, 70.3) |
| Humpback whale | | 1.1 (0.005, 1.7) | | 5.8 (0.3, 14.6) | 3.7 (0.12, 8.8) | 9.7 (0.6, 24.6) |
| Right whale | | | | | | |
| Sei whale | 1.4 (0.008, 3.0) | 0.14 (0.006, 0.3) | | 6.2 (0.2, 15.3) | 1.4 (0.04, 3.05) | 3.4 (0.05, 8.3) |
| Minke whale | 12.2 (0.5, 29.6) | 3.0 (0.01, 5.3) | 0.01 (0.00006, 0.016) | 28.6 (2.1, 69.3) | 3.2 (0.007, 10.6) | 15.3 (0.5, 38.7) |
| Pilot whale | | 1.0 (0.14, 2.3) | | 2.3 (0.3, 5.1) | 12.0 (4.1, 22.3) | |
| Bottlenose dolphin | 0.3 (0.06, 0.5) | 0.8 (0.14, 1.8) | 0.005 (0.0008, 0.01) | 0.3 (0.13, 0.5) | 0.2 (0.02, 0.4) | 0.03 (0.002, 0.08) |
| Atlantic white-sided dolphin | 1.0 (0.1, 2.5) | 2.8 (1.1, 4.8) | 0.006 (0.0005, 0.017) | 2.0 (0.9, 3.3) | 0.5 (0.03, 1.3) | 0.9 (0.3, 1.5) |
| Common dolphin | 0.09 (0.01, 0.18) | 13.5 (3.0, 28.0) | 0.02 (0.0002, 0.05) | 7.3 (0.8, 17.4) | 18.1 (4.3, 37.0) | 0.9 (0.1, 1.8) |
| Harbor porpoise | 0.17 (0.017, 0.4) | 1.1 (0.4, 2.0) | 0.004 (0.0005, 0.009) | 1.0 (0.3, 1.7) | 0.2 (0.02, 0.4) | 0.3 (0.06, 0.7) |
| Gray seal | 4.1 (1.7, 7.0) | 1.7 (0.2, 4.2) | 2.7 (0.3, 6.2) | 1.9 (0.3, 4.5) | 0.6 (0.2, 1.0) | 7.6 (3.4, 12.5) |
| Harbor seal | 9.3 (3.4, 17.0) | 19.9 (8.5, 33.7) | 12.6 (1.8, 28.3) | 12.3 (4.8, 21.3) | 1.1 (0.18, 2.9) | 24.4 (7.7, 46.5) |
| Total | 30.3 (11.1, 54.9) | 46.3 (24.0, 74.0) | 27.4 (9.6, 50.8) | 96.4 (27.7, 192.2) | 54.4 (20.3, 99.6) | 78.1 (26.7, 147.9) |

capita consumption is feasible, corresponding to 3.3–7.1% of body mass for the five odontocetes (Table 2).

The wide range of parameters for mysticetes provided a large range of daily per capita consumption estimates from 40 kg/d to 2000 kg/d, with little trend of similar estimates from the literature (Fig. 2D). More realistic estimates are intermediate values (~100–600 kg/d), corresponding to ranges of consumption between 0.3% and 2% of body mass for an average mysticete mass of 29 000 kg. The two values that appeared to be outliers were the two estimates with β = 1 (e.g., Klumov 1963, Blix and Folkow 1995), which were 2.7 and 6.1 times higher than the average of the other estimates (Fig. 2D). However, when these two parameter pairs were excluded from the mean estimate, none of the remaining daily per capita consumption estimates fell within 50% of the new mean. The inability to easily rule out any of the consumption parameter pairs from the literature highlights the uncertainty, minimal data, and lack of trend for the mysticete consumption estimates. To account for this uncertainty, the full range of consumption parameters was included in further consumption analyses for the mysticete group (Table 1).

### Annual consumption by marine mammals

Mean annual consumption for mysticetes ranged from 18 000 metric tons/yr (1 metric ton = 1 Mg) for right whales to 320 000 metric tons/yr for fin whales (Table 3), after expanding daily per capita consumption by abundance and residential ratio over the year. Probability distributions of annual consumption estimates produced by the Monte Carlo simulations were one-tailed for all marine mammal species, with large consumption estimates being possible, but generally having a very low probability. An example is given for humpback whales, which consumed a mean of 48 000 metric tons/yr with an 80% CI of 3800–120 000 metric tons/yr (Fig. 3A). The odontocetes generally consumed less than the mysticetes due to their smaller size, with average annual consumption ranging from 3500 metric tons/yr for harbor porpoise to 85 000

metric tons/yr for pilot whales (Table 3). Pinniped consumption was relatively high because of their high abundance and year-round residence in the study area. Annual gray seal consumption was estimated to average 21 000 metric tons/yr, whereas harbor seal consumption averaged 98 000 metric tons/yr (Table 3). The 12 species of marine mammals combined consumed an average of 880 000 metric tons/yr on the shelf, with an 80% CI ranging from 340 000 to 1 800 000 metric tons/yr (Table 3).

### Marine mammal diet compositions and prey-specific consumption

Because mysticetes are predominantly filter feeders or specialists in consuming small fish and invertebrates, it is not surprising that their diets were generally dominated by shrimp (32% for minke whales to 63% for fin whales), zooplankton (42% for sei whales and 85% for right whales), clupeids (30% for minke whales), and sandlance (20% for humpback whales, Appendix: Table A6). Shrimp (mostly euphausiids) was the dominant prey for mysticete annual consumption, where the 80% CIs of fin whale consumption was 15 000–540 000 metric tons/yr, followed by sei and minke whales at just below 2000 metric tons/yr to 70 000–80 000 metric tons/yr (Table 3, Fig. 4). Zooplankton was also consumed in large quantities by the mysticetes, with 80% CIs for annual consumption ranging around 2000–90 000 metric tons/yr for both fin whales and sei whales (Table 3, Fig. 4). Fish consumption was greatest for fin whales and minke whales feeding on clupeids (80% CIs ranging up to 71 000 metric tons/yr; Fig. 4), and humpback whales feeding on sandlance (80% CI of 600–25 000 metric tons/yr; Fig. 4).

