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

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A comprehensive study of the impact of predation during the years 1977–2002 on the Gulf of Maine–Georges Bank herring complex is presented. An uncertainty approach was used to model input variables such as predator stock size, daily ration, and diet composition. Statistical distributions were constructed on the basis of available data, producing informative and uninformative inputs for estimating herring consumption within an uncertainty framework. Consumption of herring by predators tracked herring abundance closely during the study period, as this important prey species recovered following an almost complete collapse during the late 1960s and 1970s. Annual consumption of Atlantic herring by four groups of predators, demersal fish, marine mammals, large pelagic fish, and seabirds, averaged just 58 000 t in the late 1970s, increased to 123 000 t between 1986 and 1989, 290 000 t between 1990 and 1994, and 310 000 t during the years 1998–2002. Demersal fish consumed the largest proportion of this total, followed by marine mammals, large pelagic fish, and seabirds. Sensitivity analyses suggest that future emphasis should be placed on collecting time-series of diet composition data for marine mammals, large pelagic fish, and seabirds, with additional monitoring focused on the abundance of seabirds and daily rations of all groups.

Keywords: Atlantic herring, consumption, ecosystem, predation, uncertainty framework.

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Introduction

The Gulf of Maine and Georges Bank regions off the northeastern USA (Figure 1) are among the more diverse, productive, and trophically complex marine temperate areas in the world (Link *et al.*, 2002; Sherman and Skjoldal, 2002). Piscivorous predators are abundant there (Read and Brownstein, 2003; Brodziak *et al.*, 2004), and include marine mammals such as humpback (*Megaptera novaeangliae*) and finback (*Balaenoptera physalus*) whales, harbour porpoise (*Phocoena phocoena)*, and harbour seals (*Phoca vitulina concolor*) (Waring *et al.*, 2002). Fish such as spiny dogfish (*Squalus acanthias*), Atlantic cod (*Gadus morhua*), bluefin tuna (*Thunnus thynnus*), and blue shark (*Prionace glauca*) are also important (Overholtz *et al.*, 2000; Schick *et al.*, 2004). A large number of marine birds, such as northern gannet (*Sula bassanus*), greater shearwater (*Puffinus gravis*), and herring gulls (*Larus argentatus*), frequent the areas (Powers and Backus, 1987). Many of these predators are resident species, but many are seasonal migrants making summer and autumn feeding forays to take advantage of the abundant prey resources.

Atlantic herring are a keystone prey species found in abundance in the Gulf of Maine–Georges Bank ecosystem, and they are common in the diets of many marine mammals, piscivorous fish, seabirds, and large pelagic fish of the region (Powers and Backus, 1987; Gannon *et al.*, 1997, 1998; Palka *et al.*, 1997; Ferland 1999; Overholtz *et al.*, 2000; Chase, 2002; Read and Brownstein, 2003). Herring biomass fluctuated greatly during the period 1977–2002 primarily because of chronic overfishing by the foreign distant water fleet in the 1970s followed by a recovery in the 1990s (Figure 2). The impact of some of these predators on herring in the region has been quantified. For example, demersal fish, marine mammals, and seabirds (Overholtz *et al.*, 1991), demersal fish (Overholtz *et al.*, 2000), and marine mammals (Read and Brownstein, 2003) have all been reviewed as predators, but the total impact of the four major groups of predators on herring has not been estimated simultaneously. Stock assessments of herring in the region currently do not explicitly take account of predation mortality, but assume that natural mortality (M) is constant over time (Overholtz *et al.*, 2004). As herring is such an important prey species, future stock assessments would do well to include species interactions or consumption by predators. To quantify this impact, total consumption by the four groups of predators will need to be estimated.

Diet composition data are available for many of the predators of the Gulf of Maine–Georges Bank herring, but these data usually cover only a few calendar years, e.g. seabirds during the period 1978–1982 (Powers and Backus, 1987), pilot whales from 1989 to 1991 (Gannon *et al.*, 1997), white-sided dolphins in 1976 and 1994 (Palka *et al.*, 1997), harbour porpoises during 1989 and 1991–1994 (Gannon *et al.*, 1998), harbour seals in 1998 and 1999 (Ferland, 1999), and bluefin tuna for the years 1988–1992

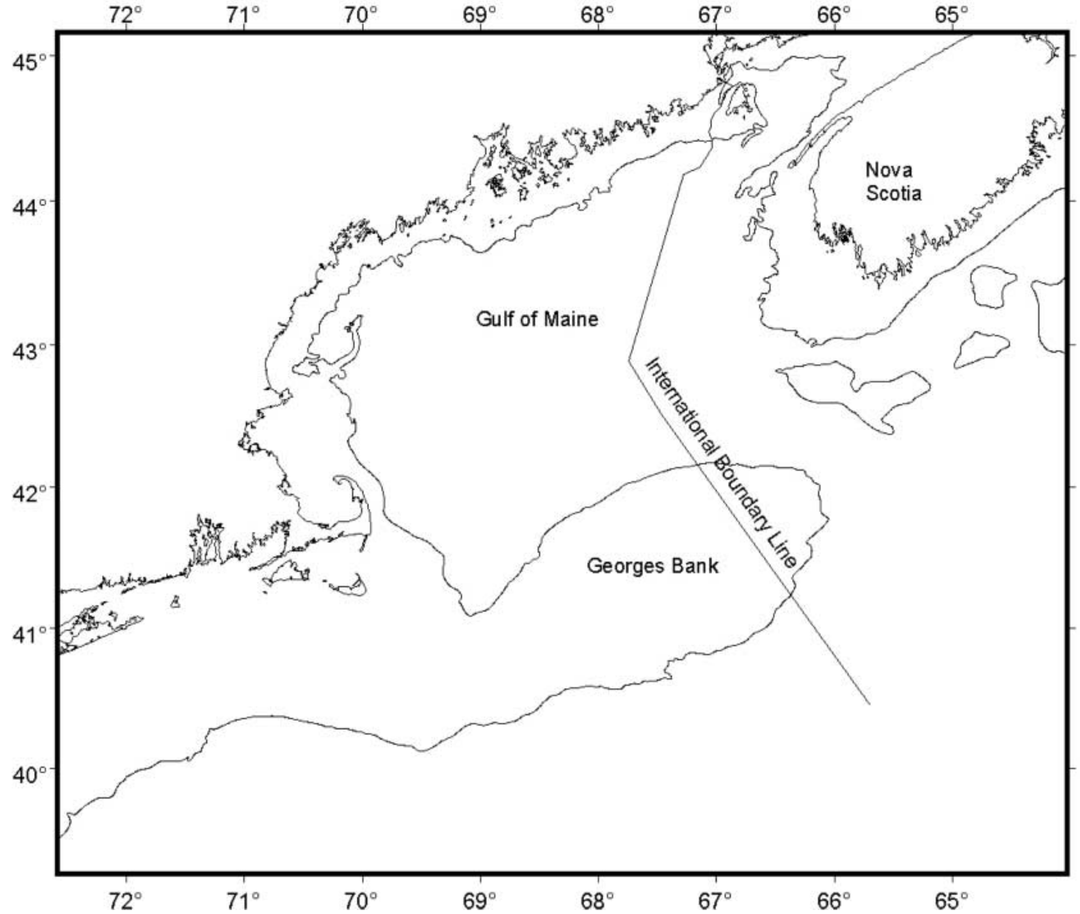

Figure 1. Location of the Gulf of Maine and Georges Bank off the eastern USA and Canada.

(Chase, 2002). For some predators, especially the larger whales, only local observational evidence and a few local empirical studies are available (Payne *et al.*, 1986; Hain *et al.*, 1995; Weinrich *et al.*, 1997). However, substantial information on cetacean food habits is available from similar ecosystems, e.g. on the Scotian Shelf (Mitchel, 1974), in the Southern Ocean, North Pacific, and North Atlantic (Kawamura, 1980), in the Barents Sea (Haug *et al.*, 1996, 2002), and in the Norwegian Sea (Tjelmeland and Lindstrom, 2005). For medium-sized pelagic and demersal predatory fish, long time-series of data exist that can be used to estimate consumption and diet composition (Link and Almeida, 2000).

The objective of this study was to estimate the consumption of Gulf of Maine–Georges Bank herring by major predator groups during the years 1977–2002. To accomplish this, an uncertainty framework was developed, and distributional and probability-based methods were used to address a range of data-poor to data-rich situations. Although the diet data for the four groups of predators that consume herring are quite different in quality and availability, all were amenable to analysis with probabilistic methods.

