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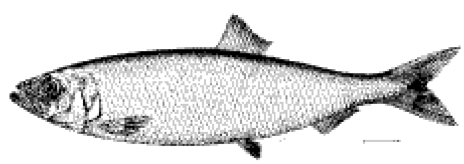
The Role of Atlantic Herring,

Clupea Harengus,

in the Northwest Atlantic Ecosystem



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DRAFT

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1.0 OVERVIEW OF ECOSYSTEM-BASED MANAGEMENT

Fisheries can alter ecosystems in several ways. They can change predator-prey dynamics, disturb physical habitat, introduce exotic species, and alter growth and mortality rates for fish species (Witherell et al. 2000; NMFS 1999). Tsou and Collie (2001b) also stated that understanding how species interactions affect population dynamics in the ecosystem is important in projecting recovery rates for exploited populations. Because of this, there may be limitations associated with traditional single species management, which may not always consider species interactions within an ecosystem. In contrast to single-species management, an ecosystem-based approach could account for the interactions a species has with its prey, predators, and competitors as well as the effects of weather and climate on fisheries. An ecosystem-based approach could also consider the effect of fishing mortality on an ecosystem (NMFS 1999).

An ecosystem-based management strategy could serve to minimize the impacts of fishing on an ecosystem while still allowing for the possibility of harvesting the resources at sustainable levels. Implementing an ecosystem-based approach should involve taking a precautionary approach to management by setting conservative catch limits, bycatch controls, establishing marine protected areas, and providing adequate monitoring and enforcement (Witherell et al. 2000).

In 1999, the Ecosystems Principles Advisory Panel drafted a report to Congress on ecosystem-based fishery management. In the report, the panel outlined a series of recommendations for implementing a Fisheries Ecosystem Plan (FEP) with the overall goal to "Maintain ecosystem health and sustainability (NMFS 1999)". The panel suggested that each regional Council develop a FEP to help address the effects fisheries have on the ecosystem. By doing this, managers may be better able to make decisions that ensure the integrity of the ecosystem while still allowing for sustainable harvesting of the resource. While the panel acknowledges that this process will be complicated, they suggested that an initial first step might be to consider how the harvesting of one species affects the dynamics of other species in the ecosystem. This may be as simple as identifying and examining predator-prey interactions. This is the approach that is taken in this paper, which is to consider the predator-prey interactions of Atlantic herring in the western north Atlantic.

2.0 OVERVIEW OF PREDATION IMPACTS ON MARINE ECOSYSTEMS

Bax (1998) summarizes the findings of several research papers on the subject of predation and offers an overview of the impacts of predation in marine fisheries. Bax acknowledged that the summary represented only a fraction of reports available, but still serves to provide insight into the potential impacts of predation on marine ecosystems. The following summary is derived from the Bax (1998) paper. The complete paper should be referenced for additional information on specific studies.

In the paper, Bax covers a wide range of predators including birds, marine mammals, fish, and invertebrates. With regard to marine mammals, Bax reports that in several studies, taking place in five different areas, marine mammals consumed more commercially important fish than the commercial fishing industry catches annually. Specific examples of marine mammal predation came from the Bering Sea, Iceland, and the North Sea. In the Bering Sea, whales and seals were estimated to consume 10% of all commercial fish stocks annually. This was in contrast to humans and birds, which consume 5% and 2% respectively. In Iceland, tooth whales were estimated to consume 850,000 tons of fish annually. In the North Sea, grey seals were estimated to consume 14.3 million (4.8%) cod age 1-4.

While predation by marine mammals may exceed that of commercial catches, there is still insufficient evidence to conclude that predation causes significant changes on fish population in marine systems. Bax suggests that population regulation does appear to occur when marine mammals have a specialized diet as opposed to a generalist diet. That is, the effects of predation are more likely to be felt when predation occurs on a single species then when it occurs on a variety of species.

Marine seabirds are also a source of heavy predation on marine ecosystems. Their high metabolic rates and high-energy requirements necessitate a high predation rate. In Oregon for example, predation by seabirds accounts for 22% of all fish production. In a 45-km area around a colony in the Shetland Isles, UK, 29% of fish production is consumed. More locally, seabirds consume 4-7% of adult herring off the Gulf Islands, Canada. Seabirds often target the same size classes as commercial fisheries, and declines in seabird populations are often associated with collapses in fish stocks. It should be noted that predation by seabirds is not always on live fish. In the North Sea, 52-66% of seabirds get their food by scavenging, with more than half of their food coming from fishery waste. This shows the potential for fishery discards to cause changes in the feeding ecology and population size of many seabirds.

Fish can also be major predators on smaller fish, larval fish, and fish eggs. Bax noted two studies in which both haddock and cod were observed to be feeding on herring eggs. These studies suggested that predation could remove 40-60% of herring eggs from a system. Bering sea yellowfin sole were estimated to have consumed 2 X 10^9 0-aged arrowtooth flounder and 80 X 10^9 0-aged Greenland halibut.

Cannibalism has also been shown to be a significant source of predation. In one study, adult northern anchovy consumed 17% of the anchovy eggs each day resulting in an overall mortality rate of 32%. Mortality by fish predation was estimated to be 2 to 35 times greater than mortality from fishing and does vary by predator species. Fishing was seen as a greater cause of mortality on larger species of fish, while predation was seen as a greater cause of mortality on smaller species.

Invertebrates are another source of predation on marine ecosystems discussed in the Bax paper (1998). Several species of squid all over the world have been shown to be significant predators in the marine ecosystem. For example, in the northeast Atlantic, over 80% of non-empty long-finned squid stomachs contained fish prey. Fish prey was also abundant in the stomachs of short-finned squid, accounting for 42% of the total prey volume. In the Gulf of Thailand, it was estimated that cephalopods consumed over 500,000 tons of prey annually in the 1980s. Other invertebrate predators include zooplankton, copepods, euphausiids, and amphipods, all of which are significant consumers of fish eggs and larvae.

3.0 INTRODUCTION TO ATLANTIC HERRING

3.1 ATLANTIC HERRING ECOLOGY AND MANAGEMENT

Atlantic herring, *Clupea harengus*, is a small schooling pelagic fish species found in great abundance on both sides of the Atlantic. In the western north Atlantic, herring range from Cape Hatteras to Labrador. Atlantic herring reach a maximum size of 43 cm and 0.68 kg and a maximum age of 15-18 years. Atlantic herring become mature between 3-4 years of age at a length of approximately 25 cm (Reid et al. 1999).

Spawning occurs in these discrete locations: southwestern Nova Scotia, coastal Gulf of Maine, and Georges Bank/Nantucket Shoals. Spawning typically occurs in the fall starting in the northern regions early in the season and ending in late fall in the southern regions. Atlantic herring primarily feed on zooplankton, which includes chaetognaths, euphausiids, and larval fish. Herring themselves are preyed upon at all stages of life by marine animals including fish, birds, and marine mammals (Reid et al. 1999; Bigelow and Schroeder 2002).

Atlantic herring are a commercially important species supporting a major fishery since pre-Colonial times (Bigelow and Schroeder 2002). Currently, herring is managed as one stock and is regulated through a single total allowable catch (TAC) or quota. The total allowable catch is distributed into four management areas. Once the TAC is reached for an area, that area becomes closed to further directed fishing.

3.2 POPULATION CHANGES OF ATLANTIC HERRING IN THE GULF OF MAINE/GEORGES BANK REGION

Overholtz and Friedland (2002) used bottom trawl survey data from the Northeast Fisheries Science Center (NEFSC) to describe the changes in the population size of Atlantic herring in the Gulf of Maine/Georges Bank region between 1968 and 1998. In their paper, the authors noted that heavy fishing from foreign fleets between 1961-1976 caused the Georges Bank portion of the population to collapse. This in turn led to a period to low herring abundance between 1971-1985. Starting in 1985, the population began to increase steadily, eventually reaching levels six times higher than the 1968 levels. Overholtz and Friedland (2002) suggested that this increase in population size occurred in a stepwise fashion with the Gulf of Maine population recovering first, followed by the Nantucket Shoals population and then the Georges Bank population. This point was supported by both bottom surveys for groundfish as well as larval fish surveys.

3.3 ATLANTIC HERRING NATURAL MORTALITY

Total mortality of a species is defined as the mortality due to fishing plus the mortality due to natural causes. Natural mortality can be further broken down into mortality due to old age and disease and mortality due to predation. With certain species like Atlantic herring, mortality due to predation can be a significant component of the total mortality of the fish. Predation mortality can even possible be greater than fishing mortality. Natural mortality rates are also dependent on the life history of the species. In general, long-lived species tend to have a lower average natural mortality, while short-lived species tend to have higher average natural mortality rates. For example, with a species that lives 10-15 years, such as Atlantic herring, a natural mortality of 0.2 appears to be a reasonable estimate.