Being primarily piscivores, the odontocetes had diets dominated by finfish and larger pelagic invertebrates including squid (72% for pilot whales), miscellaneous fish (24% for common dolphins and 50% for bottlenose dolphins), small gadids (25% for Atlantic white-sided dolphins, and 32% for harbor porpoise), and scombrids (21% for common dolphins and 14% for pilot whales); see Appendix: Table A6. Squid was the dominant prey

Table 3. Extended.

| Meso-pelagics | Misc. fish | Benthic invertebrates | Squid | Shrimp | Zooplankton | Total |
|---|---|---|---|---|---|---|
| 1.1 (0.004, 3.2) | 10.7 (0.3, 26.4) | | 11.4 (0.4, 29.3) | 200 (14.7, 538) | 34.8 (2.1, 90.2) | 316.1 (23.2. 835.6) |
| | 9.1 (0.4, 21.8) | | 0.5 (0.005, 1.0) | 17.7 (1.2, 44.5) | 1.0 (0.003, 5.8) | 48.4 (3.8, 121.5) |
| | | | | 2.7 (0.07, 6.8) | 15.1 (1.3, 38.7) | 17.7 (1.5, 45.1) |
| 1.5 (0.02, 3.2) | 3.5 (0.09, 14.9) | | 4.9 (0.19, 12.7) | 29.0 (1.8, 70.1) | 37.4 (2.9, 91.4) | 89.4 (7.2, 218.7) |
| | 1.4 (0.03, 3.4) | | 0.6 (0.009, 1.7) | 31.7 (1.9, 80.9) | 0.8 (0.01, 1.8) | (8.6) |
| 0.4 (0.03, 1.2) | 7.7 (2.3, 14.3) | 0.7 (0.09, 2.0) | 61.1 (34.5, 90.9) | | | 85.2 (48.8, 126.5) |
| 0.0015 (0.0004, 0.002) | 2.4 (1.0, 4.0) | 0.02 (0.001, 0.04) | 0.7 (0.1, 1.5) | 0.002 (0.0005, 0.004) | | 4.7 (2.1, 7.9) |
| 0.9 (0.18, 2.0) | 0.6 (0.1, 1.3) | 0.1 (0.005, 0.3) | 2.3 (1.1, 3.7) | | | 11.1 (5.4, 17.9) |
| 7.0 (1.2, 15.3) | 20.9 (6.0, 40.5) | 0.1 (0.04, 0.2) | 19.6 (4.8, 39.9) | | | 87.7 (37.7, 149.9) |
| 0.1 (0.005, 0.2) | 0.5 (0.06, 1.2) | 0.02 (0.001, 0.04) | 0.1 (0.02, 0.3) | 0.03 (0.006, 0.07) | | 3.5 (1.4, 6.1) |
| | 1.7 (0.3, 3.9) | 0.1 (0.02, 0.2) | 0.6 (0.09, 1.4) | 0.01 (0.0, 0.017) | | 20.5 (10.3, 32.5) |
| | 9.7 (3.5, 17.2) | 1.1 (0.2, 3.0) | 6.8 (1.4, 13.9) | 0.6 (0.16, 1.3) | | 97.7 (49.0, 156.8) |
| 10.7 (2.8, 29.7) | 67.3 (31.5, 114.0) | 2.2 (0.5, 6.1) | 108.6 (65.1, 158.6) | 282.7 (23.4, 738.7) | 88.8 (7.4, 226.3) | 881.0 (343.6, 1783.4) |

for the odontocetes, for which the 80% CI for pilot whale consumption of squid was 35 000–91 000 metric tons/yr (Table 3, Fig. 4). Due to their larger body sizes, pilot whales also dominated the odontocete consumption of miscellaneous fish (80% CIs of 6000–41 000 metric tons/yr), whereas common dolphins dominated the consumption of scombrids due to their abundance (80% CIs of 4300–37 000 metric tons/yr).

Pinnipeds are generalist feeders with predominantly piscivorous diets including sandlance (34% for gray seals and 25% for harbor seals), small gadids (9% for gray seals and 20% for harbor seals), large gadids (19% for gray seals and 10% for harbor seals), flatfish (14% for gray seals and 13% for harbor seals), and clupeids (10% for gray seals and 13% for harbor seals); see Appendix: Table A6. Although individual gray seals are heavier than harbor seals, annual consumption of any one prey group was greater for harbor seals due to their higher abundance, including 7800–46 500 metric tons/yr of sandlance, 8500–34 000 metric tons/yr of small gadids, 1800–28 000 metric tons/yr of flatfish, and 4800–21 000 metric tons/yr of clupeids (Table 3, Fig. 4). Gray seals primarily targeted sandlance, with an 80% CI of 3400–13 000 metric tons/yr for sandlance consumption (Table 3, Fig. 4).

For the 12 species of marine mammals combined, shrimp was the most targeted prey, with an 80% CI of the combined consumption ranging from 23 000 to 740 000 metric tons/yr (Table 3, Fig. 5A). Squid were consumed in the next greatest prey biomass, with 80% CIs of 65 000–160 000 metric tons/yr, followed by clupeids at 28 000–190 000 metric tons/yr, sandlance at 27 000–150 000 metric tons/yr, miscellaneous fish at 32 000–110 000 metric tons/yr, scombrids at 20 000–100 000 metric tons/yr, and zooplankton at 7400–230 000 metric tons/yr (Table 3, Fig. 5A).

### Sensitivity analyses of consumption estimates

Abundance was the most influential parameter when estimating annual consumption for odontocetes

(0.39–0.49 regression coefficients; Appendix: Fig. A1F–J) and most mysticetes (0.21–0.32; Appendix: Fig. A1A, B, D, E). Residence ratios were the next most influential parameter for odontocete and mysticete annual consumption estimation (0.18–0.41 and 0.12–0.16, respectively), with daily consumption parameters being the least influential (–0.43–0.03 for odontocetes). By contrast, diet was the most influential parameter for right whales (0.18 regression coefficients for both zooplankton and shrimp; Appendix: Fig. A1C) and pinnipeds (around 0.30 for harbor seal consumption of both flatfish and sandlance, as well as for gray seal consumption of clupeids and sandlance; Appendix 1: Fig. A1K, L). This is due to the abundance estimates of right whales and pinnipeds being fairly precise (CVs less than 0.34) and seals not migrating annually out of NEUS waters to the extent that some cetaceans do. Diet was also the most influential parameter when estimating consumption of individual prey groups, as seen in the example of sensitivity analyses for humpback whales (Fig. 3B–D).

### Comparing marine mammal consumption to commercial fisheries catches of prey species

For most of the six prey groups, mean marine mammal consumption was similar in magnitude or higher than commercial fisheries catch (Fig. 5B, C). Annual marine mammal consumption was 90–150% of commercial catch for large gadids, clupeids, scombrids, and flatfish, and was as much as 3–4 times higher than commercial catch for small gadids and squid (Fig. 5B, C).