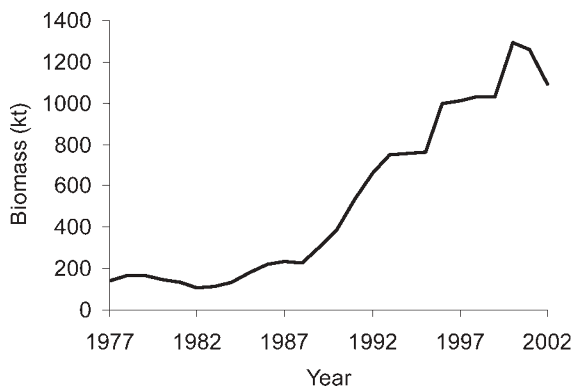

Figure 2. Herring biomass in the Gulf of Maine–Georges Bank region during the period 1977–2002.

Material and methods

Many herring predators in the Gulf of Maine–Georges Bank area are resident, e.g. silver hake (*Merluccius bilinearis*), and consume herring year-round, whereas others, such as bluefin tuna, are seasonal migrants that prey on herring for shorter periods of time. Estimating species-specific consumption requires a multi-level analysis of several important input variables, including predator biomass, residence time, daily consumption, and diet composition. Consumption can be estimated with several approaches, but for fish it is generally based on empirically derived average stomach content data and a gastric evacuation model (Olsen and Boggs, 1986). For seabirds and mammals, consumption is generally estimated using an energetics equation based on body mass (Powers and Backus, 1987; Read and Brownstein, 2003).

To model the consumption of herring by each predator during the years 1977–2002, input distributions (pert or uniform) were constructed using off-the-shelf software (@RISK; Palisade Corp., 2002) interfaced with a spreadsheet (Microsoft's EXCEL). Outputs from the model were the distribution of estimated annual consumption, a time-series of consumption point estimates, and a sensitivity analysis for the most important contributing factors in the consumption estimates. Consumption in any year was generally a linear combination of four components:

$$C(t) = \sum_{i=1}^{\text{predators}} f_i(t) * N_i(t) * c_i(t) * p_i(t), \quad (1)$$

where $C(t)$ is the annual consumption of herring, $f_i(t)$ is the fraction of the predator i stock in the Gulf of Maine–Georges Bank region, $N_i(t)$ is the abundance of predator i, $c_i(t)$ is the total annual consumption by an individual predator i, and $p_i(t)$ is the proportion of herring in the diet. Specific details for each predator group are provided subsequently. A Monte Carlo approach was used to resample the input distributions, and 5000 iterations were completed for each predator in each year. Simple percentile confidence limits (80%) were used as a measure of precision around the estimated annual consumption distributions. The consumption for a predator in any year is a distribution of 5000 values because of the Monte Carlo approach used. A simple 80% CI shows where 80% of the values are located in the output distribution between the 10 and 90% region (an example is shown later in Figure 9), and the 1977–2002 estimated average consumption trajectories.

Demersal fish

Seasonal diet data collected on Northeast Fisheries Science Center (NEFSC) bottom trawl surveys between 1977 and 2002 were examined to identify the demersal fish preying mostly on herring on the Georges Bank and in the Gulf of Maine region. In all, 12 species were identified as important predators of herring: spiny dogfish (*S. acanthias*), silver hake, Atlantic cod (*G. morhua*), pollock (*Pollachius virens*), white hake (*U. tenuis*), red hake (*U. chuss*), summer flounder (*Paralichthys dentatus*), bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), winter skate (*Leucoraja ocellata*), thorny skate (*Amblyraja radiata*), and sea raven (*Hemitripterus americanus*). We used all available seasonal stomach content data in a given year, but if seasonal data were not available for winter and summer, we substituted within-year spring data for winter and autumn data for summer, following the same conventions developed in past studies (Cohen *et al.*, 1982; Overholtz *et al.*, 2000; Link *et al.*, 2002). The same minimum predator size groupings (generally >20 to ≤40 cm) as in the work of Overholtz *et al.* (2000) were used, because of ontogenetic diet shifts.

Predator abundance during the years 1977–2002 was derived from virtual population analysis (VPA) stock size estimates (Gulf of Maine cod, Georges Bank cod), stock assessment results (spiny dogfish), and autumn groundfish survey analyses (Azarovitz, 1981; NEFSC, 2002a, 2003). Age (2+) abundance was used as initial population stock size for the Georges Bank and Gulf of Maine cod stocks. For spiny dogfish, loess smoothed biomass was converted to numbers with mean weight data, for size groups 39–79 cm and 80+cm. These are the sizes of dogfish that consume fish, particularly herring. Stock abundance for the other predatory fish was obtained by converting smoothed autumn survey biomass (kg tow^{-1}) to total biomass using weighting factors from Clark and Brown (1977), or in the case of goosefish, sea raven, thorny skates, and winter skate, weighting factors from gear efficiency experiments (NEFSC, 2002b). Biomass estimates were converted to total number by applying calculated values of mean weight. This procedure was used because survey abundance estimates (number per tow) were highly variable, had large year effects, and are subject to recruitment events, whereas survey biomass estimates are more stable over time. The estimates of abundance were offset 1 y forward to serve as start-year values for estimates of consumption. As many of the predators were heavily exploited during the years 1977–2002, often resulting in large declines in quarterly abundance in a given year, quarterly estimates of total mortality (Z) were applied to the start-beginning year stock size to estimate abundance by quarter.

Quarterly consumption was estimated from a relationship based on average stomach content data and gastric evacuation rate (Eggers, 1977; Elliott and Persson, 1978; Pennington, 1985):

$$C = 24RS^{\gamma}, \quad (2)$$

where C is daily consumption (in g), S the mean stomach content (g), γ is assumed equal to 1, 24 is the number of hours in a day, and R is the evacuation rate per hour, i.e.

$$R = \alpha e^{\beta T}, \quad (3)$$

where α and β are fitted constants, and T is the quarterly mid-point bottom temperature (°C) (Figure 3). α and β values in Equation (3) were assumed to be 0.004 and 0.115, respectively (Durbin *et al.*, 1983; Overholtz *et al.*, 2000). Daily consumption estimates were resolved to a quarterly resolution by expansion (91.25 d).

Bottom water temperatures were available from NEFSC research trawl surveys conducted during the study years (Holzworth and Mountain, 1992). An average annual model of bottom water temperature during the period 1977–2002 was constructed for the area between the northern Mid-Atlantic and the Gulf of Maine, and annual anomalies from this model were calculated. Temperatures in this average model fluctuated over a range from 5 to 10°C on an annual basis. The model is a Fourier

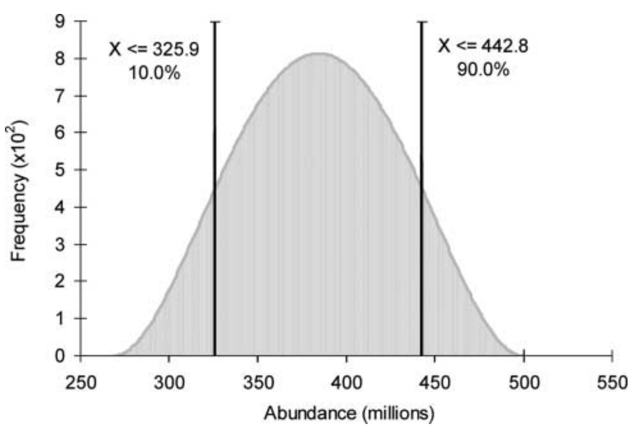

Figure 3. Distribution of spiny dogfish abundance (millions), with 80% CI.

decomposition fitted to annual and semi-annual cycles, and is explained in detail in Mountain and Holzworth (1973). For each calendar year, annual anomalies were added to this average curve, producing estimated temperatures for each Julian date in a given year. The temperature midpoints of each quarter and year were then available for use in the gastric evacuation model, a temperature-dependent process.

For each of the 12 demersal fish predators of herring, distributions of each of three variables (abundance, consumption, and % herring in the diet) were developed for each year from 1977 to 2002. Predator abundance was assumed to be uncertain, so a pert distribution (modified beta distribution; Palisade Corp., 2002) was constructed with a 30% CV on abundance (see Figure 3 as an example for spiny dogfish). This distribution was chosen because it is simple, is easy to make symmetrical, can be fitted easily, and has insignificant tails. Distributions such as the normal or log-normal require more knowledge about the shape, tails, and the underlying assumptions.