Scientists at the Northeast Fisheries Science Center are currently examining the relationship of predation to overall natural mortality. What is known already is that predation in an ecosystem can change year-to-year based on changes in the biomass of both the predator and prey.

In the Atlantic herring assessment presented at the Transboundary Resource Assessment Committee (TRAC) assessment meeting, Overholtz et al. (2003) presented a graph, Figure 1, on the relationship between natural mortality to total landings. The graph demonstrates that before 1985, landings were greater than natural mortality. Between roughly 1985 and 1990, landings and natural mortality were approximately equal. After 1990, natural mortality exceeded landings (Figure 1).

Overholtz et al. (1991) also estimated age-specific mortality rates for the five major prey species in the ecosystem between 1988-1992. Table 1 shows how natural mortality changes over time for a given species. The table also describes how natural mortality changes with age and illustrates at which stage a species is most vulnerable to predation. The changes in natural mortality reflect the changes in that species biomass as well as the biomass of the predator. Table 1 also provides a means to compare natural mortality rates between species. The natural mortality rates will indicate which species are being consumed at a higher rate and thus may represent a more important prey species to the ecosystem.

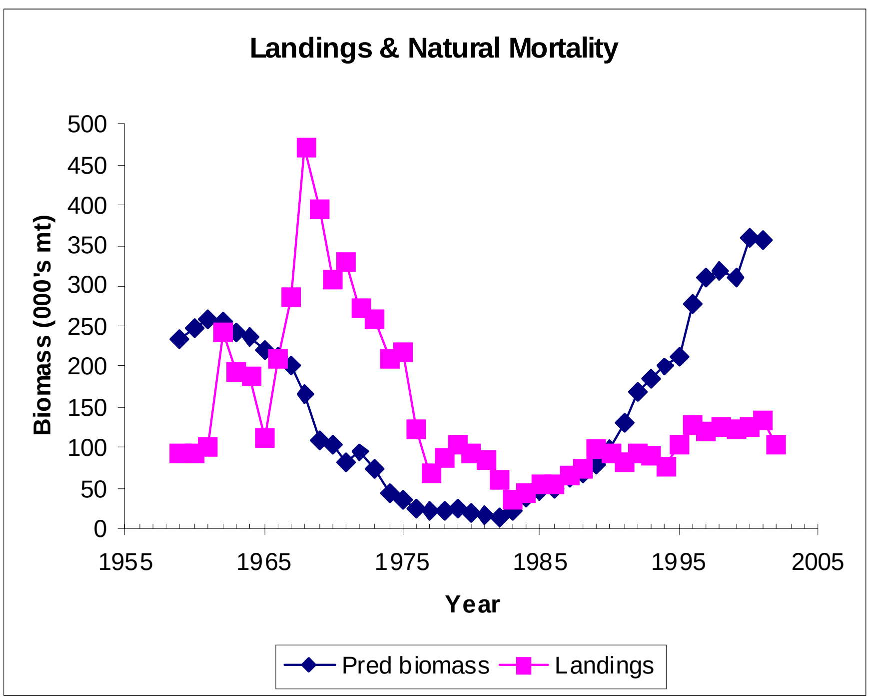

Figure 1 Losses to Natural Mortality (000's t) and Landings During 1959-2002 (Overholtz et al. 2003)

Year	Age 1	2	3	4	5	6+
1988						
Sandeel	0.46	0.65	0.32	0.17	0.00	0.00
Mackerel	0.54	0.29	0.20	0.02	0.02	0.01
Herring	0.12	0.27	0.13	0.09	0.07	0.06
Silver hake (N)	0.43	0.40	0.30	0.03	0.03	0.00
Silver hake (S)	0.30	0.23	0.17	0.05	0.03	0.00
1989						
Sandeel	0.77	0.28	0.14	0.08	0.00	0.00
Mackerel	0.85	0.43	0.30	0.03	0.03	0.02
Herring	0.16	0.28	0.13	0.09	0.07	0.06
Silver hake (N)	1.02	0.93	0.68	0.06	0.05	0.00
Silver hake (S)	0.34	0.26	0.19	0.45	0.30	0.00
1990						
Sandeel	0.72	0.31	0.15	0.08	0.00	0.00
Mackerel	1.07	0.71	0.60	0.03	0.03	0.02
Herring	0.18	0.34	0.16	0.10	0.09	0.07
Silver hake (N)	0.70	0.65	0.50	0.04	0.03	0.00
Silver hake (S)	0.24	0.19	0.14	0.03	0.02	0.00
1991						
Sandeel	0.69	0.28	0.14	0.75	0.00	0.00
Mackerel	1.06	0.71	0.53	0.04	0.03	0.02
Herring	0.18	0.36	0.17	0.11	0.09	0.07
Silver hake (N)	0.67	0.62	0.48	0.05	0.04	0.00
Silver hake (S)	0.20	0.16	0.11	0.02	0.02	0.00
1992						
Sandeel	1.07	0.44	0.21	0.11	0.00	0.00
Mackerel	1.09	0.78	0.60	0.04	0.04	0.03
Herring	0.21	0.40	0.19	0.12	0.10	0.09
Silver hake (N)	0.96	0.90	0.73	0.09	0.07	0.00
Silver hake (S)	0.22	0.17	0.12	0.02	0.01	0.00

Table 1 Age-Specific Predation Mortality Rates for the Five Prey Species in the Pelagic Ecosystem for 1988-1992 (Overholtz et al. 1991)

4.0 ATLANTIC HERRING AS A PREY SPECIES

This section examines the relationship between Atlantic herring and their predators only. No other prey species are considered in this section. Predation on Atlantic herring in relation to other prey species is considered in Section 5.0 of this document.

4.1 PREDATION ON ATLANTIC HERRING BY GROUNDFISH SPECIES

Overholtz et al. (1991) used diet information as well as predator/prey abundance to estimate the amount of herring consumed for several key groundfish predators. Spiny dogfish, while not a groundfish species, is included in Table 2. Values presented here are estimates of average consumption between 1988-1992.

Predator	Herring consumed (tons)
Silver Hake (north stock)	457
Silver Hake (south stock)	1,013
Atlantic Cod	173
Spiny Dogfish	4,255
Total	5,898

Table 2 Average Consumption (tons) by Piscivorous Fish on Atlantic Herring Between 1988-1992 (Overholtz et al. 1991)

4.1.1 Atlantic Cod (*Gadus morhua*)

Atlantic cod, *Gadus morhua*, is a significant predator on Atlantic herring, not only in the Gulf of Maine ecosystem, but also in several other ecosystems in the North Atlantic. Comparing the impacts of herring predation by cod in different ecosystems is useful in characterizing the significance of cod predation in the Gulf of Maine ecosystem. For example, the degree of predation on herring may be different in other ecosystems if cod have more of less other prey species from which to choose. This could change the reliance of cod on herring as a prey and thus make the predator-prey relationship stronger or weaker depending on the situation. Determining this relationship for other ecosystems provides a means for comparing for the relationship in the Gulf of Maine ecosystem.

4.1.1.1 Cod on the Northeast Continental Shelf

Several sources cite Atlantic cod as a major predator on Atlantic herring in the Gulf of Maine-Georges Bank area (Fahay et al. 1999; Bowman 2000; Link and Garrison 2002; Langton 1982; Overholtz el al. 1991; Bigelow and Schroeder 2002). A few of these sources attempt to quantify the amount of herring consumed by cod over time. Link and Garrison (2002) sampled 15,000 cod stomachs from a NEFSC bottom trawl survey. The researchers observed that Atlantic herring is a major prey item for Atlantic cod greater than 50-cm. Cod consumed herring in significant amounts in the Gulf of Maine, Scotian Shelf, Georges Bank, and southern New England regions, but not in the Mid-Atlantic Bight region. In the regions where cod was consumed, it was consumed year-round with the highest consumption rates in the summer and winter and the lowest rates in the spring. Consumption rates also varied within the time series of the data. Between 1973 and 1975, herring made up 15% of the diet composition of cod. Between 1976 and 1980, herring made up 17% of the diet.

Another study conducted within this time series (1977-1980) found that herring made up an average of 5.9% of the diet for cod greater than 61-cm (Bowman et al. 2000). Most of these stomachs were sampled only from the Gulf of Maine. Between 1981 and 1985, the percent composition of herring in the diet of cod decreased to 2% (Link and Garrison 2002). This decrease in composition corresponds to a decrease in the abundance of herring in the environment (Overholtz and Friedland 2002). As the population of herring began to increase in the mid 1980s, so did the consumption of herring by cod. Between 1986 and 1990, the percentage of herring observed in cod stomachs increased to 12%. It again increased to 25% between 1991 and 1998 (Link and Garrison 2002). Consumption of herring by cod was also modeled during this time period (1988-1992). This study suggested that Atlantic cod consumed an average of 173 tons of herring between 1988 and 1992 (Overholtz et al. (1991).