### Discussion

#### Daily per capita consumption parameters

As reported in previous studies (e.g., Kleiber 1975), analyses of α and β consumption parameters suggested that reasonable ranges of marine mammal consumption estimates could be achieved with β values close to 0.75. However, consumption parameters associated with
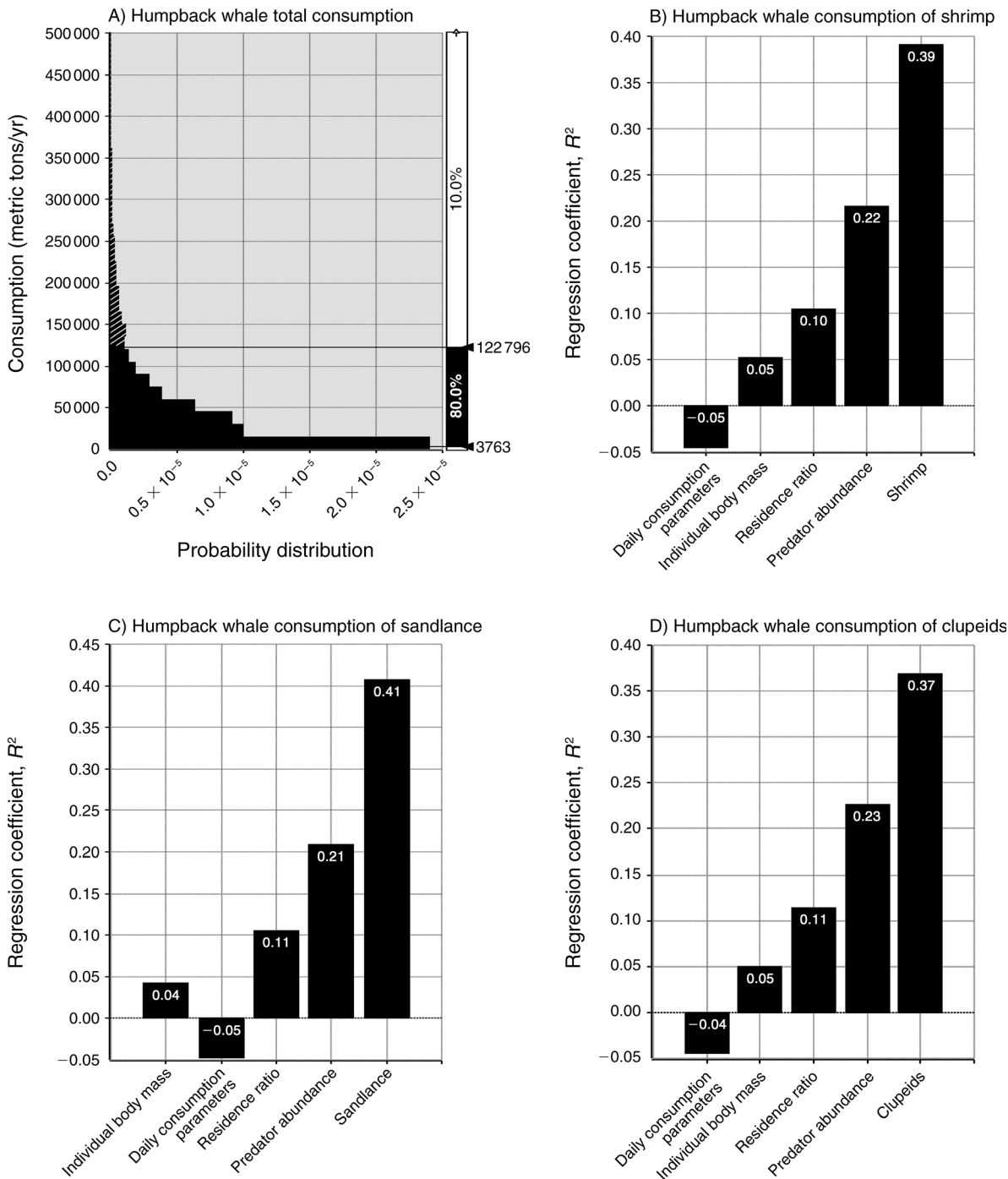
FIG. 3. (A) Probability distribution of annual consumption (metric tons/yr) by humpback whales on the Northeast U.S. continental shelf study area, where the black bar to the right represents the 80% CI of annual consumption in metric tons (=Mg), and regression sensitivity results of input parameters vs. humpback whale consumption of (B) shrimp, (C) sandlance, and (D) clupeids. The 10% CI in the right open bar is only the upper variation; the lower 10% CI is not shown. Residence ratio is the proportion of the marine mammal stock found in the study area by season (see *Methods: Marine mammal abundance*).

similar daily per capita consumption estimates can result in drastically different consumption estimates when $\alpha$ and $\beta$ values are combined independently (Fig. 2A), illustrating why $\alpha$ and $\beta$ consumption values should not be considered independently. A better method for incorporating uncertainty of consumption parameters may be to sample from pairs of consumption parameters. When parsed into similar species groups, a pattern generally emerged showing $\alpha$ and $\beta$ values that fell along a contour of similar daily per capita consumptions. The
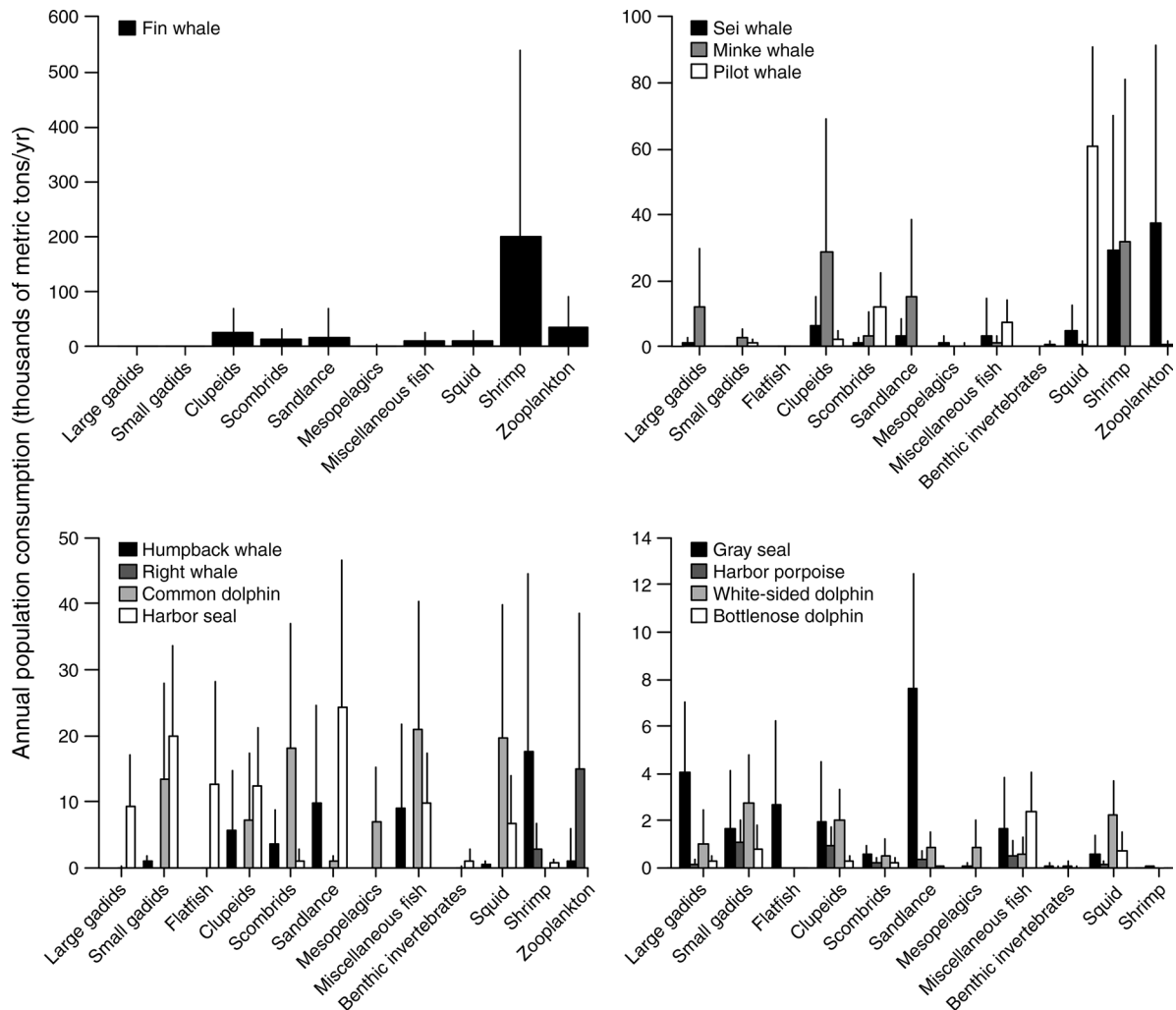
FIG. 4. Annual consumption of prey groups by marine mammal species on the Northeast U.S. continental shelf. Vertical bars represent the 80% CIs.