The density function for the pert distribution can be written as

$$f(x) = \frac{(x - \min)^{\alpha 1 - 1}(\max - x)^{\alpha 2 - 1}}{B(\alpha 1,\ \alpha 2)(\max - \min)^{\alpha 1 + \alpha 2 - 1}}, \tag{4}$$

where the distribution is based on inputs, pert (min, m.likely, max), B is the beta function, and

$$\mu = \frac{\min + 4 * \text{m.likely} + \max}{6},\ \text{and}\ \alpha 1 = 6\left[\frac{\mu - \min}{\max - \min}\right]$$
$$\text{and}\ \alpha 2 = 6\left[\frac{\max - \mu}{\max - \min}\right]. \tag{5}$$

The distribution for each year was centred on the estimate of annual biomass (m.likely), and a minimum (min) and maximum (max) value were determined such that the minimum value was 1 standard deviation (s.d.) less than the mean, and the maximum was 1 s.d. greater than the mean, with the s.d. calculated as $0.3 \times$ mean (30% CV).

The annual distribution was centred on the predator abundance estimate, and minimum and maximum values (both 1 s.d. from the point estimate) were calculated for each year. CVs on the demersal fish survey abundance data ranged from 15 to 30%, so a value of 30% was used to parameterize the pert distribution for all 12 predators. The same approach was used in preparing distributions for quarterly consumption where empirical CVs ranged from 30 to 50%, so a CV of 0.5 was used; the percentage herring in the predator diet averaged about a 30% CV, so a CV of 0.3 was used. Therefore, CVs for each of the input variables for the demersal fish were based on rough averages or the highest value from the empirical data.

Marine mammals

Available literature on the stomach contents of marine mammals in the Gulf of Maine–Georges Bank region as well as observational evidence was used to determine a list of important herring predators (Gannon *et al.*, 1998; Read and Brownstein, 2003). Eight species were considered important, including fin whales, humpback whales, minke whales (*B. acutorostrata*), pilot whales (*Globicephala* sp.), harbour porpoise, Atlantic white-sided dolphins (*Lagenorhynchus acutus*), harbour seals, and grey seals (*Halichoerus grypus*). Stock size, daily ration (percentage body weight, %BW), and percentage of herring in diets were used in deriving marine mammal consumption estimates of herring. For fin whales, stock size estimates were modified to account for the percentage of the western North Atlantic stock in the region. For harbour porpoise and Atlantic white-sided dolphin, the percentage of the total stock in the area was also considered in the analyses.

Mammal stock-size estimates were available from shipboard and aircraft surveys conducted during the 1990s (Waring *et al.*, 2002). For most species, only a single stock-size estimate was available from a survey, but rates of population increase were provided in the stock assessments (Waring *et al.*, 2002). For each of the eight marine mammal stocks, a time-series of population abundance estimates was produced by calculating a survival rate [$\ln(1 + r)$, where r is the rate of increase] from the rate of population increase for that stock, and using the negative of this value to decrement the recent survey stock size estimate back through time to 1977. A positive rate of increase was applied to produce stock-size estimates in years following the survey estimate up to 2002. Distributions were constructed for each year from 1977 to 2002 by assuming a pert distribution and using the s.d. supplied in each stock assessment (Waring *et al.*, 2002). The distribution was centred on the point estimate for each year, and a minimum and maximum value were calculated with the available s.d. in the same manner as for demersal fish. Therefore, a CV on mammal abundance was calculated from the available empirical data provided in each stock assessment.

Estimates of daily ration of marine mammals were available from Read and Brownstein (2003), based on a cetacean energetics equation (Innes *et al.*, 1987) relating consumption to body mass:

$$C = \omega M^{\tau}, \tag{6}$$

where C is daily consumption (kg d^{-1}), M is mammal body mass (kg), and ω and τ are parameters, 0.123 and 0.80, respectively (Innes *et al.*, 1987). A pert distribution was used to describe the proportional daily ration of mammals using the available estimates for each species. A CV of 30% was assumed for this variable, on the basis of the empirical information for demersal fish (see previous section).

Diet composition data were used to estimate the proportion of herring in the diets of each mammal, but local data were not available for the large whales. However, there are short-term studies on harbour seals, harbour porpoise, pilot whales, and Atlantic white-sided dolphins (Selzer *et al.*, 1986; Payne and Selzer, 1989; Overholtz and Waring, 1991; Gannon *et al.*, 1997, 1998; Palka *et al.*, 1997; Ferland, 1999; Williams, 1999). There are also many years of observations of feeding behaviour and associated prey for the larger whales (Brown *et al.*, 1979; Overholtz and Nicolas, 1979; Payne *et al.*, 1986; Hain *et al.*, 1995). Therefore, marine mammal diet data from other North Atlantic regions were used in combination with local observations to estimate the proportion of herring in the diet. Studies on fin whales, humpback whales, minke whales, and harbour porpoise suggest that they are euryphagous, with one or two preferred prey species plus several other items in their diets (Kawamura, 1980; Gannon *et al.*, 1998). Local observational evidence suggests that these cetaceans now prey heavily on Atlantic herring, but during the 1970s and 1980s consumed other species, principally sandlance (*Ammodytes americanus*; Overholtz and Nicolas, 1979; Payne *et al.*, 1986; Payne and Selzer, 1989). Similarly, the primary prey in the diet of demersal fish in the region switched from sandlance in the late 1970s through the mid-1980s, to herring in the 1990s and subsequently (Overholtz *et al.*, 2000; Link and Garrison, 2002).

The approach used to determine mammal diet proportions therefore depended on knowledge and data from other ecosystems, local and regional empirical information, and inferences from empirical data for predatory fish in the region (Sergeant, 1963; Kawamura, 1980; Payne *et al.*, 1986; Hain *et al.*, 1995; Palka *et al.*, 1997; Weinrich *et al.*, 1997; Overholtz *et al.*, 2000). The approach also assumed that encounter rates by predators are directly related to prey abundance. Therefore, the encounter rate for predators on herring during the early 1980s would have been low, whereas recently it has been much higher. Recent diet percentages for herring would likely not exceed 40–70% in the Gulf of Maine and Georges Bank region, because many alternative prey such as Atlantic mackerel (*Scomber scombrus*), sandlance, Atlantic saury (*Scomberesox saurus saurus*), butterfish (*Peprilus triacanthus*), and krill (*Meganyctiphanes norvegica*) are abundant (Brown *et al.*, 1979; Overholtz *et al.*, 2000; Collette and MacPhee, 2002; Link *et al.*, 2002).

It was assumed that mammals had smaller percentages of herring in their diets during the late 1970s and early 1980s when herring abundance was low, and much higher percentages thereafter. These low and high values were used to anchor the lower and upper regions of a diet proportion curve for each species during the whole period 1977–2002. Several interim data points were chosen by inspection to transition the curve between the low and high values. A spline smoother was used to fit a curve between the points (SPLUS, 2001; Figure 4). It provides for a simple transition between low and high herring abundance without making any elaborate assumptions. Spline smoothers utilize a polynomial method to fit a piecewise curve through a set of points. In this case, a fifth order polynomial was used because it allowed for flattening of the curve in the low and high regions of herring abundance.

Overall, this method assumes that large predators have difficulty locating prey that is not abundant, easily find prey when that prey is abundant, and smoothly transition between the two extremes. A uniform distribution was used to describe the diet compositions of marine mammals, because their dietary estimates were the most uncertain of the various inputs used to model their consumption. The spline-smoothed trajectories (1977–2002) for each species were used to centre uniform distributions with a range in CV of $\pm$50%. The uniform distributional approach and higher CV were chosen to reflect a much greater level of uncertainty than used for the distributions of fish diet composition. This provided for a very wide range in herring in the mammal diets, e.g. in 2002, the proportion of herring in the diet of finback was allowed to range from 0.25 to 0.76.

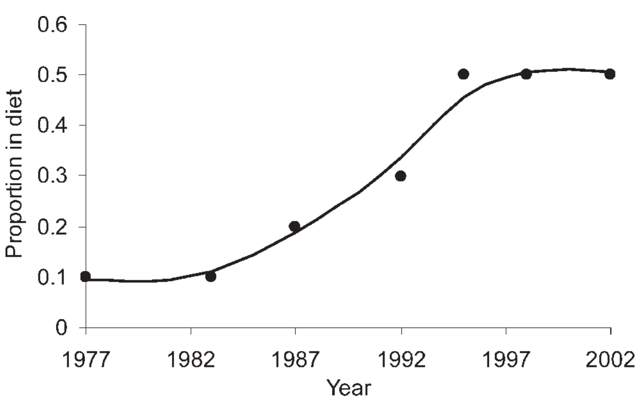

Figure 4. Spline smooth of proportion of herring in finback whale diets, 1977–2002.

Unlike most of the marine mammals in the region, harbour seals are extremely euryphagous and consume a variety of fish (Ferland, 1999; Williams, 1999). Atlantic herring constitute only a small proportion of their diet, with the winter/spring percentage lower than that of summer and autumn (Payne and Selzer, 1989; Ferland, 1999; Williams, 1999). A spline-smoother approach was also used for harbour seals, but the percentages only ranged from 4 to 7% during Quarters 1 and 2, and between 7 and 13% during Quarters 3 and 4.