4.1.1.2 Cod in the Gulf of St. Lawrence

Atlantic cod populations have demonstrated similar trends in the southern Gulf of St. Lawrence - a decrease in biomass over time. Swain and Sinclair (2000) discuss the cod recruitment dilemma in the southern Gulf of St. Lawrence. The dilemma is that, while cod showed high recruitment when stocks were low in the 1970s, they are now showing low recruitment rates with the stock still being at a low level. To examine the cause of this dilemma, researchers examined the pelagic fish biomass in the area, mainly herring and mackerel. Herring and mackerel have been known to be strong consumers of cod eggs and larvae in other areas like the North and Baltic seas. While, Swain and Sinclair (2000) acknowledge that there is not actual data to suggest that that predation on cod eggs is occurring, the opportunity for it is there. Spawning of cod coincides with a time of heavy feeding by herring and mackerel.

Researchers also examined trends in pelagic fish abundance to see if there were any correlations with pelagic fish biomass and cod recruitment. Herring and mackerel biomass declined in the late 1960s and early 1970s much as the cod biomass did. In examining the recruitment rate of cod for this time, researchers saw that although biomass of pelagic fish and cod were low, recruitment of cod was high. When the biomass of herring and mackerel increase in the 1990s, researchers saw that cod recruitment was low. The authors concluded that there was a strong negative relationship between pelagic fish biomass and recruitment rate of cod in the southern Gulf of St. Lawrence (Swain and Sinclair 2000).

Hanson and Chouinard (2002) caution that it is important, when modeling predation impacts on an ecosystem, to have information on diets of the predators that are specific to that ecosystem. For example, information on the diets of Scotian Shelf or Grand Banks cod cannot be used to describe southern Gulf of St. Lawrence cod because certain aspects of the community are not common to all three systems. Consequently, when researchers modeled the diet of Atlantic cod in the southern Gulf of St. Lawrence, specific information was used for that ecosystem. Between 1959 and 1980, it was found that herring were not a significant part of the diet (2% for cod 46-60cm and 9% for cod 61-75cm). Between 1987 and 1999, the significance of herring in the diet of cod increased to 17% and 54% for cod 46-60cm and 61-75cm respectively. This trend is consistent with other studies, which show that when populations of herring are low, consumption rates of herring are also low. This was the case in the 1970s when herring were virtually non-existent in the diet of cod (Schwalme and Chouinard 1999).

Another study on the diet of southern Gulf of St. Lawrence cod suggested that cod feed on herring at all times of the year (Schwalme and Chouinard 1999). Data on the diet of cod for this study were collected between 1991-1993, a time when herring stocks were increasing. Researchers found that, for small cod (40-51cm), herring comprised 7.1%, 13.7%, and 3.8% by weight for spring/fall, summer, and winter diets respectively. For large cod (51-61cm), herring comprised 46.5%, 25%, and 35% by weight for spring/fall, summer, and winter diets respectively (Schwalme and Chouinard 1999).

4.1.2 Haddock

Juvenile haddock were collected for stomach content analysis between 1953 and 1976 (Bowman 1981). Atlantic herring were found to comprise only a fraction of the diet of juvenile haddock (< 2%). In a study conducted on the diet of adult haddock, based on stomachs collected between 1977-1980, no Atlantic herring were found in the stomachs of haddock (Bowman et al. 2000). This suggests that herring constitutes only a minor role in the diet of haddock. That is, haddock only prey on herring during their larval stage and may only do so opportunistically.

4.1.3 Silver Hake (Whiting)

Bowman (1984) analyzed 2,622 silver hake (whiting) stomachs between 1973-1976. Stomach samples were obtained from three areas: the Mid-Atlantic region, southern New England, and Georges Bank. Through stomach content analysis, Bowman determined that the diet of silver hake was comprised mainly of fish (80.0%). With regard to Atlantic herring, research suggested that predation varied between sexes, different size classes, different regions, and seasons. It was determined that the female whiting were feeding on herring, while the males were feeding primarily on crustaceans. In females, Atlantic herring accounted for 3.2% of the total weight of the diet.

The amount of herring in the diet of silver hake also varies according to the length of the fish. Silver hake first start feeding on herring between 31-35 cm, with herring accounting for 5.4% by weight of the diet. Between 36-40 cm, herring accounts for 3.8% by weight of the total diet. For silver hake greater than 41 cm, herring accounts for 2.8% by weight of the diet. Regionally, herring accounts for 3.2%, 1.3%, and 5% by weight in the Mid-Atlantic, southern New England, and Georges Bank regions respectively. In all three regions, whiting predation on herring occurs mainly in the fall.

Garrison and Link (2000) produced a similar study examining the diet of silver hake. This study was more extensive then the previous study, sampling over 35,000 silver hake stomachs between 1973-2000. Analysis of percent weight of herring in the diet was conducted for both different sizes of silver hake and different regions sampling. Silver hake were broken down into three size classes: small (<20 cm), medium (20-50 cm), and large (>50 cm). It was estimated the herring made up <2%, 7%, and 15% of the diet for small, medium, and large silver hake respectively. By area, herring accounts for <1%, 7%, 13%, 6%, and 12% for herring caught in the Mid-Atlantic bight, southern New England, Georges Bank, Gulf of Maine, and SW Scotian Shelf regions respectively.

4.1.4 American Plaice

Atlantic herring may be a dietary component of American plaice in specific regions. In the essential fish habitat source document for American plaice, Johnson et al. (1999) suggest that herring make up an important part of the diet for plaice in Sheepscot Bay, Maine and Passamaquoddy Bay, Canada. No other regions contained documented instances of plaice predation on herring (Bowman 2000; Bigelow and Schroeder 2002).

4.1.5 Summer Flounder

Predation on Atlantic herring by summer flounder primarily occurs in the Mid-Atlantic and southern New England regions (Bowman et al. 2000). Stomach content analysis from the same study showed that summer flounder 41-45 cm in size contained 5.5% by weight of Atlantic herring. Stomachs of summer flounder 56-60 cm contained 13.4% herring by weight (Bowman et al. 2000). In a similar study, Link et al. (2002b) found that the percentage by weight of herring in the diet of summer flounder averaged 8% over the last 10 years.

4.1.6 Atlantic Halibut

In the essential fish habitat source document for Atlantic halibut, Cargnelli et al. (1999) give a mostly qualitative description of the diet. In the document, the authors state that the diet of Atlantic halibut greater than 80 cm is predominantly made up of fish. Atlantic herring is a component of that diet, but no quantitative numbers are provided. Bowman (2000) offers a more detailed account of the diet of Atlantic halibut. In the report, it is stated that herring are preyed on by halibut between 41-50 cm, and constitute 11.1% of the total halibut diet. Herring were not reported to be part of the diet for halibut 51-60 cm, but reappear in halibut 61-70 cm, accounting for <0.1% of the total diet. Atlantic halibut >70 cm were reported to have a diet that contained 0.2% herring by total weight.

There were also regional differences identified in the Bowman (2000) report. Herring were reported to be consumed by halibut in the Gulf of Maine region and inshore north of Cape Hatteras, with the majority of herring consumed in the latter region. In a similar study, Link et al. (2002b) collected 229 Atlantic halibut stomachs. Based on stomach content analysis, herring was determined to comprise an estimated 4% of the total diet of halibut.

4.1.7 Pollock

Both Cargnelli et al. (1999) and Bigelow and Schroeder (2002) cite Atlantic herring as the major fish prey of pollock in the Gulf of Maine. No specific amounts were provided in either reference. In a diet analysis study for northwestern Atlantic fish, it was reported that Atlantic herring were not found in the stomachs of pollock for all specimens sampled (Bowman et al. 2000).

4.1.8 Longhorn Sculpin

Bigelow and Schroeder (2002) suggest that Atlantic herring are preyed upon by longhorn sculpins. No data exist on amounts of herring consumed.

4.2 PREDATION ON ATLANTIC HERRING BY MONKFISH

Monkfish (goosefish) greater than 30 cm have been documented to prey on Atlantic herring. The essential fish habitat source document for monkfish only qualitatively described the diet and suggested that herring are one of many fish species preyed upon (Steimle et al. 1999). Bowman (2000) reported that Atlantic herring accounts for 0.8% of the diet for monkfish >90 cm, and that the majority of predation occurs in the southern New England region.

4.3 PREDATION ON ATLANTIC HERRING BY SPINY DOGFISH

Spiny dogfish are opportunistic feeders, preying upon many different species including Atlantic herring (Bigelow and Schroeder 2002; McMillan and Morse 1999). Bowman et al. (1984 and 2000) characterized the diet of spiny dogfish by analyzing the contents of dogfish stomachs. In the 1984 study, 10,167 stomachs were sampled between 1969 and 1982. It was found that the amount of Atlantic herring in the diet of dogfish changed dramatically over the course of the study. Between 1969 and 1972, herring accounted for an estimated 0.5% of the total weight of the diet. In 1979, the amount of herring in the diet increased to 6.4% of the total weight. Starting in 1981, percent volume was used to estimate importance in the diet of dogfish. In 1981, herring were found to comprise 2.2% of the total volume of prey in the diet of dogfish. This dramatically increased in 1982 to a value of 13.4% (Bowman et al. 1984). These data suggest that the relative importance of Atlantic herring to the diet of spiny dogfish has increased between 1969 and 1982.