points that deviated more than 50% from the mean consumption estimates produced exceptionally high or low daily per capita consumption values that may not be representative of general feeding habits. For the pinnipeds, the two high outlying points were from growing juvenile otariids (fur seals and sea lions) that had significantly higher ingestion rates than adult otariids (Innes et al. 1987*b*), and from a generic rate of all mammals that Hammill et al. (1995) borrowed from Kleiber (1975), which may differ from pinniped ingestion rates. For the odontocetes, the two low outlying points were both from aggregations of all marine mammals (Kleiber 1975, Innes et al. 1987*b*), which may not be representative of the higher metabolic rates expected for odontocetes (Spitz et al. 2010).

Using our criteria to select consumption parameters, we obtained ranges of daily per capita consumption that agreed with previous empirical estimates of daily consumption (Gaskin 1982, Trites et al. 1997) and

followed biological theories such as smaller odontocetes having higher energy requirements needed to thermo-regulate smaller body sizes in cold water, and to support their active life styles (Spitz et al. 2010). However, in the case of mysticetes where very few empirical data exist and previous studies have used a broad range of parameters to estimate consumption, it was not possible to determine outliers. Thus, a broader range of consumption parameters was used to incorporate the full uncertainty associated with the estimates. This range should be refined as additional research is conducted to ground-truth the estimates of $\alpha$ and $\beta$ for these large cetaceans.

*Estimates of consumption by marine mammals*

An important result from this study was the characterization of uncertainty for the marine mammal consumption estimates. Confidence intervals for annual consumption estimates varied by factors of two to
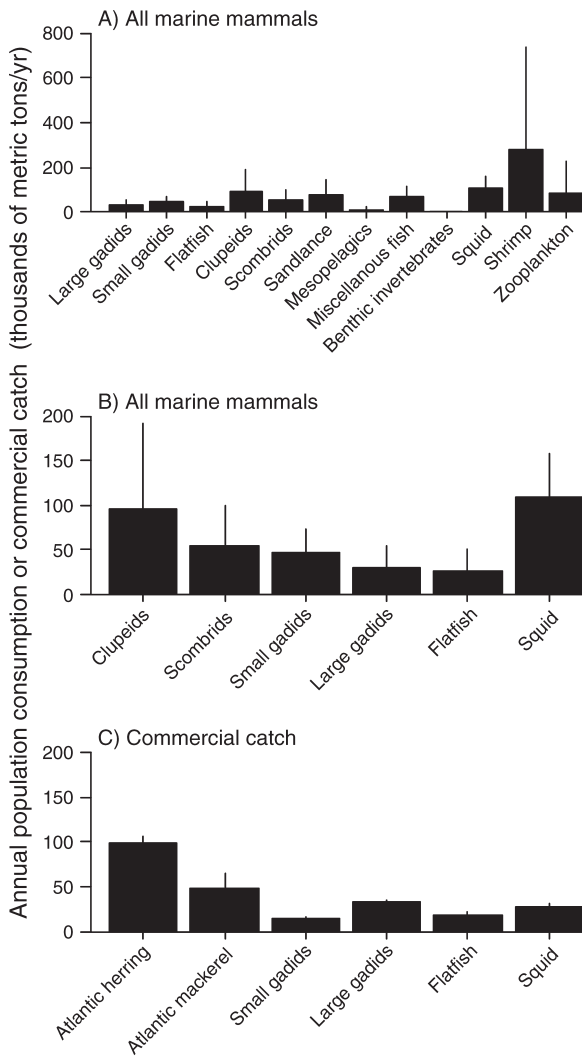
FIG. 5. (A) Total consumption for all marine mammals by prey group, (B) total consumption of commercially important prey for all marine mammals, and (C) commercial catch by species group. Solid squares represent means. Vertical bars represent the 80% CIs for marine mammal consumption and CVs for commercial catch.

almost 40, and incorporated the uncertainty of each input parameter. These orders of magnitude for uncertainty estimates are similar to those in previous studies (Mohn and Bowen 1996, Overholtz and Link 2007), and appropriate caveats should be included to address this uncertainty when estimating marine mammal consumption and prey removal, or when incorporating either of these into ecosystem models.

Daily per capita consumption estimates varied greatly, illustrating the need to understand why these estimates varied and to improve techniques to better confine these ranges. Some studies estimated daily per capita consumption similar to that found in this study (Markussen et al. 1992, Read and Brownstein 2003), whereas others (Smith and Gaskin 1974, Stevick et al.

2008) reported individual cetacean consumption to be 1.5–2.5 times higher than mean estimates found in this study. Studies that estimated higher daily consumption generally focused on areas and times of high productivity and concentrated feeding activity for marine mammals (Bushuev 1986, Leaper and Lavigne 2007). Others estimated individual daily consumption rates that were toward the lower end (Hain et al. 1992, Folkow et al. 2000, Tamura et al. 2009). Discrepancies may be due to assumptions made about residence time, feeding during migrations, or due to the empirical method used to determine daily consumption, such as stomach content (e.g., Víkingsson 1997). In general, mean mass of stomach contents reported in previous research (Fontaine et al. 1994) was less than daily consumption estimates, which could indicate that most species fed more than once a day. Given the variability of previous approaches and results, we assert that our approach provides one method to bound these estimates in the context of annual mean consumption.

Sensitivity analyses indicated that abundance estimates and residency ratios were the most influential parameters when estimating mysticete and odontocete annual consumption. This reflects the relatively high CVs for these two factors. Due to the lack of information on the proportion of the year that many of these species inhabit the shelf and the unknown interannual variability in this proportion, we assumed a 50% CV. If this assumed value were too high, the relative importance of this factor would be overestimated. A large component of the CVs for the abundance estimates is due to the fact that the species are naturally highly aggregated. Additionally, CVs for on-shelf abundance estimates naturally increased over CVs for the entire population.