Herring account for only a small fraction of the diet of pilot whales, mainly because the two species scarcely overlap. Diet studies suggest that prey such as squid (*Loligo pealii*) and mackerel are more important to pilot whales than herring (Waring *et al.*, 1990; Overholtz and Waring, 1991; Gannon *et al.*, 1997). The range of pilot whales in the region is also mostly on the fringe of the distribution of herring (Waring *et al.*, 2002). The proportion of herring in pilot whale diets was assumed to be low (~5%) during the years 1970–1987, increasing thereafter to about 20% in the late 1990s because of the increases in herring biomass.

Abundance surveys for marine mammals in the Gulf of Maine were designed to estimate the population size of each species in the region (Waring *et al.*, 2002). However, harbour porpoise, Atlantic white-sided dolphins, and minke whales are present in significant proportions of their populations on the eastern side of the Bay of Fundy, or on the Scotian Shelf, or in offshore areas on the outer shelf/slope break of Georges Bank (Waring *et al.*, 2002). As these population components do not overlap with the Gulf of Maine–Georges Bank herring complex, they were excluded from the analysis. Pert distributions for the proportion of these stocks in the area were parameterized using CVs ranging from 15 to 30%, depending on species. These CVs were chosen on the basis of the seasonal distributions of each species.

Large pelagic fish

Bluefin tuna, shortfin mako shark (*Isurus oxyrinchus*), and blue shark are the primary large pelagic predators of herring in the region (Kohler and Stillwell, 1981; Stillwell and Kohler, 1982; Chase, 2002; ICCAT, 2003). A slightly different approach was developed for this group of herring predators, because daily ration data were available as percentage body weight (%BW) consumed per day (Chase, 2002); therefore, biomass instead of numbers was used as an input variable. Input variables that were modelled for the three large pelagic predatory species were therefore predator biomass, proportion of the population in the region, daily ration (%BW), and proportion of herring in the diet.

Bluefin tuna biomass (age 3+) was obtained from a VPA for this species run in 2003 (ICCAT, 2003). Only age 3+ tuna were considered because younger fish are frequently found outside the region during the summer feeding season, and generally they do not prey on herring (Mason, 1976; Holliday, 1978; Chase, 2002). As stock abundance information is not available for either blue or mako shark, we developed a ratio method using Japanese longline ICCAT data (1978–1988, 5640 sets) for the US EEZ (Hoey *et al.*, 2002). For blue shark, we used the ratio between blue shark and bluefin tuna catch per set data from Hoey *et al.* (2002) to produce an expansion factor (1.5) to scale blue shark numbers during the years 1977–2002 to bluefin tuna numbers (ICCAT, 2003) during the same period. Next, a weighted average drawn mean weight

(24.59 kg) was calculated from MRFSS recreational mean weight data (24.59 kg) and multiplied by a factor of 1.96 to convert to wet weight (48.19 kg; Cortes, 2002). Biomass estimates for the period 1977–2002 were then obtained by multiplying estimated blue shark numbers by 48.59 kg fish^{-1}. For shortfin mako shark, we used the ratio between mako shark and bluefin tuna from Hoey *et al.* (2002) to produce a raising factor (0.0476) to scale mako numbers during the years 1996–2000 to bluefin tuna numbers for the same period. Again, a weighted average drawn mean weight (22.36 kg) was calculated from recreational mean weight data (22.36 kg), and multiplied by 1.96 to convert to wet weight (43.83 kg; Cortes, 2002). Biomass estimates were then derived in the same manner as for blue shark. Lacking any empirical information on the precision of abundance estimates for these three species, biomass estimates for the three large pelagic species were modelled using pert distributions and an assumed CV of 30%.

The residence period of large pelagic fish in the Gulf of Maine varies among species, with bluefin tuna present from July to October, blue shark from May to October, and mako shark from June to October. We assumed that about 50% of the bluefin tuna and 25% of the blue shark and shortfin mako shark biomass was resident during these times (Stillwell and Kohler, 1982; Kohler, 1987; Chase, 2002). A pert distribution was used to model the stock proportions for each species in the region, using an assumed 30% CV, because less is known about the seasonal distribution of these species in the region than for marine mammals.

The estimated daily ration (%BW) for bluefin tuna (3.2% BW per day) was derived by averaging the published estimates that were available (Tiews, 1978; Young *et al.*, 1997; Chase, 2002; ICCAT, 2003) and calculating a standard deviation (s.d. 1.4%). Blue shark and shortfin mako shark estimates of daily ration (0.56 and 1.0 %, respectively, both with CVs of 50%) were taken from the literature (Stillwell and Kohler, 1982; Kohler, 1987).

A spline-smoothed diet proportion approach was used for bluefin tuna much the same as for the marine mammals. Chase (2002) reported that herring accounted for 50% of the diet of bluefin tuna during the years 1988–1992. This value was used to centre a uniform distribution during the period 1988–1992 with a CV of 50%. During earlier years (1977–1987), herring were of lesser importance in the diet of bluefin, and values of 15–20% were used (Holliday, 1978; Eggleston and Bochenek, 1990). From 1993 to 2002, it was assumed that 60% of the bluefin tuna diet was herring (range 30–90%). For blue shark and shortfin mako shark, diet percentages during the years 1977–2002 were assumed to range from 10 to 20% with a CV of 50%, and from 5 to 10% with a CV of 50%, respectively (Kohler and Stillwell, 1981; Stillwell and Kohler, 1982; Kohler, 1987; Overholtz *et al.*, 2004). Again, as in the case of mammals, a higher CV was used to reflect the level of uncertainty in the diet proportions.

Seabirds

Approximately 20 species of seabird are found in the Northeast Shelf ecosystem, and most are moderately abundant, especially over Georges Bank (Schneider and Heinemann, 1996). However, no large-scale surveys of seabird populations have been conducted in the area since 1988. The Gulf of Maine and Georges Bank region are generally thought of as seasonal feeding areas, with few species actually nesting locally. Eight seabird species are important predators of herring: northern fulmar (*Fulmarus glacialis*), black-legged kittiwake (*Rissa tridactyla*), northern gannet (*S. bassanus*), herring gull (*L. argentatus*), great black-backed gull (*L. marinus*), and shearwaters (greater shearwater *P. gravis*, sooty shearwater *P. griseus*, and Cory's shearwater *Calonectris diomedae*). As the three species of shearwater are similar in size and greater shearwaters are by far the most abundant species in the region, their abundance was combined into one aggregate group. Quarterly estimates of seabird numbers, daily ration, and the proportion of herring in seabird diets were the variables that were estimated with an uncertainty framework.

Schneider and Heinemann (1996) provide the mean and standard deviation in relative density for 18 species of seabird during the years 1978–1988 from annual surveys conducted by the Manomet Observatory. As seasonal abundance data are not available, the information in Powers (1983, Appendix 5) was used to derive quarterly abundance estimates for the seabird species. The Powers (1983) data were standardized to the highest quarterly value to obtain the seasonal scaler for the mean value provided in Schneider and Heinemann (1996). Then, standard and yearly deviations from the mean for each species were used to estimate the number of seabirds per square kilometre. This was then expanded to the total region to estimate the quarterly abundance of birds during the period 1978–1988 as:

$$N_{ij} = [D_{ij} * \mathrm{SD}_i + \mu_i] * \mathrm{SC}_{ij} * A,$$

where N_{ij} is the quarterly abundance, D_{ij} the annual deviation from the mean density μ_i, SD_i the standard deviation, SC_{ij} the quarterly scaler, A the total area for the northern Mid-Atlantic–Gulf of Maine region, i the species, and j is the quarter.

It was assumed that the seasonal distribution of seabirds had not changed over time. As no estimates of abundance exist since 1988, the average abundance during the years 1984–1988 (the five most recent years of the series) was used for the balance of the study period, 1989–2002. Anecdotal evidence suggests that seabird numbers have been stable (T. L. Evans, pers. comm.) recently.

Estimates of daily ration for each of the six seabird groups were obtained from Powers and Backus (1987). These were used in pert distributions with CVs of 30%. Diets of seabirds are generally euryphagous, with numerous items and low frequencies of occurrence. Most seabird prey is generally unavailable except on occasion at the surface, when seabirds associate with marine mammals that are foraging, or from fishery discards (Powers and Backus, 1987; Pierotti, 1988). Available data from 1981 and 1982 indicate that herring were scarce in the diets of seabirds in the region then (Powers and Backus, 1987). The diet data for the six species-groups were examined, and percentages were used to centre uniform distributions with a CV of 50%. During the period 1977–2002, the percentage of herring in seabird diets ranged from a low of 2–5% for great black-backed gulls to a high of 5–15% for northern gannets. A spline approach was used to estimate the proportion of herring in the seabird diets over time, with the lowest proportion applied during the late 1970s and early 1980s when herring were scarce, and higher proportions in the late 1990s when herring were more common.