Bowman et al. (2000) again estimated the composition of the diet of spiny dogfish in a 2000 paper. In this paper, predation by length and area was examined. Atlantic herring were first observed in the diet of dogfish between 71-80 cm, accounting for 2.9% of the diet by weight. Atlantic herring were again found in the diet of dogfish between 91 and 100 cm, accounting for 1.3% of the diet by weight. When predation was examined by area, only the southern New England and inshore north of Cape Hatteras regions documented evidence of dogfish predation on herring (Bowman et al. 2000).

The consumption of herring by spiny dogfish was again modeled in 1998. Link et al. (2002a) report that the Atlantic herring that were preyed upon by dogfish were mainly age 1-3 fish. Researchers also estimated that the amount of herring consumed by dogfish in 1998 was around 67,000 tons. Researchers also estimated that numerically, dogfish consumed 848,000,000 individual herring in 1998.

4.4 PREDATION ON ATLANTIC HERRING BY PELAGIC FISH SPECIES

4.4.1 Bluefin Tuna

Atlantic bluefin tuna migrate into the waters off of coastal New England during the warm months of the year, presumably to feed on concentrations of prey. Bluefin tuna are opportunistic feeders that prey on finfish, crustaceans, and cephalopods (Bigelow and Schroeder 2002; Chase 2002). Chase (2002) conducted a detailed study on the diet of Atlantic bluefin tuna in five regions of the northeast United States (Jefferies Ledge, Stellwagen Bank, Cape Cod Bay, Great South Channel, and south of Martha's Vineyard). In each of these areas, Atlantic herring and Atlantic mackerel are the main pelagic fish species consumed. It should be noted that Atlantic herring occurs less frequently in the regions south of New England.

Sampling of Atlantic bluefin tuna stomachs took place between 1988 and 1992. In all, 819 stomachs were sampled with 568 containing prey. Stomach content analysis showed that herring occurred most in the diet of tuna in the Jefferies Ledge region, (74% of stomachs sampled) and accounted for 87.2% of the total weight of all prey species consumed by tuna from 1988-1992. Herring were also abundant in the diets in the Stellwagen Bank and Great South Channel regions, occurring in 14% and 27.3% of the stomach sampled and accounting for 6% and 48.4% of the total weight of the prey, respectively. Herring occurred less frequently in the diets of tuna in the Cape Cod Bay and South of Martha's Vineyard, occurring only in 8.3% and 2.1% of the stomachs sampled and accounting for only 3.1% and 2.5% of the total weight of the prey, respectively. With regard to length, Atlantic herring consumed were between 18-27 cm, which corresponds to age-2 to age-4 fish in the western Gulf of Maine (Chase 2002).

Increases in commercial catches of Atlantic bluefin tuna have occurred in areas in which Atlantic herring abundance has also increased (western Gulf of Maine and Great South Channel) and decreased in areas south of the Gulf of Maine. This change in the distribution of bluefin tuna may be due to increases in foraging opportunities on Atlantic herring in areas where herring are most abundant (areas off of New England and north). This may explain why herring are more often found in the diet of tuna in these areas and less in the areas south of New England (Chase 2002).

4.4.2 Swordfish

Swordfish, like tuna, are a highly migratory fish. They are also opportunistic feeders, preying on pelagic fishes and squids (Bigelow and Schroeder 2002). In a study conducted by Bowman et al. (2000), Atlantic herring were estimated to make up 0.2% of the total weight of the prey in the stomach of swordfish.

4.4.3 Bluefish

Bluefish spawn in the spring and move north following the Gulf Stream. Bluefish are present in the waters off the northeast continental shelf in the summer and fall. Bluefish are voracious predators of pelagic fishes and squids (Bigelow and Schroeder 2002). Bluefish stomachs were examined during the autumn of 1994 and 1995. Both young-of-the-year (989) and adult (275) bluefish stomachs were collected from the U.S. northeast continental shelf (Buckel et al. 1999).

Stomach content analysis showed that no Atlantic herring were consumed by young-of-the-year bluefish. Atlantic herring accounted for 11.3 and 17.6% (1994 and 1995 respectively) of the total weight of prey consumed by adults (Buckel et al. 1999).

In a similar study, Bowman et al. (2000) found that Atlantic herring consumed by bluefish 31-40 cm accounted for 2.3% of the total prey weight. This predation occurred in the inshore north of Cape Hatteras region. Different regions in which the studies took place most likely explain this difference in contribution of Atlantic herring to the diet of bluefish. Predation on herring is specific to the region in which it occurs; given that two different predation rates were found, the importance of herring to bluefish is likely dependent on where predation occurs.

4.4.4 Striped Bass

Adult striped bass from the Chesapeake Bay, Delaware Bay, and Hudson River stocks migrate north in the spring and summer. Typically, the striped bass that undergo these migrations are females, as females tend to be larger than males, and larger fish migrate further (Nelson et al. 2003). Sampling for stomach contents was conducted in three areas off the coast of Massachusetts (north shore, Cape Cod Bay, and Nantucket Sound) between 1997 and 2000. 3,006 striped bass were sampled with 1,720 containing prey. Diet analysis was broken down into the three areas. Atlantic herring in the north shore region were found in 3.4% of the samples, accounting for 5.8% of the total prey weight. In the Cape Cod Bay region, herring were found in 0.2% of the samples, accounting for 0.1% of the total prey weight. No herring were found in the Nantucket sound region (Nelson et al. 2003). It is possible that diet composition reflects the patterns of herring abundance in the region.

4.4.5 Black Sea Bass

Atlantic herring were reported to be a component of the diet of black sea bass in inshore areas south of Cape Hatteras. Bowman et al. (2000) reported that black sea bass between 21-25 cm had a stomach content that contained 2.3% herring by weight.

4.4.6 Atlantic Salmon

Bigelow and Schroeder (2002) report than Atlantic herring are a component of the diet of Atlantic salmon. No specific predation rates were provided.

4.5 PREDATION ON ATLANTIC HERRING BY SHARKS AND SKATES

4.5.1 Porbeagle Shark

According to Bigelow and Schroeder (2002), Atlantic herring is a major prey for porbeagle sharks in the Gulf of Maine. No specific predation rates were provided in the reference.

4.5.2 Thresher Shark

Thresher sharks prey on small pelagic fish such as herring, menhaden, and bluefish (Bigelow and Schroeder 2002). No specific predation rates were provided.

4.5.3 Blue Shark

In a diet study of northwestern Atlantic fish, blue sharks were reported to be a major predator of fish, with fish accounting for 51.8% of the total weight of their diet. Atlantic herring comprise 0.4% by weight of that diet (Bowman et al. 2000).

4.5.4 Smooth Hammerhead Shark

In the same study by Bowman et al., Atlantic herring were found to comprise 17% of the total weight of prey in the diet of smooth hammerhead sharks (Bowman et al. 2000).

4.5.5 Dusky Shark

In the Mid-Atlantic region, clupeids were estimated to comprise 1.5% of the total weight of the prey of the dusky shark (Bowman et al. 2000).

4.5.6 Barndoor Skate

Barndoor skates are reported in Bigelow and Schroeder (2002) to prey on Atlantic herring. In a study conducted by Bowman et al. 2000, barndoor skates were found to prey on only decapod crustaceans.

4.5.7 Thorny Skate

Thorny skates were observed to prey on Atlantic herring in the Gulf of Maine region inshore north of Cape Hatteras. Thorny skates between 61-70 cm had a diet that contained 63.5% Atlantic herring by weight. Thorny skates >90 cm had a diet that contained 20.8% Atlantic herring by weight (Bowman et al. 2000).

4.5.8 Little Skate

Atlantic herring were found to constitute a minor portion of the diet for little skates (Packer et al. 2003).

4.5.9 Winter Skate

Large winter skates have been reported to be consumers of Atlantic herring (Bigelow and Schroeder 2002; Packer et al. 2003). Link et al. (2002a) estimated that winter skates consumed as average of 928 tons of Atlantic herring in 1998. This was estimated this to equal roughly 9,220,000 individual fish.

4.6 PREDATION ON ATLANTIC HERRING BY INVERTEBRATES AND MISCELLANEOUS FISH SPECIES

4.6.1 Short-Finned Squid (Illex)

Invertebrates such as squid can also be a major predator to Atlantic herring. In a study conducted in Newfoundland, 17,729 short-finned squid stomachs were sampled from 1980-1993. Diet was determined through analyzing the otoliths found in the stomachs. In the study, 1,868 stomachs contained a total of 8,251 otoliths. Atlantic herring accounted for less than 3% of the otoliths sampled (Dawe et al. 1997). Analysis of the otoliths also suggested that the herring consumed were between 39-137 mm in length (Dawe et al. 1997). It is also possible that larger fish were consumed with out consuming the otoliths.