Diet compositions had relatively low impacts on estimated annual consumption because animals have to consume minimum quantities of food to sustain themselves, regardless of what prey items they consumed. However, when estimating the annual consumption of a specific prey group by a marine mammal species, the effect of diet composition was generally the most influential, as was found in previous studies (Shelton et al. 1997, Overholtz and Link 2007). Although perhaps initially counterintuitive, it is rational that abundance or daily per capita consumption estimates for a marine mammal species make little difference in determining consumption of prey species that are rarely eaten. Accurate marine mammal abundance and annual residency estimates are therefore critical for annual marine mammal consumption estimates or modeling, and diet compositions are especially important when specific prey groups are being considered.

It is important to estimate predation based on specific temporal and regional overlap of predators and prey in any ecosystem. Studies that have included marine mammal abundance data from the entire NEFSC

marine mammal survey area to estimate consumption (Read and Brownstein 2003, Overholtz and Link 2007) may substantially overestimate prey-specific consumption for prey species that are largely confined to shelf waters. One of the greatest differences between this study and previous studies is that the marine mammal abundance estimates were reduced to only the abundance on the NEUS shelf, which removed the percentage of the population that may be feeding on other prey (Craddock and Polloni 2009). In addition to spatial overlap, temporal overlap with prey is also very important in estimating predation, especially for highly mobile and migratory predators such as whales. To account for migration of mammals outside of the NEUS shelf during portions of the year, this study included a residency ratio and expanded daily per capita consumption to only the relevant portion of the year in which predators and prey overlap. When accounting for these differences, the annual consumption estimates for most marine mammals were generally comparable to those of previous studies (e.g., Hain et al. 1992, Read and Brownstein 2003, Overholtz and Link 2007).

Although input parameters may be improved by continued research, this work shows that estimating the general range of metabolic demand of these mammals can be executed. This information has been used directly in stock assessments to improve natural mortality estimates for prey species (NEFSC 2012). Accurate consumption estimates are also important for improving marine mammal interactions in ecosystem models, which can be used to address questions regarding trade-offs between fishery yields and marine mammal prey requirements (e.g., Gerber et al. 2009, Morissette et al. 2010, 2012). Additionally, estimates of marine mammal consumption can be used to improve growth estimates and projections of marine mammal stock recovery, because prey availability can affect growth and successful reproduction (Haug et al. 2002, Klanjscek et al. 2007, Hlista et al. 2009). Therefore, understanding the food requirements of marine mammals is important for monitoring the health of the populations, which can be especially critical for endangered species.

## Comparing marine mammal consumption to commercial fisheries catches of prey species

The comparison of marine mammal consumption to commercial fisheries catch presented in this study provides an order-of-magnitude contrast of these consumption estimates. Mean marine mammal consumption for all prey groups that primarily contain commercially harvested prey is similar in magnitude or greater than commercial catch, as found in other areas of the world (Trites et al. 1997, Tamura and Ohsumi 2000). On the NEUS shelf, the large amount of prey consumed illustrates the importance of marine mammal consumption in the ecosystem, and the need for further research to determine the interactions that this con-

sumption has with species at other trophic levels of the ecosystem.

Although consumption by marine mammals may be similar in magnitude to commercial fishing for some commercially important prey groups, this study agrees with previous research that the majority of the total consumption occurs on prey not targeted by commercial fishing (Hammill and Stenson 2000, Kaschner 2004, Savenkoff et al. 2008), such as euphausiids and sandlance, or on prey groups that are abundant, such as squid and, in some years, clupeids. Although commercially targeted shrimp such as pandalids are included in the prey category "shrimp," euphausiids constitute the vast majority of the biomass consumed in the shrimp prey category. Similarly, squid prey in diet studies often included species not targeted by commercial fisheries (Gonzalez et al. 1994, Trites et al. 1997), and the two squid species commercially targeted in the NEUS are currently not considered to be overfished (NEFSC 2006, 2011). In addition, marine mammals often select smaller sizes of prey than are targeted by commercial fisheries (Bowen et al. 1993, Gannon et al. 1998). Thus, direct and indirect interactions between marine mammal consumption and commercial fishing may be lower than expected from total consumption estimates.

Predation on groundfish is of particular interest in this study area, especially in eastern Canadian waters where seal populations have increased substantially in recent years (Waring et al. 2011), and fisheries closures have been implemented because of low cod populations. Estimates from this study indicate that, on average, gray seals consumed 12% of the amount of large gadids harvested by commercial fisheries, and harbor seals consumed 28%. This consumption includes several species of gadids, some of which are currently at high population abundance, such as haddock (NEFSC 2008a). Although we were unable to fully investigate interannual variability of marine mammal diets, it is likely that cod consumption by seals in the United States is currently a relatively low percentage of the large gadid prey consumption, because Atlantic cod stocks are currently overfished (NEFSC 2008b), and predation mortality from seals decreases with prey abundance (Savenkoff et al. 2007). Therefore, consumption of cod is likely to be comparable to that in previous research and is likely to be lower than in Canadian waters (Mohn and Bowen 1996). Some studies indicate that the higher seal predation rates in Canada may be contributing to the slow cod recovery in that region, but the lower seal populations in U.S. waters may not have the same impact on cod stocks. Additionally, seals are unlikely to have caused declines in cod stocks in the United States, as studies indicate that even with the relatively high levels of predation in Canada, overfishing was more likely the cause of the cod stock collapse than was predation (Mohn and Bowen 1996, Bundy et al. 2009).

Caveats for comparing marine mammal consumption to fisheries catch include the fact that consumption could not be estimated by individual prey species, because taxonomic detail of published prey items varied widely. Diet compositions also had to be drawn from distant regions for many marine mammals, resulting in prey category approximations based on species of similar taxa. Additionally, most prey groups contain species that are not commercially targeted, and therefore may overestimate marine mammal consumption relative to commercial fishery catch. Caution should therefore be used when comparing marine mammal consumption and commercial catch for prey groups. Additional context can be provided by comparing marine mammal consumption to fish consumption for similar prey. A recent stock assessment of Atlantic herring (NEFSC 2012), which incorporated marine mammal consumption estimates from this work, found that annual consumption of herring by 13 top predator fish species generally ranged from estimates similar to those of marine mammal consumption to five times higher. Also in our study area, Overholtz and Link (2007) found that Atlantic herring consumption by demersal fish was generally greater than consumption by marine mammals. Globally, Trites et al. (1997) found that fish consumption in the Pacific was two to more than 20 times the marine mammal consumption of prey groups. Bundy et al. (2009) found that although piscivorous fish consumption was higher than marine mammal consumption in four northwest Atlantic ecosystems prior to cod collapse, this consumption has been at least partially replaced by marine mammal consumption as seal populations have increased. However, Bundy et al. (2009) found that resource overlap indices were low between marine mammal consumption and commercial fisheries catch, and that marine mammals generally targeted lower trophic level species than did fisheries. In general, marine mammal consumption is similar to or lower than fish consumption of similar prey groups.