Results

Results are presented for only one species in each group, then followed by the results for the predator group as a whole.

Demersal fish

Herring as a proportion of the diet composition of demersal fish changed markedly over the period 1977–2002. From the late

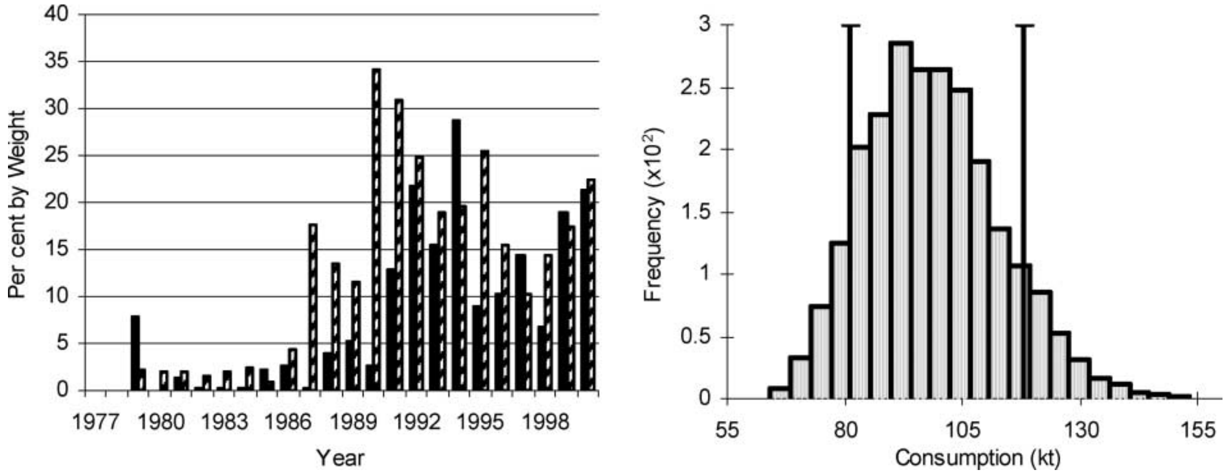

Figure 5. Diet percentages for herring (by weight) (spring-black bars, autumn-cross hatched bars) for spiny dogfish during the period 1977–2000, and consumption of herring by spiny dogfish during 1991, with range and 80% CI (81 000–118 000 t).

1970s through the mid-1980s, herring accounted for just a small percentage of the diet (by weight) of spiny dogfish (Figure 5). However, when herring started to recover in the late 1980s, 10–35% of the diet of spiny dogfish consisted of herring (Figure 5). Estimated consumption of herring by spiny dogfish averaged only a few thousand tonnes from the late 1970s to the mid-1980s, peaked at nearly 100 000 t in 1991, declined to about 28 000 t in 1997, and has subsequently fluctuated about 50 000 t (Figure 5). During the peak year of herring consumption in 1991, herring predation by dogfish ranged from 54 000 to 159 000 t, with an 80% CI of 81 000–118 000 t (Figure 5).

As a group, predatory demersal fish had a major impact on the herring stock during the study years 1977–2002. Consumption was relatively low in the late 1970s and early 1980s, increased in the late 1980s, and peaked in the early to mid-1990s (Figure 6). Spiny dogfish and silver hake were by far the largest consumers of herring, followed by the two cod stocks, white hake, and goosefish (Figure 6). The other seven species had smaller impacts individually, but as a whole consumed a significant quantity of herring. Total consumption by demersal fish ranged from a few thousand tonnes in the early 1980s, peaked at >200 000 t during the period 1991–1994, then stabilized at an average of 135 000 t from 1998 onwards (Figure 6).

Marine mammals

The total consumption of herring by marine mammals was less than by demersal fish. Herring consumption by harbour porpoises averaged slightly over 5000 t during the years 1977–1981,

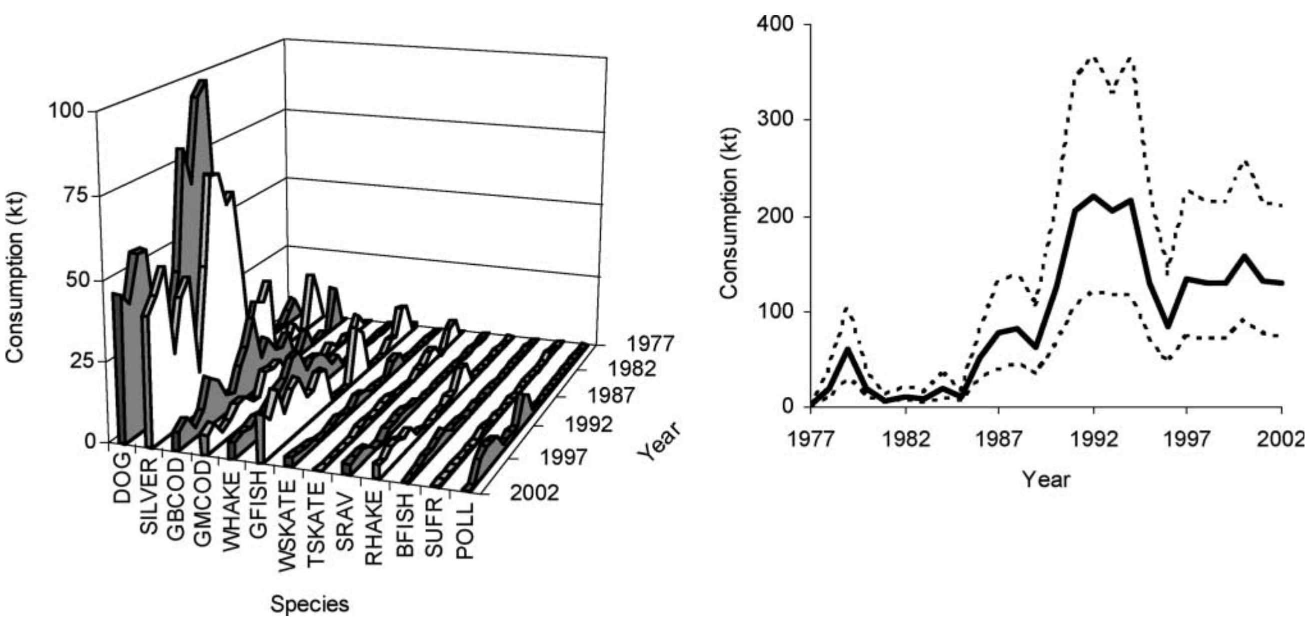

Figure 6. Consumption of herring by demersal fish (spiny dogfish, DOG; silver hake, SILVER; Georges Bank cod, GBCOD; Gulf of Maine cod, GMCOD; white hake, WHAKE; goosefish, GFISH; winter skate, WSKATE; thorny skate, TSKATE; sea raven, SRAV; red hake, RHAKE; bluefish, BFISH; summer flounder, SUFR; and pollock, POLL) during the years 1977–2002, and the total consumption of herring by demersal fish during the same years, with 80% CI.

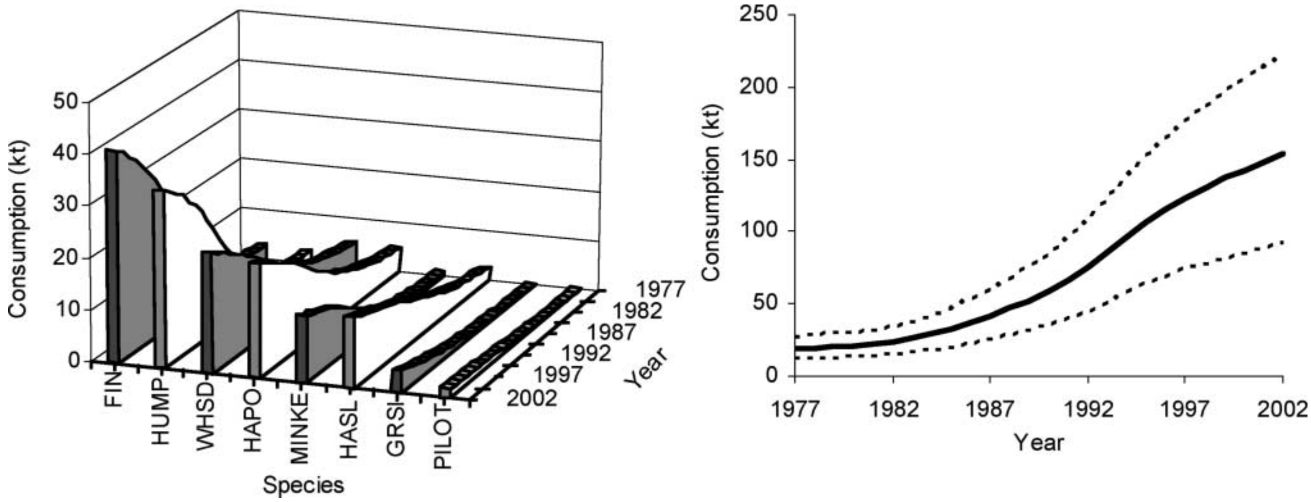

Figure 7. Consumption of herring by marine mammals (fin whale, FIN; humpback whale, HUMP; white-sided dolphin, WHSD; harbour porpoise, HAPO; minke whale, MINKE; harbour seal, HASL; grey seal, GRSL; and pilot whale, PILOT) during the years 1977–2002 and the total consumption of herring by marine mammals during the same years, with 80% CI.