4.6.2 Long-Finned Squid (Loligo)

Cargnelli et al. (1999) suggested in the essential fish habitat source document for long-finned squid, that herring are among the many prey species. It was noted that long-finned squid greater than 16 cm feed on fishes and other squids.

4.6.3 Miscellaneous Fish

Tilefish, alewife, hickory shad, and Atlantic tomcod were all reported to be predators on small Atlantic herring. It should be noted that while herring is a component of the diet of each of these fish, it is not a major component for any of them. In each of these cases, reports are all qualitative, with no predation rates provided (Bigelow and Schroeder 2002; Steimle et al. 1999).

4.7 PREDATION ON ATLANTIC HERRING BY MARINE MAMMALS

4.7.1 Marine Mammals in the Gulf of Maine (GOM)

4.7.1.1 Harbor Seals

Stomachs from 53 harbor seals from southern New England were used to examine the composition of the diet. Atlantic herring were found in 1.8% of the stomachs sampled (Seltzer et al. 1986).

4.7.1.2 Harbor Porpoises

Harbor porpoises from the Gulf of Maine and Bay of Fundy are considered a single population (Gannon et al. 1998). Porpoises move south into the Gulf of Maine in the fall then disperse over the continental shelf in the winter. Because of their small size and limited energy stores, porpoises must remain close to their prey at all times. A study conducted by Gannon et al. (1998) examines the diet of 95 porpoises killed in gillnets during the fall of 1989 and 1991-1994. Porpoises were categorized based on sex, maturity, and reproductive condition. In all, Atlantic herring were found in 78% of all non-calf stomachs sampled. While herring were not an abundant prey number wise, accounting for only 7% of the prey by number, herring accounted for 44% of the total mass ingested. This suggests that porpoises are eating few large-sized prey and many small-sized prey. In fact, what was observed was that Atlantic herring were the largest prey consumed, averaging 254 mm (range 159-339 mm).

When separated into maturity stage and sex, calves were found to consume the least amount of herring. Herring only occurred in 15% of the calves sampled, accounting for 11% of the total mass ingested. In juvenile males, herring occurred in 89% of the samples, accounting for 44% of the ingested mass. In juvenile females, herring occurred in 75% of the samples, accounting for 66% of the ingested mass. In mature specimens, Atlantic herring occurred in 79% and 70% of the samples, and accounted for 66% and 35% of the total mass ingested for males and females respectively.

It was concluded that Atlantic was the most predominant prey for porpoises during the fall season. It was also suggested that while herring are a major prey for porpoises in the fall, it is a more significant prey for porpoises in the summer when porpoises are in the Bay of Fundy. This is discussed in a later section on Canadian Harbor porpoises.

4.7.1.3 Pilot Whales

Conflicting reports are available on the importance of Atlantic herring in the diet of pilot whales. Overholtz and Waring (1991) did not find any amount of Atlantic herring in their study of pilot whales. Gannon et al. (1997b) examined pilot whales stranded from Delaware to North Carolina. In this study, the authors included partial (trace) remains of prey as well as whole prey. What the authors found was that in eight whale specimens, herring had a frequency of occurrence of 12.5%, accounting for 1.3% of the total mass ingested. In a similar study looking at 30 pilot whales caught in the distant water fleet mackerel fishery, Gannon et al. (1997a) found that trace amounts of herring occurred in 23.3% of the samples, while whole Atlantic herring occurred in 18.2% of the samples.

Both regional differences in diet as well as low sample size could play a role in explaining the different results of the three studies. For instance, if herring actually represent a small percentage of pilot whale diet, then the likelihood of encountering herring in stomach samples decreases with sample size. Regionally, if herring are more abundant in a certain area, then the likelihood of finding herring in the stomachs of predators that are also feeding in that area increases.

4.7.1.4 Humpback Whales

Research on humpback whale predation on Atlantic herring has been primarily based on observations of behavior. Humpback whales are a highly migratory species that breed in the winter in the warm tropical waters then migrates north into more productive feeding grounds off the northeast United States. Weinrich et al. (1997) noted a change in the distribution of humpbacks starting in the late 1970s. The change in distribution involved a shift from Georges Bank and the northern Gulf of Maine to Stellwagen Bank and the Great South Channel. This shift in distribution was attributed to a collapse in the herring population, a major prey for whales, followed by an increase in sand lance populations on Stellwagen Bank.

The distribution of humpback whales again changed in the late 1980s as researchers documented a gradual and continuous decrease in the number of whales on Stellwagen Bank coupled with an increase in the number of whales spotted on Jefferies Ledge. It was hypothesized that due to the recovery of Atlantic herring populations, humpback whale distribution shifted back to the pre-collapse state (Weinrich et al. 1997).

4.7.2 Marine Mammals in Canadian Waters

Hammill and Stenson (2000) estimated the consumption rates for four pinniped species in Canadian waters. The specific rates, as they pertain to Atlantic herring, are provided in the next four sections. In addition to consumption, length of Atlantic herring consumed was also estimated for each of the predator species. The results from this paper are provided in Table 3.

	<30cm		>30cm	
Seal species	**Tons**	**% of total**	**Tons**	**% of total**
Harp seal	16,984	95.0	894	5.0
Hooded seal	901	72.0	351	28.0
Grey seal	6,938	84.0	1,322	16.0
Harbor seal	268	62.9	158	37.1
Total	25,091	90.2	2,725	9.8

Table 3 Consumption (tons) of Atlantic Herring by Seals in 1996 in the Northern Gulf of St. Lawrence, by Size Group of Prey (Hammill and Stenson 2000)

4.7.2.1 Harp Seals

Modeling consumption was again utilized to quantify the amount of Atlantic herring consumed by several pinniped species in the Atlantic waters off of Canada. Hammill and Stenson (2000) used information on energy requirements, population size, diet composition, and seasonal changes in distribution to generate these estimates. From this model, harp seals were estimated to consume 48,858 tons of Atlantic herring in 1996.

4.7.2.2 Hooded Seals

Using the same model, Hammill and Stenson (2000) estimated that hooded seals consumed 6,003 tons of Atlantic herring in Canadian waters in 1996. Atlantic herring consumption was also modeled for hooded seals in the Gulf of St. Lawrence. Hooded seals are present in this area for only six months each year. The model used two values for mortality (M) to estimate annual consumption rates. The estimates presented here in Table 4 represent tons consumed for an M of 0.13 and 0.07 respectively (Hammill et al. 1997). In addition to consumption rates, prey length was also estimated. Results indicated that 55% of herring consumed were between 21 and 30 cm, and 45% were between 31 and 40 cm (Hammill et al. 1997).

Year	Tons consumed	
	M= 0.13	M= 0.07
1991	623	675
1992	638	748
1993	654	829
1994	670	919
1995	687	1,018

Table 4 Estimated Total Fish Consumption (tons) of Atlantic Herring by Hooded Seals During the Six Month Period That They Were Present in the Gulf of St. Lawrence (Hammill 1997)

4.7.2.3 Grey Seals

Grey seal consumption was estimated through diet analysis as well as modeling. Between September 1988 and November 1990, 528 seals were sampled on the Scotian Shelf, with 143 containing prey (Bowen et al. 1993). Samples were collected through most months of the year. When the diet of grey seals was compared by season, results showed that Atlantic herring occurred in 18.8% of the summer samples and accounted for 65.8% of the total mass ingested. Conversely, herring occurred in only 4.5% of the winter samples, accounting for 9% of the total mass ingested. This suggests that grey seals feed more heavily on Atlantic herring during the summer months than they do during the winter months.

When diet was compared between maturity levels, results showed that herring occurred in 10.2% of the samples from pups, accounting for 38.5% of the total mass ingested. Herring occurred in 15.6% of the adult samples, accounting for 43.6% of the total mass ingested. Mean length of Atlantic herring consumed was 34.5cm. There is also a great deal of overlap between the sizes of herring consumed by grey seals and those taken in the commercial fishery. This suggests that there is the possibility for competition between seals and humans for Atlantic herring (Bowen et al. 1993).

Hammill and Stenson (2000) also modeled grey seal consumption of herring by taking into account population size, diet composition, and seasonal changes in distribution. It was estimated that grey seals consumed an average of 27,228 tons of Atlantic herring in Canadian waters in 1996.

4.7.2.4 Harbor Seals

Harbor seal predation on Atlantic herring was also estimated through the same model in the Hammill and Stenson (2000) paper. Results demonstrated that harbor seals were estimated to consume 1,559 tons of Atlantic herring in 1996 in Canadian waters.