Although the estimates from this study indicate that marine mammal consumption may be important to specific prey taxa, attempts to increase prey populations by reducing marine mammal populations may in fact have no, or detrimental, effects on prey populations (Morissette et al. 2006, Savenkoff et al. 2008, Gerber et al. 2009, Morissette et al. 2012). This may be due to indirect trophic effects (Butterworth et al. 1995, Punt and Butterworth 1995, Yodzis 1998). As in any system, the many secondary effects that occur from the removal of top predators such as marine mammals may lead to unknown or undesirable consequences to ecosystems (Yodzis 2000, Springer et al. 2003). Therefore, studies that do not incorporate the indirect predation effects (e.g., Stefánsson et al. 1997, Butler et al. 2006) may be oversimplifying the system when speculating that the presence of marine mammals negatively impacts commercially targeted stocks. This is illustrated by the fact that predation by other fish in the ecosystem may be comparable to, or even an order of magnitude higher than, consumption by marine mammals (Trites et al. 1997, Overholtz and Link 2007, Bundy et al. 2009).

## Conclusions

The global controversies surrounding how much and of what marine mammals consume, their interactions with fisheries, and how these factors impact their protection, are prominent management issues (e.g., Savenkoff et al. 2008, Corkeron 2009, Gerber et al. 2009) that require reliable estimates of marine mammal consumption and uncertainty to be addressed. We have provided reasonable parameter ranges to estimate per capita consumption, and any parameters outside of these ranges should be questioned. Further, we have demonstrated that marine mammal abundance and residency were most influential when estimating marine mammal consumption, and diet compositions were most influential when estimating consumption of particular prey. Although many confidence intervals that we provide are large, we have demonstrated that they can be quantified. Given the challenges of improving empirical estimates, quantifying consumption uncertainty is important, and we recommend that future efforts similarly provide ranges bounding any estimates of marine mammal consumption.

Finally, marine mammal consumption maybe similar in magnitude to fisheries removals for some prey taxa. However, evaluating such consumptive removals needs to address the specific spatiotemporal overlap of the predators and prey in the local ecosystem. Furthermore, when applying consumptive removals in a management context, broader ecosystem considerations need to be incorporated, such as indirect food web interactions (Punt and Butterworth 1995, Yodzis 2000, Gerber et al. 2009). Certainly, ascertaining the scope, extent, and impact of these species interactions remains an important challenge, and detailed information on marine mammal consumption is needed. The approach that we present here elucidates a more quantitatively rigorous manner in which to approach and contextualize such estimates. Doing so represents an important step as marine mammal and fisheries science move toward ecosystem-based fisheries management (Leaper and Lavigne 2007, Forcada et al. 2009, Link 2010).

### Literature Cited

Benoît, H. P., and D. P. Swain. 2008. Impacts of environmental change and direct and indirect harvesting effects on the dynamics of a marine fish community. Canadian Journal of Fisheries and Aquatic Sciences 65:2088–2104.

Blix, A. S., and L. P. Folkow. 1995. Daily energy expenditure in free living minke whales. Acta Polytechnica Scandinavica 153:61–66.

Bowen, W. D., J. W. Lawson, and B. Beck. 1993. Seasonal and geographic variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on the Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences 50:1768–1778.

Brodie, P. F. 1975. Cetacean energetics, an overview of intraspecific size variation. Ecology 56:152–161.

Bundy, A., J. J. Heymans, L. Morissette, and C. Savenkoff. 2009. Seals, cod and forage fish: A comparative exploration of variations in the theme of stock collapse and ecosystem change in four Northwest Atlantic ecosystems. Progress in Oceanography 81:188–206.

Bushuev, S. G. 1986. Feeding of minke whales, *Balaenoptera acutorostrata*, in the Antarctic. Report of the International Whaling Commission 36:241–245.

Butler, J. R. A., S. J. Middlemas, I. M. Graham, P. M. Thompson, and J. D. Armstrong. 2006. Modelling the impacts of removing seal predation from Atlantic salmon, *Salmo salar*, rivers in Scotland: A tool for targeting conflict resolution. Fisheries Management and Ecology 13:285–291.

Butler, J. R. A., et al. 2008. The Moray Firth Seal Management Plan: an adaptive framework for balancing the conservation of seals, salmon, fisheries and wildlife tourism in the UK. Aquatic Conservation: Marine and Freshwater Ecosystems 18:1025–1038.

Butterworth, D. S., A. E. Punt, W. H. Oosthuizen, and P. A. Wickens. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 3. Modelling the dynamics of the Cape fur seal *Arctocephalus pusillus*. South African Journal of Marine Science 16:161–183.

Corkeron, P. 2009. Reconsidering the science of scientific whaling. Marine Ecology Progress Series 375:305–309.

Craddock, J. E., and P. T. Polloni. 2009. Food habits of small marine mammals from the Gulf of Maine and from slope waters off the Northeast US coast. Year 3, Final Interim Report. Northeast Fisheries Science Center, National Oceanic and Atmospheric Administration, Woods Hole, Massachusetts, USA.

DeMaster, D. P., C. W. Fowler, S. L. Perry, and M. F. Richlen. 2001. Predation and competition: the impact of fisheries on marine-mammal populations over the next one hundred years. Journal of Mammalogy 82:641–651.

Fogarty, M. J., and S. A. Murawski. 1998. Large-scale disturbance and the structure of marine system: Fishery impacts on Georges Bank. Ecological Applications 8:S6–S22.

Folkow, L. P., L. Haug. K. T. Nilssen, and E. S. Nordoy. 2000. Estimated food consumption of minke whales *Balaenoptera acutorostrata* in Northeast Atlantic waters in 1992–1995. North Atlantic Marine Mammal Commission Scientific Publications 2:65–80.

Fontaine, P.-M., M. O. Hammill, C. Barrette, and M. C. Kingsley. 1994. Summer diet of the harbour porpoise (*Phocoena phocoena*) in the Estuary and the Northern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences 51:172–178.

Forcada, J., D. Malone, J. A. Royle, and I. J. Staniland. 2009. Modelling predation by transient leopard seals for an ecosystem-based management of Southern Ocean fisheries. Ecological Modelling 220:1513–1521.

Gannon, D. P., J. E. Craddock, and A. J. Read. 1998. Autumn food habits of harbor porpoises, *Phocoena*, in the Gulf of Maine. Fishery Bulletin 96:428–437.

Gaskin, D. E. 1982. Metabolic rate and energy budget in cetaceans. The ecology of whales and dolphins. Heinemann, Exeter, New Hampshire, USA.

Gerber, L. R., L. Morissette, K. Kaschner, and D. Pauly. 2009. Should whales be culled to increase fishery yield? Science 323:880–881.

Gonzalez, A. F., A. Lopez, A. Guerra, and A. Barreiro. 1994. Diets of marine mammals stranded on the northwestern Spanish Atlantic coast with special reference to Cephalopoda. Fisheries Research 21:179–191.

Hain, J. H., M. J. Ratnaswamy, R. D. Kenney, and H. E. Winn. 1992. The fin whale, *Balaenoptera physalus*, in waters of the Northeastern United States Continental Shelf. Report of the International Whaling Commission 42:653–699.

Hammill, M. O., M. S. Ryg, and B. Mohn. 1995. Consumption of cod by the Northwest Atlantic grey seal in Eastern Canada. Pages 337–348 in A. S. Bliz, L. Walloe, and O. Ultang, editors. Whales, seals, fish and man. Elsevier Science B.V., New York, New York, USA.