increased to an average of 12 000 t in the early 1990s, and peaked at 22 000 t in 2002 (Figure 7), with an 80% CI of 13 000–33 000 t (Figure 8). The other mammals in this group exhibited similar patterns of herring consumption during the years 1977–2002.

Herring consumption by all marine mammals increased steadily over the time horizon 1977–2002, peaking in 2002 (Figure 7). Fin whales and humpback whales consumed the greatest quantities (Figure 7), and by 2002, these two species were eating 41 000 t and 34 000 t, respectively, of herring. Harbour porpoise, white-sided dolphin, harbour seals, and minke whales consumed large amounts of herring during the same period (Figure 7). Estimates of total consumption of herring by marine mammals increased from 19 000 t in 1977 to 153 000 t in 2002 (Figure 7).

Large pelagic fish

Bluefin tuna were by far the largest consumer of herring of the large pelagic fish predators. From the mid-1980s to 2002, bluefin tuna consumed increasing amounts of herring. Bluefin tuna annually consumed an average of 10 000 t of herring during the years 1977–1981, 14 000 t from 1988 to 1992, and 23 000 t during the years 1998–2002 (Figure 9). In 2002, herring consumption

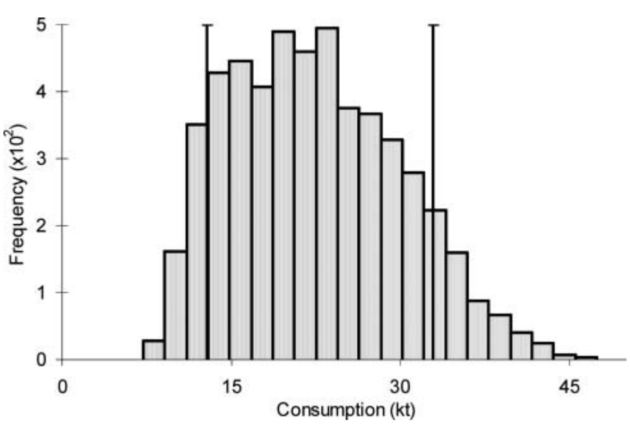

Figure 8. Consumption of herring by harbour porpoise during 2002, with 80% CI (13 000–33 000 t).

was estimated at 25 000 t, with a range between 7000 and 56 000 t, and an 80% CI of 14 000–36 000 t (Figure 10). Blue shark and shortfin mako shark displayed similar, but lower, trends over time.

Consumption by large pelagic fish increased during the study period. Bluefin tuna consumed between 7000–25 000 t annually, and blue sharks between 300 t and 1100 t (Figure 9). The diet of shortfin mako shark contained a small proportion of herring, with annual consumption estimates ranging between 8 t and 23 t from 1977 to 2002 (Figure 9). Total consumption by this predatory group ranged from 8 000 to 26 000 t during the period 1977–2002 (Figure 9), a relatively small value compared with demersal fish and marine mammals.

Seabirds

Seabirds as a group had a much lesser consumption of herring than the other groups of predators. Annual consumption of herring by shearwaters averaged just 1000 t during the period 1977–1991 (Figure 11), but thereafter it increased, averaging 2500 t during the years 1992–1996, and 3000 t from 1997 to 2002 (Figure 11). Shearwater consumption in 2002 was estimated to be 3000 t, ranging from 2000 t to 4000 t, with an 80% CI of 2000–4000 t (Figure 12).

As a group, seabirds consumed comparatively little herring. The two largest consumers in the group were northern gannets and shearwaters, followed by black-backed and herring gulls (Figure 11). Black-legged kittiwakes and northern fulmars accounted for very little at all. Group consumption declined from the late 1970s through the mid-1980s (Figure 11), then increased in the late 1990s to stabilize at a slightly higher level. Total annual consumption by the group ranged from 2000 t to 10 000 t during the whole period 1977–2002, 10 000 t during 1977 and 1978, declining to just 3000 t from 1979 to 1986, then increasing slightly to average 6000 t during the period 1987–1995 and 9000 t from 1996 (Figure 11). Estimated consumption of herring by seabirds in 2002 was still 9000 t, with an 80% CI between 6000 t and 11 000 t.

Total consumption by all predators

Together, the four groups of predators consumed a significant amount of herring in the Gulf of Maine–Georges Bank region.

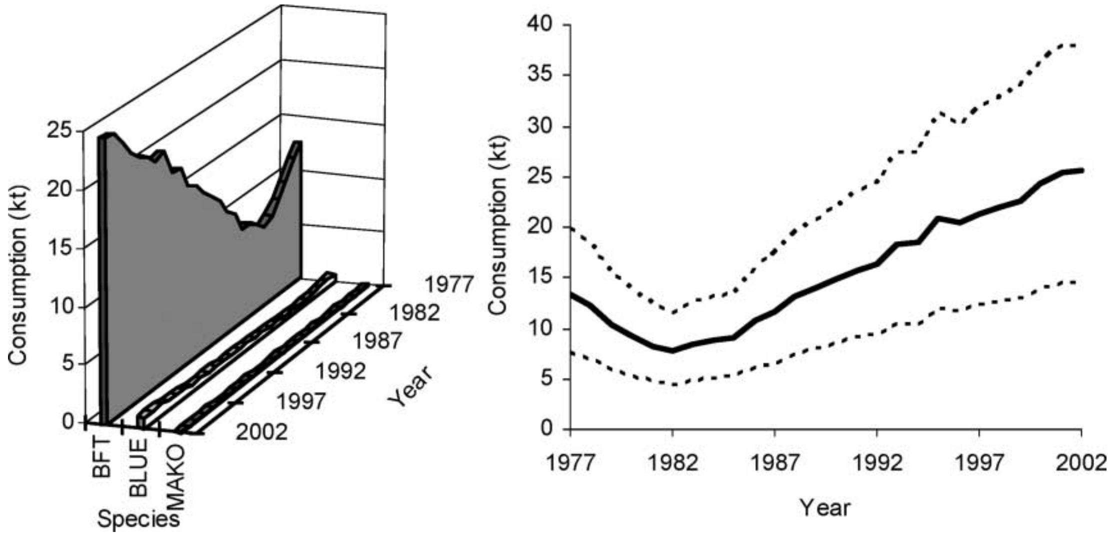

Figure 9. Consumption of herring by large pelagic fish (bluefin tuna, BFT; blue shark, BLUE; shortfin mako shark, MAKO) during the years 1977–2002, and the total consumption of herring by large pelagic fish during the same years, with 80% CI.

Demersal fish consumed the largest quantity (200 000+ t in the early 1990s), followed by marine mammals (75 000 t at the same time; Figure 13). Herring consumption by the two groups in recent years is still similar, at about 130 000 t by demersal fish and 150 000 t by marine mammals (Figure 13). Large pelagic fish, primarily bluefin tuna, were the next most important predatory group, consuming about 26 000 t in 2002, followed by seabirds, the least important of the four groups, which accounted for just 9 000 t in the same year (Figure 13).

Total consumption of herring by all groups increased from an annual average of 57 000 t during the early part of the study period, 1977–1982, to average 13 000 t from 1986 to 1989, then 294 000 t from 1990 to 1994, followed by a decline and a subsequent resurgence to a recent average (1998–2002) of 311 000 t (Figure 13).