4.7.2.5 Harbor Porpoises

Harbor porpoises in the western Atlantic comprise a single stock. Gannon et al. (1998) focused on the autumn distribution of harbor porpoises in the Gulf of Maine (see Section 4.7.1.2). Recchia and Read (1989) describe the diet of harbor porpoises during their spring/summer distribution in the Bay of Fundy. In this study, 160 stomachs were sampled from June to September between 1985 and 1987. Atlantic herring was the dominant prey species found in the diet of harbor porpoises, occurring in 88.2% of the samples and accounting for 64% of the total mass ingested (Recchia and Read 1989). The mean size of Atlantic herring consumed was 265 mm.

Consumption was also compared between offshore and inshore areas of the Bay of Fundy from 1985-1987 (Table 5). No drastic differences were observed except in 1986 when herring accounted for 83.2% of the total mass ingested in the inshore area and 28.5% of the total mass ingested in the offshore area. Consumption also varied between time periods. Between 1969 and 1972, herring occurred in 57.7% of the stomachs sampled. Between 1985 and 1986, herring occurred in 97.2% of the samples (Recchia and Read 1989).

	% Occurrence	**% Mass Ingested**
1985 inshore	94.7	44.9
1985 offshore	93.3	95.1
1986 inshore	87.5	83.2
1986 offshore	82.1	28.5
1987 offshore	87.9	96.2

Table 5 Comparison of Diets of Harbor Porpoises From the Inshore and Offshore Areas

4.7.3 Modeling Marine Mammal Consumption

Overholtz et al. (1991) used diet information and predator and prey abundance to estimate the amount of herring consumed for several key predators in the Northeast Region (Georges Bank to Cape Hatteras). Values presented in Table 6 are estimates of average consumption between 1988-1992.

Predator	**Herring consumed (tons)**
Humpback	2,586
Finback	9,959
Minke	366
Pilot	2,803
White-sided dolphin	1,487
Harbor porpoises	684
Harbor seal	1,433
Total	**36,264 tons**

Table 6 Average Consumption (tons) by Marine Mammals on Atlantic Herring Between 1988-1992 (Overholtz et al. 1991)

4.8 PREDATION ON ATLANTIC HERRING BY MARINE BIRDS

Little is known about what effect predation by marine birds has on Atlantic herring. References on the subject have been mainly qualitative, with no consumption rates provided (Axelsen et al. 2001; Bigelow and Schroeder 2002; Hislop and MacDonald 1989; Reid et al. 1999). Overholtz et al. (1991) estimated the amount of herring consumed by seabirds by considering seasonal estimates of seabird abundance and daily consumption rates for the different bird species. The model examined three groups of seabirds: northern gannet, shearwater, and black-legged kittiwakes. From this model it was estimated that northern gannet and shearwater consume an average of 2,827 and 247 tons of herring respectively, between 1988 and 1992 (Overholtz et al. 1991). Black-legged kittiwakes were not estimates to consume any Atlantic herring.

5.0 PREDATION ON ATLANTIC HERRING IN RELATION TO OTHER POTENTIAL PREY SPECIES

A list of prey species in the northwest Atlantic was compiled by using species descriptions from Bigelow and Schroeder (2002). Species were considered to be prey if they are consumed by several different predators. As a result, the following list does not represent every possible prey and their predators in the region. The list is intended to provide some perspective on other available prey in the region and begin to identify ecological interactions between important fish species.

Prey	Known Predators
Alewife	Bluefish, weakfish, striped bass, dusky shark, spiny dogfish, salmon, monkfish, cod, pollock, and silver hake
American plaice	Spiny dogfish, blue shark, little skate, cod, silver hake, monkfish, and bluefish
American shad	Spiny dogfish, angle shark, seals, monkfish, bluefish
Atlantic cod	Cod, four spot flounder, spiny dogfish, sea raven, skates, hakes, squid, and harp seal. Large cod have few enemies like sharks and seals.
Atlantic hagfish	Groundfish, cod, spiny dogfish, harbor seals, and harbor porpoises
Atlantic herring	Preyed upon by nearly every pelagic predator, also groundfish, marine mammals, and birds.
Atlantic mackerel	Whales, porpoises, sharks, tunas, bluefish, bonito, striped bass, other sharks, hake, pollock, monkfish, weakfish, cod, and silver hake
Atlantic menhaden	Are prey for nearly every piscivorous fish, marine mammal, and sea bird in the Gulf of Maine
Atlantic round herring	Consumed by a wide variety of pelagic predators including fish, sea birds, and marine mammals
Atlantic salmon	Only large predators such as sharks, tunas, and marine mammals
Atlantic saury	Squids, swordfish, marlins, sharks, tunas, hake, cod, pollock, dolphin, whales, and birds
Atlantic silverside	Bluefish, striped bass, sea robin, dolphins, birds, and crabs
Bay anchovy	Bluefish, striped bass, summer flounder, weakfish, spiny dogfish, smooth dogfish, several other fish, and sea birds

Table 7 List of Possible Prey Species in the Gulf of Maine and Their Predators (Bigelow and Schroeder 2002)

Prey	Known Predators
Blueback herring	Spiny dogfish, eel, cod, silver hake, white hake, Atlantic halibut, bluefish, weakfish, striped bass, seals, gulls, and terns
Bluefish	Sharks, cod, bluefish, summer flounder, and birds
Butterfish	30 species of fish and squid including haddock, silver hake, swordfish, bluefish, weakfish, and summer flounder
Capelin	10 fish species, 5 marine mammals, and 9 marine bird species are known predators (most notably are cod and haddock)
Cunner	Cod, sea raven, smooth dogfish, white hake, skates, sculpins, tomcod, birds
Cusk	Spiny dogfish, winter skate, cod, white hake, monkfish, fawn cusk-eel, sea raven, summer flounder, hooded seal, and grey seal
Fawn cusk-eel	Conger eel, skates, spiny dogfish, cod, pollock, hakes, monkfish, sculpin, sea raven, and flounders
Fourbeard rockling	Spiny dogfish, little skate, monkfish, cod pollock, red and white hakes, and sea raven
Monkfish	Small individuals: swordfish, sharks, and many species of fish
Gulf stream flounder	14 species of fish including spiny dogfish, spotted hake, windowpane, red hake, silver hake, little skate, and cod
Haddock	Juvenile haddock are eaten by spiny dogfish, skates, cod, haddock, pollock, cusk, hakes, monkfish, sea raven, bluefish, halibut and gray seals
Halibut	Seals, sharks, spiny dogfish, and monkfish
Lantern fish (several species)	Pollock, cod, hake, swordfish, bigeye tuna, opah, common dolphin, and harbor porpoises
Little skate	Sharks, other skates, cod, monkfish, sea raven, sculpin, bluefish, summer flounder and grey seal
Longhorn sculpin	Cod, spiny dogfish, winter skate, sea raven, little skate, monkfish, white hake, and sculpins
Northern pipefish	Smooth dogfish, cod, sea raven, black sea bass, weakfish, oyster toadfish, and bluefish
Ocean pout	18 species of fish including spiny dogfish, skates, cod, hakes, sea raven, and bluefish
Pollock	Spiny dogfish, monkfish, lobster, minke whale, grey seal, harbor seal and pollock
Rainbow smelt	Cod, salmon, striped bass, bluefish, seals, and birds
Red hake	Spiny dogfish, cod, monkfish, silver hake, skates, hakes, sea raven, sculpin, and bluefish
Redfish	Little skate, cod, pollock, silver hake, white hake, monkfish, redfish, bluefish, and wolffish
Sand lance	Whales, seals, (many fish)
Scup	Several species of elasmobranchs and bony fish
Shorthorn sculpin	Smooth skate, clearnose skate, cod, haddock, sea raven, and black sea bass
Silver hake	A partial list: spiny dogfish, little skate, monkfish, pollock, cod, haddock, spotted, red, and white hakes, redfish, sea raven, bluefish, mackerel, swordfish, flounders, and harbor porpoises

Table 7 List of Possible Prey Species in the Gulf of Maine and Their Predators (Bigelow and Schroeder 2002)

Prey	Known Predators
Spotted hake	Spiny dogfish, monkfish, smooth dogfish, silver hake, windowpane flounder, and summer flounder
Striped cusk-eel	Skates, spiny dogfish, cod, monkfish, and flounders
Summer flounder	Spiny dogfish, blue shark, little skate, cod, silver hake, monkfish, and bluefish
Weakfish	Weakfish, bluefish, sharks, skates, monkfish, and summer flounder
Weitzman's pearlside	Cod, pollock, silver hake, Atlantic herring, and harbor porpoises
White hake	Sandbar shark, white hake, cod, Atlantic puffin, and arctic tern
Windowpane fl	16 species of sharks, skates, and bony fish
Winter flounders	Spiny dogfish, blue shark, little skate, cod, silver hake, monkfish, and bluefish
Wrymouth	Spiny dogfish, thorny skate, monkfish, cod, haddock, white hake, sea raven, and redfish
Yellowtail Flounder	Spiny dogfish, blue shark, little skate, cod, silver hake, monkfish, and bluefish

Table 7 List of Possible Prey Species in the Gulf of Maine and Their Predators (Bigelow and Schroeder 2002)

5.1 GROUNDFISH

Overholtz et al. (1991) estimated the amount of prey consumed by several species of groundfish as well as for spiny dogfish, by taking into account seasonal estimates of predator and prey abundance as well as daily consumption rates for the predator species between 1988-1992. The predators examined at in the model were silver hake, Atlantic cod, and spiny dogfish. The prey species in this model were sandeel, Atlantic mackerel, Atlantic herring, and silver hake. Silver hake were separated into northern and southern stocks. The results of the model are provided in Table 8 (average tons consumed). It should be noted that estimates generated after the original paper was published, represent predicted estimated based on the variables of the model.