Hammill, M. O., and G. B. Stenson. 2000. Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbor seals (*Phoca vitulina*) in Atlantic Canada. Journal of Northwest Atlantic Fishery Science 26:1–23.

Haug, T., U. Lindstrom, and K. T. Nilssen. 2002. Variations in minke whale (*Balaenoptera acutorostrata*) diet and body condition in response to ecosystem changes in the Barents Sea. Sarsia 87:409–422.

Hinga, K. R. 1979. The food requirements of whales in the southern hemisphere. Deep Sea Research 26:569–577.

Hlista, B., H. Sosik, T. L. Martin, R. Kenney, and M. Moore. 2009. Seasonal and interannual correlations between right-whale distribution and calving success and chlorophyll concentrations in the Gulf of Maine, USA. Marine Ecology Progress Series 394:289–302.

Innes, S., D. M. Lavigne, W. M. Earle, and K. M. Kovacs. 1987a. Estimating feeding rates of marine mammals from heart mass to body ratios. Marine Mammal Science 2:227–229.

Innes, S., D. M. Lavigne, W. M. Earle, and K. M. Kovacs. 1987b. Feeding rates of seals and whales. Journal of Animal Ecology 56:115–130.

Kaschner, K. 2004. Modeling and mapping resource overlap between marine mammals and fisheries on a global scale. Dissertation. Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, Vancouver, British Columbia, Canada.

Kenney, R. D., M. A. M. Hyman, and H. E. Winn. 1985. Calculation of standing stocks and energetic requirements of the cetaceans of the Northeast United States outer Continental Shelf. NOAA Technical Memorandum NMFS-F/NEC-41. National Oceanic and Atmospheric Administration, Washington, D.C., USA.

Kenney, R. D., G. P. Scott, T. J. Thompson, and H. E. Winn. 1997. Estimates of prey consumption and trophic impacts of cetaceans in the USA Northeast Continental Shelf Ecosystem. Journal of Northwest Atlantic Fishery Science 22:155–171.

Klanjscek, T., R. M. Nisbet, H. Caswell, and M. G. Neubert. 2007. A model for energetics and bioaccumulation in marine mammals with applications to the right whale. Ecological Applications 17:2233–2250.

Kleiber, M. 1975. The fire of life: An introduction to animal energetics. R. E. Kreiger, Huntington, New York, USA.

Klumov, S. K. 1963. Food and helminth fauna of whalebone whales (*Mystacoceti*) in the main whaling regions of the world ocean. Trudy Instituta Okeanologii 71:94–194.

Laerm, J., F. Wenzel, J. E. Craddock, D. Weinand, J. McGurk, M. J. Harris, G. A. Early, J. G. Mead, C. W. Potter, and N. B. Barros. 1997. New prey species for Northwestern Atlantic humpback whales. Marine Mammal Science 13:705–711.

Lavigne, D. M. 1996. Ecological interactions between marine mammals, commercial fisheries, and their prey: Unraveling the tangled web. Pages 59–71 *in* W. A. Montevecchi, editor. Studies of high latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems. Canadian Wildlife Service Minister of Supply and Services Canada, Ottawa, Canada.

Leaper, R., and D. Lavigne. 2007. How much do large whales eat? Journal of Cetacean Research and Management 9:179–188.

Lindstrom, U., S. Smout, D. Howell, and B. Bogstad. 2009. Modelling multi-species interactions in the Barents Sea ecosystem with special emphasis on minke whales and their interactions with cod, herring and capelin. Deep Sea Research II 56:2068–1079.

Link, J. S. 2010. Ecosystem-based fisheries management: confronting tradeoffs. Cambridge University Press, New York, New York, USA.

Link, J. S., C. A. Griswold, E. T. Methratta, and J. Gunnard, editors. 2006. Documentation for the Energy Modeling and Analysis eXercise (EMAX). U.S. Department of Commerce, Northeast Fisheries Science Center Reference Document 06-15.

Lockyer, C. 1981. Growth and energy budgets of large baleen whales from the Southern hemisphere. Volume 3:379–487 *in* J. G. Gordon, J. Goodman, and G. A. Soave, editors. Mammals in the seas. FAO Fisheries Series 5, Food and Agriculture Organization of the United Nations, Rome, Italy.

Lundström, K., O. Hjerne, S.-G. Lunneryd, and O. Karlsson. 2010. Understanding the diet composition of marine mammals: Grey seals (*Halichoerus grympus*) in the Baltic Sea. ICES Journal of Marine Science 67:1230–1239.

Markussen, N. H., M. Ryg, and C. Lydersen. 1992. Food consumption of the NE Atlantic minke whale (*Balaenoptera acutorostrata*) population estimated with a simulation model. ICES Journal of Marine Science 49:317–323.

Mohn, R., and W. D. Bowen. 1996. Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod. Canadian Journal of Fisheries and Aquatic Sciences 53:2722–2738.

Morissette, J., K. Kaschner, and L. R. Gerber. 2010. 'Whales eat fish'? Demystifying the myth in the Caribbean marine ecosystem. Fish and Fisheries 11:388–404.

Morissette, L., M. Castonguay, C. Savenkoff, D. P. Swain, D. Chabot, H. Bourdages, M. O. Hammill, and J. M. Hanson. 2009. Contrasting changes between the northern and southern Gulf of St. Lawrence ecosystems associated with the collapse of groundfish stocks. Deep Sea Research II 56:2117–2131.

Morissette, L., V. Christensen, and D. Pauly. 2012. Marine mammal impacts in exploited ecosystems: would large scale culling benefit fisheries? Plos One 7:e43966.

Morissette, L., M. O. Hammill, and C. Savenkoff. 2006. The trophic role of marine mammals in the northern Gulf of St. Lawrence. Marine Mammal Science 22:74–103.

Murie, D. J. 1987. Experimental approaches to stomach content analyses of piscivorous marine mammals. Pages 147–163 *in* A. C. Huntly, D. P. Costa, G. A. J. Worthy, and M. A. Catellini, editors. Approaches to marine mammal energetics. Society for Marine Mammalogy Special Publication No. 1. Blackwell, Lawrence, Kansas, USA.

NEFSC. 2006. 42nd Northeast Regional Stock Assessment Workshop (42nd SAW) stock assessment report, Part A: Silver hake, Atlantic mackerel, and northern shortfin squid. U.S. Department of Commerce, Northeast Fisheries Science Center Reference Document 06-09a, Woods Hole, Massachusetts, USA.

NEFSC. 2008a. 47th Northeast Regional Stock Assessment Workshop (47th SAW) assessment report. U.S. Department

of Commerce, Northeast Fisheries Science Center Reference Document 08-12a, Woods Hole, Massachusetts, USA.

NEFSC. 2008b. Assessment of 19 Northeast Groundfish Stocks through 2007: Report of the 3rd Groundfish Assessment Review Meeting (GARM III). Northeast Fisheries Science Center, Woods Hole, Massachusetts, 4–8 August 2008. U.S. Department of Commerce, Northeast Fisheries Science Center Reference Document 08-15, Woods Hole, Massachusetts, USA.