Sensitivity analysis

Because of the uncertainty framework and Monte Carlo approach used in this analysis, it is possible to do a comprehensive investigation of the sensitivity of model results to input data for any given year. The metric evaluated in the sensitivity analysis was the correlation between the output variable, herring consumed, and the various input variables. The coefficient for each input–output pair was based on the Spearman rank correlation between herring consumption and a set of sampled input values for each input variable. For each year, the 5000 realizations of each input and output value were ranked, and the correlation for this set of 5000 ranked pairs was calculated for each input value. Only the final year in the series, 2002, was selected to illustrate results for all the predator groups, because the output for all years would be voluminous. However, other years in the time-series were examined, and sensitivity results for those years produced the same conclusions as 2002.

Depending on the predator group, model outputs for herring consumed are more sensitive to one input variable than another. As an example for one species, minke whales, consumption of herring was correlated (from highest to lowest) with the proportion of herring in the diet, proportion in the area, daily ration, and stock size (Figure 14).

In general, herring consumption is most sensitive to the estimates of average stomach content for demersal fish, the percentage of herring in the diet of marine mammals and large pelagics, and to the daily ration for seabirds (Table 1). Daily ration and proportion of herring in the diet were the most significant input variables for all four predatory groups, whereas stock size was generally the least important. In most cases where the proportion of the stock in the area was also modelled, it too was more highly correlated than stock size, with the exception of bluefin tuna (Table 1).

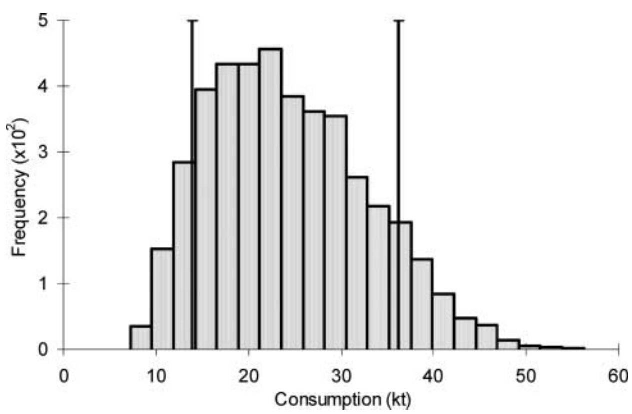

Figure 10. Consumption of herring by bluefin tuna in 2002, with 80% CI (14 000–36 000 t).

Discussion

The Gulf of Maine–Georges Bank herring stock complex completely recovered from low biomass levels during the late 1980s and 1990s, and herring now occupy their historical range (Overholtz and Friedland, 2002). Consumption of herring by the four predatory groups analysed here averaged more than 300 000 t annually between 1998 and 2002. In comparison, landings in the herring fishery in the region averaged just 100 000 t in recent years

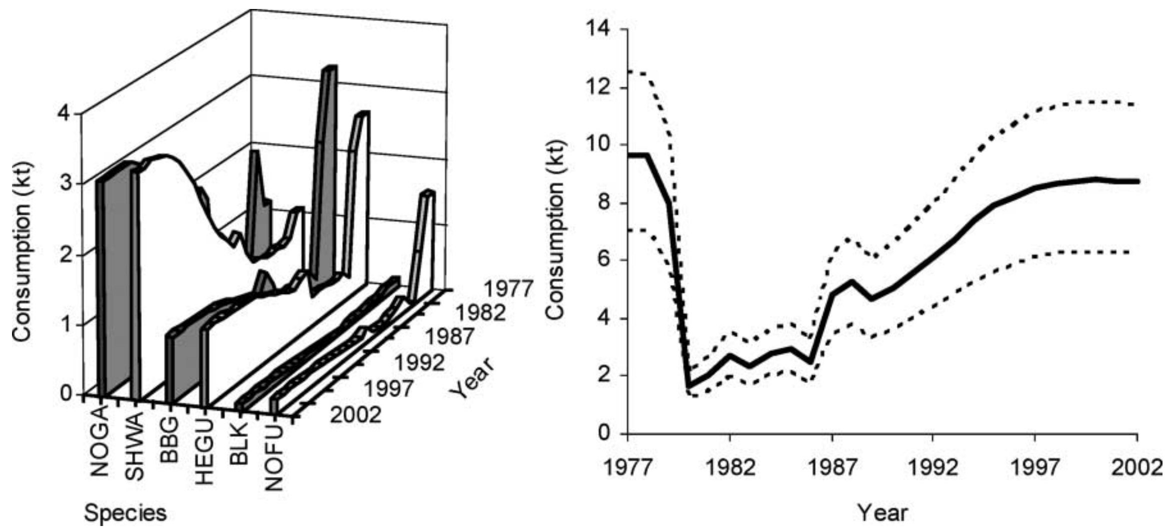

Figure 11. Consumption of herring by various seabirds (northern gannet, NOGA; shearwater, SHWA; black-backed gull, BBG; herring gull, HEGU; black-legged kittiwake, BLK; and northern fulmar, NOFU) during the years 1977–2002, and the total consumption by seabirds during the same years, with 80% CI.

(Overholtz *et al.*, 2004). Bax (1991) also found that catches were generally much smaller than consumption in other ecosystems, such as the Benguela Current, the North Sea, and the eastern Bering Sea.

Consumption of herring closely followed herring abundance during the years 1977–2002, declining in the late 1970s and early 1980s, as herring became scarcer and other prey fish (such as sandlance) increased (Fogarty *et al.*, 1991; Overholtz *et al.*, 2000). Beginning in the late 1980s, herring again became the major prey item in the diets of many predators of the region, and currently remain very important to them all. However, the total consumption of herring by demersal fish declined significantly in the mid-1990s after spiny dogfish, cod, and white hake were overfished. For example, most of the large female spiny dogfish that prey heavily on fish were removed by a directed fishery for spiny dogfish that developed in the early 1990s (NEFSC, 2003). Herring biomass continued to increase, however, suggesting perhaps that herring abundance can at least potentially be linked to consumptive removals by predators (Tsou and Collie, 2001). Despite the decline in demersal fish and their consumption of herring during

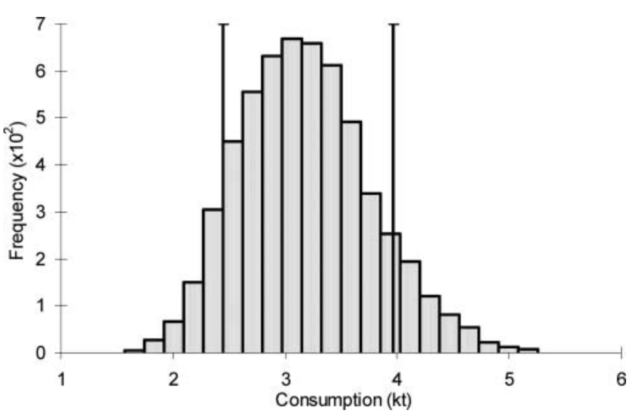

Figure 12. Consumption of herring by the shearwater group during 2002, with 80% CI (2000–4000 t).

the 1990s, total herring consumption remained relatively constant, because the abundance of marine mammals continued to increase. Such continued increases in marine mammal abundance and hopefully recovery of depleted demersal fish stocks will increase the natural impacts on the herring resource.

The estimate of total consumption from this study is the first comprehensive analysis that includes all the major predators of Atlantic herring in the Gulf of Maine–Georges Bank region. Consumption by demersal fish and marine mammals estimated in this study is of the same order of magnitude as previously reported (Overholtz *et al.*, 2000; Tsou and Collie, 2001; Read and Brownstein, 2003). Refined estimates from this study, however, suggest that herring consumption by demersal fish is 20–30% lower than the point estimates in Overholtz *et al.* (2000). For example, the current study estimated that 206 000 t (80% CI, 116 000–328 000 t) were consumed in 1991, whereas the previous study estimated 273 000 t. This difference is likely because of improvements in the analysis of diet composition, use of a better temperature model, inclusion of quarterly estimates of stock size for the predators, and the uncertainty framework used in the current analysis. Similarly for marine mammals, estimates of consumption of herring are of the same magnitude, but lower by 50% on average in the present study. For example, the estimate of herring consumed by marine mammals in 1991 from the current study is 73 000 t (80% CI, 20 000–156 000 t), whereas in a previous study the estimate was 141 000 t (CI 94 000–190 000 t; Read and Brownstein, 2003). The reasons for the lower estimate in the present study are likely due to improved estimates of the number of marine mammals in the area through accounting for the percentage of the stocks in the region, improved estimates of diet composition, and the use of an uncertainty framework in the current analysis.