Prey	Predator				Total
	Silver hake (N)	Silver hake (S)	Atlantic cod	Spiny dogfish	
Sandeel	5,798	22,000	18,307	64,962	111,067
A. mackerel	338	7,541	3,692	167,463	179,024
A. herring	457	1,013	173	4,255	5,898
Silver hake (N)	5,275	0	6,046	11,995	23,316
Silver hake (S)	0	10,137	3,879	3,353	17,369
Total consumption	11,869	40,690	32,096	252,018	336,673

Table 8 Average Consumption (tons) by Piscivorous Fish on the Five Prey Species in the Pelagic Ecosystem for 1988-1992 (Overholtz et al. 1991)

5.1.1 Atlantic Cod

Atlantic cod are major consumers of fish, crustaceans and squids in the Gulf of Maine ecosystem (Bigelow and Schroeder 2002; Link and Garrison 2002). Analysis of stomach samples showed that the diet of Atlantic cod shifts with age. Small Atlantic cod (<10 cm) feed mainly on mysids. Shrimp and other small crustaceans also constitute a minor portion of the diet (Bowman et al. 2000; Link and Garrison 2002). Medium-sized cod (10-30 cm) primarily prey upon crustaceans, including pandalids, amphipods, and shrimp, as well as mollusks.

While crustaceans such as crabs and decapods constituted the majority of the diet for cod 30-80 cm in length, in this study, the inclusion of fish in the diet became more frequent. This marks a shift to an adult diet, which is characterized by an increased occurrence of fish in the stomachs (Bowman et al. 2000; Link and Garrison 2002). Fish commonly found in the diet during the adult stage included silver hake and sand lance (the majority), as well as Atlantic herring and other gadids (Bowman et al. 2000). Large cod (>80 cm) were much more piscivorous than smaller-sized cod. Common fish prey included Atlantic herring, sand lance, dogfish, silver hake, and other cod. In addition to fish, large cod also consume squids, crabs, and shrimp.

The diet of Atlantic cod also varied by geographic region. Atlantic cod in the Scotian Shelf region primarily preyed upon echinoderms, followed by decapods and small amounts of fish. In the Gulf of Maine region, silver hake and herring were the common prey items, followed by illex squid. Fish, including sand lance and gadids, constituted the majority of the cod diet in Georges Bank, followed by decapods. Atlantic cod in the southern New England region also feed on fish such as dogfish, sand lance, and cod (Bowman et al. 2000).

These two studies suggest that while cod are considered generalist predators, they do show preferences for particular prey items. In the majority of areas sampled, adult cod preferred fish prey (including herring, silver hake, and sand lance) and larger invertebrates, such as squids, crabs, and shrimps. It has also been indicated that the diet of Atlantic cod generally reflects the availability of prey in the environment. For example, the occurrence of sand lance and Atlantic herring in the diet increased when these prey species were abundant in areas where Atlantic cod occurred (Link and Garrison 2002).

5.1.2 Silver Hake

The diet of silver hake (whiting) also changes from juvenile to adult. The diet of small silver hake is mainly comprised of euphausiids as well as pandalids (Bowman et al. 2000; Garrison and Link 2000), copepods, and amphipods (Bigelow and Schroeder 2002). Fish and squid become an important part of diet for silver hake >20 cm, comprising 80% of the diet (Bigelow and Schroeder 2002). Bowman et al. (2000) report than sand lance is the main prey for silver hake 20-30 cm in length. In contrast, Garrison and Link (2000) report than Atlantic herring is the main prey species. Other fish prey of importance includes mackerel, silver hake, and other clupeids and scombrids. Cephalopods, euphausiids, and decapods are also important components of silver hake diet, but not as important as fish.

The difference of opinion between studies on the major prey species could be due to different sampling regions. Research has demonstrated that the diet of silver hake does vary by region.

Garrison and Link (2000) reported that in the southern regions, the diet of silver hake contained a higher proportion of sand lance, cephalopods, and amphipods, while the diet in the northern regions contained more pelagic fish, euphausiids, and shrimp.

Bowman et al. (2000) also reported that while fish were the main prey in all areas, specific species dominance varied by area. In the southern areas such as inshore north of Cape Hatteras, the Mid-Atlantic, and southern New England regions, sand lance and silver hake were the main fish prey. In the northern regions such as Georges Bank, the Gulf of Maine, and the Scotian Shelf, Atlantic herring was the main fish prey, followed by silver hake, mackerel, and sand lance. This variation in prey preference is most likely explained by availability of a particular species in each area.

5.1.3 Haddock

Atlantic herring were found to only comprise a small portion of the juvenile haddock diet (Bigelow and Schroeder 2002; Bowman 1981). Juvenile haddock feed mainly on small crustaceans such as amphipods (Bigelow and Schroeder 2002; Bowman 1981; Bowman et al. 2000). In addition, juvenile haddock also consume euphausiids, shrimp, mysids, and polychaetes. Fish prey constituted a minor portion of the diet and included herring, silver hake, and bothidae (Bowman 1981). Adult haddock feed mainly on crustaceans and echinoderms (Bowman et al. 2000).

The diet of haddock also varies by region. Scotian Shelf haddock feed mainly on polychaetes, followed by echinoderms and crustaceans. Gulf of Maine and Georges Bank haddock feed mainly on echinoderms, followed by crustaceans and polychaetes. Haddock in southern New England feed mainly on polychaetes, followed by crustaceans and echinoderms. In the Mid-Atlantic region, haddock were found to feed entirely on amphipods (Bowman et al. 2000).

5.1.4 American Plaice

American plaice are considered to be specialist predators feeding mainly on echinoderms (Bigelow and Schroeder 2002; Johnson et al. 1999; Link et al. 2002b). In a diet study conducted on American plaice, echinoderms were found to comprise >70% of the diet (Link et al. 2002b). In addition to echinoderms, American plaice also consume small quantities of polychaetes, shrimps, small crustaceans, and small fish such as herring (Bigelow and Schroeder 2002).

5.1.5 Summer Flounder

Fish and cephalopods constitute the majority of the adult summer founder diet (Bigelow and Schroeder 2002; Bowman et al. 2000; Link et al. 2002b). Link et al. (2002b) found that fish and cephalopods comprised over 80% of the diet in 8,938 stomachs sampled. Specific species included loligo squid, sand lance, Atlantic herring, and anchovies. Bowman et al. (2000) also suggested that round herring (*Etrumeus teres*) and illex squid are also consumed by adult summer flounder. The juvenile summer flounder is comprised of decapods, fish (silver hake and round herring), and mysids (Bowman et al. 2000).

5.1.6 Atlantic Halibut

Atlantic halibut feed primarily on a wide variety of fishes including skates, herring, capelin, cod, cusk, haddock, silver hake, redfish, sand lance, sculpins, wolffish, grenadiers, mackerel, and flounders (Bigelow and Schroeder 2002). Link et al. (2002b) suggested that gadids, crabs, small pelagic fish, and squids comprised the majority of the halibut diet. In 229 stomachs sampled, gadids accounted for 22% of the prey, followed by crabs (12%), illex squid (10%), silver hake (10%), and herring (<5%). Bowman et al. (2000) found a similar pattern with fish accounting for 65.7% by weight of the prey, followed by cephalopods (18.5%) and crustaceans (15.4%).

5.1.7 Pollock

The diet of juvenile pollock is primarily made up of euphausiids and crustaceans. In addition, amphipods, decapods, isopods, and copepods are also found in the diet of juvenile pollock (Bigelow and Schroeder 2002; Cargnelli et al. 1999). Adults prey mainly on pelagic crustaceans, followed by small fish and squids (Cargnelli et al. 1999). Euphausiids were observed as the dominant prey overall in the diet.

Fish and squid become more important to diet for pollock >61 cm. Atlantic herring were reported to be the most dominant fish prey (Cargnelli et al. 1999), and pollock were also reported to feed extensively on Atlantic herring spawn (Bigelow and Schroeder 2002). Other species of fish include cod, haddock, silver hake, sand lance, redfish, and pollock (Bigelow and Schroeder 2002). Bowman et al. (2000) reported a similar pattern for prey preference of pollock with crustaceans observed as the major prey overall and fish becoming a major prey in pollock >61 cm. However, despite previous studies stating that Atlantic herring was the major fish prey, no herring was found in the stomachs of pollock sampled in the study (Bowman et al. 2000).