NEFSC. 2010. 50th Northeast Regional Stock Assessment Workshop (50th SAW) assessment report. U.S. Department of Commerce, Northeast Fisheries Science Center Reference Document 10-17, Woods Hole, Massachusetts, USA.

NEFSC. 2011. 51st Northeast Regional Stock Assessment Workshop (51st SAW) assessment report. U.S. Department of Commerce, Northeast Fisheries Science Center Reference Document 11-02, Woods Hole, Massachusetts, USA.

NEFSC. 2012. 54th Northeast Regional Stock Assessment Workshop (54th SAW) Assessment Summary Report. U.S. Department of Commerce, Northeast Fisheries Science Center Reference Document 12-14, Woods Hole, Massachusetts, USA.

Overholtz, W. J. 2006. Estimates of consumption of Atlantic herring (*Clupea harengus*) by bluefin tuna (*Thunnus thynnus*) during 1970–2002: An approach incorporating uncertainty. Journal of Northwest Atlantic Fishery Science 36:55–63.

Overholtz, W. J., and J. S. Link. 2007. Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine–Georges Bank Atlantic herring (*Clupea harengus*) complex during the years 1977–2002. ICES Journal of Marine Science 64:83–96.

Overholtz, W. J., and G. T. Waring. 1991. Diet composition of pilot whales *Globicephala* sp. and common dolphins *Delphinus delphis* in the Mid-Atlantic Bight during spring 1989. Fishery Bulletin 89:723–728.

Palisade. 2011. @RISK Professional for Excel. Version 5.7. Palisade, Ithaca, New York, USA.

Payne, P. M., and L. A. Selzer. 1989. The distribution, abundance and selected prey of the harbor seal, *Phoca viulina concolor*, in Southern New England. Marine Mammal Science 5:173–192.

Punt, A. E., and D. S. Butterworth. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals *Arctocephalus pusillus* and the Cape hakes *Merluccius capensis* and *M. paradoxus*. South African Journal of Marine Science 16:255–285.

Read, A. J., and C. R. Brownstein. 2003. Considering other consumers: Fisheries, predators, and Atlantic herring in the Gulf of Maine. Conservation Ecology 7(7):2.

Savenkoff, C., L. Morissette, M. Castonguay, D. P. Swain, M. O. Hammill, D. Chabot, and J. M. Hanson. 2008. Interactions between marine mammals and fisheries: Implications for cod recovery. Pages 107–151 *in* J. Chen and C. Guo, editors. Ecosystem ecology research trends. Nova Science Publishers, Hauppauge, New York, USA.

Savenkoff, C., D. P. Swain, J. M. Hanson, M. Castonguay, M. O. Hammill, H. Bourdages, L. Morissette, and D. Chabot. 2007. Effects of fishing and predation in a heavily exploited ecosystem: Comparing periods before and after the collapse of groundfish in the southern Gulf of St. Lawrence (Canada). Ecological Modelling 204:115–128.

Shelton, P. A., W. G. Warren, G. B. Stenson, and J. W. Lawson. 1997. Quantifying some of the major sources of uncertainty associated with estimates of harp seal prey consumption. Part II: Uncertainty in consumption estimates associated with population size, residency, energy requirement and diet. Journal of Northwest Atlantic Fishery Science 22:303–315.

Sigurjónsson, J., and G. A. Víkingsson. 1997. Seasonal abundance of and estimated food consumption by cetaceans in Icelandic and adjacent waters. Journal of Northwest Atlantic Fishery Science 22:271–287.

Smith, A. D. M., et al. 2011. Impacts of fishing low–trophic level species on marine ecosystems. Science 333:1147–1150.

Smith, B. E., and J. S. Link. 2010. The trophic dynamics of 50 finfish and 2 squid species on the Northeast US Continental Shelf. NOAA Technical Memorandum NMFS NE 216:640. National Marine Fisheries Service, Woods Hole, Massachusetts, USA. http://www.nefsc.noaa.gov/nefsc/publications/

Smith, G. J. D., and D. E. Gaskin. 1974. The diet of harbor porpoises (*Phocoena* (L.)) in coastal waters of eastern Canada, with special reference to the Bay of Fundy. Canadian Journal of Zoology 52:777–782.

Spitz, J., E. Mourocq, J.-P. Leauté, J.-C. Quéro, and V. Ridoux. 2010. Prey selection by the common dolphin: Fulfilling high energy requirements with high quality food. Journal of Experimental Marine Biology and Ecology 390:73–77.

Springer, A. M., J. A. Estes, G. B. van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, K. A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? Proceedings of the National Academy of Sciences USA 100:12223–12228.

Stefánsson, G., J. Sigurjónsson, and G. A. Víkingsson. 1997. On dynamic interactions between some fish resources and cetaceans off Iceland based on a simulation model. Journal of Northwest Atlantic Fishery Science 22:357–370.

Stevick, P. T., L. S. Incze, S. D. Kraus, S. Rosen, N. Wolff, and A. Baukus. 2008. Trophic relations and oceanography on and around a small offshore bank. Marine Ecology Progress Series 363:15–28.

Swain, D. P., and G. A. Chouinard. 2008. Predicted extirpation of the dominant demersal fish in a large marine ecosystem: Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences 65:2315–2319.

Tamura, T., K. Konishi, T. Isoda, R. Okamoto, T. Bando, and T. Hakamada. 2009. Some examinations of uncertainties in the prey consumption estimates of common minke, sei and Bryde's whales in the western North Pacific. International Whaling Commission Scientific Committee Paper SC/61/JR2.

Tamura, T., and S. Ohsumi. 2000. Regional assessments of prey consumption by marine cetaceans in the world. International Whaling Commission Scientific Committee Paper SC/52/E6.

Trites, A. W., V. Christensen, and D. Pauly. 1997. Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. Journal of Northwest Atlantic Fishery Science 22:173–187.

Trzcinski, M. K., R. Mohn, and W. D. Bowen. 2006. Continued decline of an Atlantic cod population: How important is gray seal predation? Ecological Applications 16:2276–2292.

Víkingsson, G. A. 1997. Feeding of fin whales (*Balaenoptera physalus*) off Iceland—diurnal and seasonal variation and possible rates. Journal of Northwest Atlantic Fishery Science 22:77–89.

Waring, G. T., E. Josephson, K. Maze-Foley, and P. E. Rosel, editors. 2011. U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments—2011. NOAA Technical Memorandum NMFS NE 221. National Marine Fisheries Service, Woods Hole, Massachusetts, USA. http://www.nefsc.noaa.gov/nefsc/publications/

Yodzis, P. 1998. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. Journal of Animal Ecology 67:635–658.

Yodzis, P. 2000. Diffuse effects in food webs. Ecology 81:261–266.

Yodzis, P. 2001. Must top predators be culled for the sake of fisheries? Trends in Ecology and Evolution 16:78–84.

## Supplemental Material

### Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/13-1656.1.sm