Medium-sized predatory fish are the leading consumers in many marine ecosystems, including the eastern Bering Sea, the North Sea, and the Barents Sea (Bax, 1991). The current study supports this finding in terms of consumption of herring in the Gulf of Maine and Georges Bank. Not only did demersal fish consume more herring than any other group of predators, but in

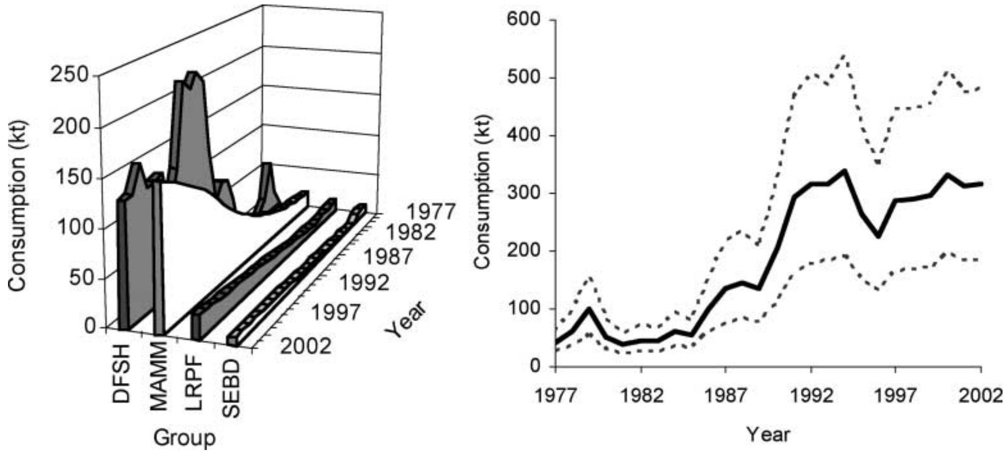

Figure 13. Consumption of herring by the four groups of predators (DFSH, demersal fish; MAMM, marine mammals; LRPF, large pelagic fish; SEBD, seabirds) during the years 1977–2002, and the total consumption of herring by all predators during the same years, with 80% CI.

the early 1990s this group consumed more herring than the other three groups combined. Marine mammals were second in importance in terms of herring consumption, as they were for several of the ecosystems reported in Bax (1991). Marine mammals are major consumers of fish in the Gulf of Maine–Georges Bank region, with a total fish consumption exceeding a million tonnes annually (Kenney *et al.*, 1995). However, this estimate includes several species of prey fish (including herring) residing on the continental shelf, as well as a number of fish that live along the shelf/slope break and farther offshore. Estimated total consumption of all fish prey by 12 species of piscivorous demersal fish in the Georges Bank region averaged about 2 million tonnes during the years 1977–1990, and 1.2 million tonnes in the late 1990s (Overholtz *et al.*, 2000). If marine mammal populations continue to expand, consumption of forage fish by predatory fish and marine mammals may become nearly equal.

The probability methods used in this analysis to capture uncertainty proved useful, especially given that the quality of the input data varied from poor to excellent. When empirical estimates of the mean and CV of an input variable were available (such as the mean stomach content data for demersal fish, or stock sizes for marine mammals) they could be readily incorporated into informative input distributions. Similarly, less well-determined inputs (such as the percentage of herring in the diets of several marine mammals), relevant local information, studies from similar species and systems, and expert opinion were combined to produce input distributions that were less informative, but relevant and conditioned on the quality of the available data. Data qualification approaches of this type are now becoming more common as the need for complex multispecies and ecosystem modelling advice has increased (Christensen and Pauly, 1995; Shelton *et al.*, 1997; Pauly *et al.*, 2002; Christensen and Walters, 2004). Future improvements to the approach might include more work on the development of priors based on a full Bayesian modelling analysis (Brodziak *et al.*, 2004). In addition, although herring appear to be the keystone prey fish in this ecosystem, non-linear predator responses to alternative prey could also be incorporated into the uncertainty framework developed here.

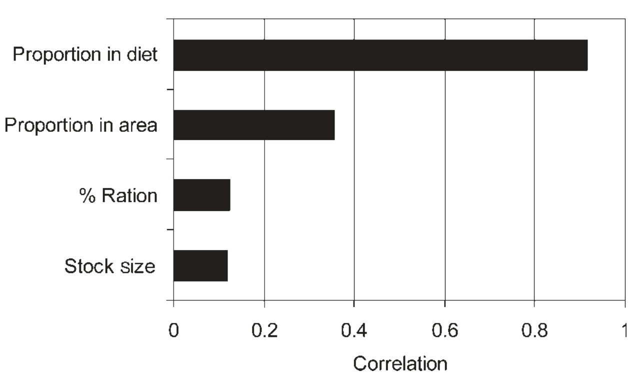

Figure 14. Correlation results from sensitivity analysis between input variables (Proportion in diet, Proportion in area, % ration (%BW per day), and stock size) and herring consumed for minke whales during 2002.

The sensitivity analyses suggest that diet composition data and daily consumption estimates are generally more important than predator stock size for estimating herring consumption by marine mammals, large pelagic fish, and seabirds. This result seems counter-intuitive, because it would appear that the number of predators should most influence their consumption of prey. However, the distributions used to model the percentage of herring in the diets of these predators were uninformative (uniform distributions), so the results were highly dependent on this input. Also, the high CVs that were used for the uniform distributions greatly influenced the results. For demersal fish, daily consumption was most influential, followed equally by the percentage of herring in the diet, and predator stock size. Even in this case, predator stock size is not the most influential variable. These results suggest that more attention should be focused on estimating the food habits and daily rations of piscivorous predators. There has been extensive monitoring of fish diets in the region over the past 40 y (Link *et al.*, 2002), but more research on the estimation of consumption is warranted. Although it is difficult to obtain information on the diets of marine mammals, new methods such as stable isotope analysis, using tissue samples, could be useful (Estrada *et al.*, 2003). Information on large pelagic fish and seabird diets is scant and would benefit greatly from direct monitoring programmes that collect a time-series of information over a minimum of at least 5 y.

Table 1. Results of sensitivity analysis for 2002 for all the predator species.

Species	% Herring	Ration	Stock size	% in area
Spiny dogfish	0.268	0.446	0.269	NA
Silver hake	0.350	0.563	0.353	NA
Georges Bank cod	0.447	0.760	0.431	NA
Gulf of Maine cod	0.338	0.549	0.339	NA
White hake	0.344	0.547	0.331	NA
Summer flounder	0.390	0.877	0.390	NA
Thorny skate	NA	NA	NA	NA
Winter skate	0.428	0.743	0.440	NA
Bluefish	0.429	0.764	0.443	NA
Sea raven	0.431	0.758	0.442	NA
Pollock	NA	NA	NA	NA
Red hake	0.419	0.731	0.432	NA
Goosefish	0.431	0.744	0.438	NA
Fin whales	0.865	0.406	0.275	NA
Humpback whales	0.717	0.403	0.407	NA
Habour porpoise	0.821	0.390	0.078	0.365
Atlantic white-sided dolphins	0.816	0.338	0.206	0.188
Harbour seals	0.601	0.398	0.211	NA
Minke whales	0.915	0.125	0.119	0.356
Grey seals	0.886	0.376	0.088	NA
Pilot whales	0.894	0.313	0.143	NA
Bluefin tuna	0.586	0.568	0.377	0.372
Blue shark	0.754	0.501	0.283	0.297
Shortfin mako shark	0.769	0.486	0.271	0.261
Northern gannet	0.407	0.658	0.286	NA
Shearwaters	0.458	0.596	0.321	NA
Great black-backed gull	0.377	0.705	0.241	NA
Herring gull	0.392	0.704	0.240	NA
Black-legged kittiwake	0.672	0.541	0.447	NA
Northern fulmar	0.498	0.632	0.315	NA

Values are the Spearman rank correlation between the quantity of herring consumed and the percentage of herring in the diet (% herring), the daily ration (ration), the stock abundance of the predator (stock size), and the percentage of the predator stock in the region (% in area). NA, not applicable.

The information from this analysis may be useful in developing stock assessment advice for Atlantic herring in the region. Including biological interactions and their impacts in stock assessments and multispecies models is an important step in predicting sustainable yields and developing realistic estimates of biological reference points for key prey species (ICES, 1989; Overholtz *et al.*, 1991; Hollowed *et al.*, 2000). Reference points such as maximum sustainable yield (MSY) and the biomass at MSY (B_{MSY}) are often smaller and larger, respectively, when biological interactions are considered (Hollowed *et al.*, 2000). Lacking these considerations, an over-optimistic picture of sustainable yield may result, and important trophic links may be severed if a prey resource is overfished. Atlantic herring, because of their small average size, are vulnerable to a wide variety of predators over their entire lifespan, unlike many other prey fish that grow to larger size as they age and exit the window of vulnerability. The fishery for herring harvests the same size groups that predators consume, so in effect the two are competing for the same fish (Overholtz *et al.*, 2000). This is why the expectation of yield and biological reference points may be quite different when predation on prey fish is included in the accounting method.

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