5.1.8 Longhorn Sculpin

Longhorn sculpins are benthic scavengers, feeding on a wide variety of fish and invertebrates. The majority of their diet consists of crustaceans such as crabs. Fish are another group commonly found in their diet. Prey species include Atlantic herring, eels, sand lance, sculpins, eelpout, and yellowtail flounder as well as fish larvae. In addition, sculpins have been known to consume shrimp, amphipods, hydroids, muscles, squids, and annelid worms (Bigelow and Schroeder 2002).

5.2 MONKFISH

Monkfish are opportunistic predators, feeding on a variety of benthic and pelagic species (Steimle et al. 1999). The three main groups of prey were crustaceans, mollusks, and fish. Fish comprised the majority of prey species for all sizes of monkfish, while cephalopods were only important in monkfish >40 cm. For monkfish <20 cm, silver hake and sand lance were the major prey species. Silver hake became the dominant prey in monkfish >20 cm. Atlantic herring were also an important prey species in larger monkfish (Bowman et al. 2000). Other prey included spiny dogfish, skates, eels, mackerel, Atlantic menhaden, smelt, weakfish, cunner, tautog, black sea bass, butterfish, pufferfish, sculpins, sea raven, searobins, Atlantic tomcod, cod, haddock, hake, witch and other flounders, and squid (Steimle et al. 1999).

Monkfish diet also varies by region. Squid, clupeids, silver hake, and American plaice were more important to the monkfish diet in the Gulf of Maine. In contrast, little skates, red hake, monkfish, and sand lance were more important to the diet in southern New England (Bigelow and Schroeder 2002).

5.3 SPINY DOGFISH

Bowman et al. (1984) compiled a detailed study on the diet of spiny dogfish. In their study, 10,167 stomachs were sampled. Results suggested that fish were the most important prey group. Some of the major fish species found included Atlantic herring, Atlantic mackerel, sand lance, Atlantic cod, haddock, capelin, menhaden, river herring, red hake, silver hake, white hake, and spotted hake. In addition to fish, dogfish also prey on squid, crustaceans, ctenophores, jellyfish, polychaetes, sipunculids, amphipods, shrimps, crabs, snails, octopods, sea cucumbers, and bivalves (Bigelow and Schroeder 2002; Bowman et al. 1984; Bowman et al. 2000; McMillan and Morse 1999). It has been suggested that scallop viscera from scallop fishery discards has become an important component of the diet of dogfish as well (Bowman et al. 1984). This wide variety of prey species shows the opportunistic predatory nature of spiny dogfish.

Bowman et al. (1984) also describe a shift in the diet of spiny dogfish between 1969 and 1980 based on prey availability. Between 1969-1972, the abundance of Atlantic herring was declining. At the same time, Atlantic mackerel abundance was at high levels and constituted the highest percentage of the dogfish diet (23%) for the entire time series. Between 1973 and 1976, the biomass of mackerel began to decline, where as the biomass of herring began to show signs of recovery. This caused the amount of mackerel found in the diet of dogfish to decrease while the amount of herring in the diet increased. Also during this time, the two major squid species (loligo and illex) were increasing in biomass, and their representation in the diet of dogfish also increased. During the final time period of the study (1977-1980) herring and mackerel stocks were at low biomass levels, so was their contribution to the dogfish diet. These data show that the fluctuation in the diet of dogfish mirrors the changes in prey biomass in their environment. Spiny dogfish appear to consume whichever prey species is in greatest abundance and switch preference when that prey becomes less available.

Link et al. (2002a) modeled the consumption of prey by spiny dogfish in 1998. Table 9 summarizes the findings of the study and provides estimates of the amount and numbers consumed for several prey species.

Prey Species	Mean Weight Consumed (tons)	Estimated Number Consumed
Haddock	3	163,000
Atlantic Herring	67,660	848,000,000
Atlantic Cod	34	2,150,000
Yellowtail Flounder	553	5,420,000
Atlantic Mackerel	32,895	392,000,000
Silver Hake	15,326	346,000,000
Summer Flounder	1,084	19,900,000
American Plaice	411	9,180,000

Table 9 Mean Annual Consumption and Mean Estimate of Number Consumed by Spiny Dogfish (Link et al. 2002a)

5.4 PELAGIC SPECIES

5.4.1 Bluefin Tuna

Atlantic bluefin tuna migrate into the waters off New England during the warm months of the year to feed. Bluefin tuna are considered to be opportunistic predators, feeding on a wide variety of finfish, cephalopods, and crustaceans (Chase 2002). To quantify the diet of bluefin tuna in New England waters, Chase (2002) sampled 819 stomachs for prey preference. In the 568 stomachs that contained prey, 21 species of teleost, 2 species of elasmobranches, and roughly 9 different invertebrate species were found. Out of all the prey found, squid (loligo and illex), sand lance, Atlantic herring, Atlantic mackerel, and bluefish were most common and accounted for 88% of the total stomach contents (Chase 2002). Sand lance and Atlantic herring were observed to be the major prey for bluefin tuna in the Gulf of Maine.

In addition, Chase (2002) examined the diet of bluefin tuna in different regions of the Gulf of Maine. On Jefferies Ledge, Atlantic herring was the dominant prey, occurring in 74% of the stomach samples and accounting for 87% of the prey biomass. Squids (illex and loligo) were found in 50% of the samples but only accounted for 2% of the estimated prey biomass. Atlantic mackerel was the third most common prey in this area, occurring in 32% of the samples. Other prey also occurring in the bluefin tuna diet in this region included menhaden and pollock. On Stellwagen Bank, sand lance was the dominant prey item, occurring in 80% of the samples and accounting for 70% of the estimated prey biomass. Other notable prey items included Atlantic herring, squids, spiny dogfish, and mackerel. Sampling in Cape Cod Bay found no dominant prey species. The most common prey in this area was the fig sponge. Additional prey species included the spiny dogfish, bluefish, mackerel, skates, and herring.

Bluefin tuna in the Great South Channel were observed to primarily feed on sand lance, which were found in 62% of the stomachs sampled and accounted for 28% of the estimated prey biomass. Atlantic herring were the second most common prey species, occurring in 27% of the samples and accounting for 48% of the estimated prey biomass. Squid were also an important prey item, followed by bluefish and mackerel. Squid were the most important prey species in tuna sampled south of Martha's Vineyard. As a group, squid were found in 60.4% of the stomach samples and accounted for 12.9% of the total estimated prey biomass. Mackerel was the second most common prey, occurring in 33.3% of the samples and accounting for 56.2% of the prey weight. Atlantic herring, silver hake, and butterfish also constituted a portion of the diet in this region.

These data suggest that Atlantic bluefin tuna do not specialize in terms of specific prey. The regional differences in their diet may reflect regional differences in prey abundances. Tuna may therefore consume whatever prey are abundant in a given region at any given time.

5.4.2 Swordfish

Swordfish are another highly migratory pelagic fish species that occur in the northwest Atlantic. Diet studies have shown that swordfish feed primarily on illex squid, which constituted 67.4% of the diet (Bowman et al. 2000). The same study suggested that fish were also a major prey group, accounting for 32.5% of the diet. Fish prey includes Atlantic herring, Atlantic mackerel, menhaden, bluefish, silver hake, butterfish, argentines, and rattails (Bigelow and Schroeder 2002; Bowman et al. 2000).

5.4.3 Bluefish

Bluefish are found to consume a wide variety of prey, which includes 28 species of fish and 10 species of invertebrates (Bigelow and Schroeder 2002). The diet of adult bluefish is dominated by pelagic schooling species such as squid, clupeids, and butterfish (Bigelow and Schroeder 2002). Buckel et al. (1999) examined the stomachs of over 1,200 bluefish stomachs in 1994 and 1995. The dominant prey species were, in order of preference, butterfish, squid, round herring (*Etrumeus teres*), and Atlantic herring. Bowman et al. (2000) found similar results, suggesting squid are the main prey species followed by fish.

5.4.4 Striped Bass

Striped bass migrate north to New England waters in the spring and summer to feed. Prey preference was examined on these feeding grounds from 1997 to 2000. In all, 3,006 striped bass stomachs were sampled with 1,720 containing prey. Overall, fish and crustaceans were the most dominant prey groups in the diet (Nelson et al. 2003). Prey preference varied by geographic region. Atlantic herring were the most important fish prey in the north shore region, less important prey in the Cape Cod region, and absent in the diet in the Nantucket Sound region. This suggests that striped bass preference for herring is less in the southern regions than in northern regions. Conversely, preference for sand lance is greater in the two southern regions (Cape Cod Bay and Nantucket Sound) than the northern region (north shore region) (Nelson et al. 2003). Preference for squid also showed regional variation, as squid comprised a larger proportion of striped bass diet in the two southern regions.

Bigelow and Schroeder (2002) report that striped bass prey on eel, herring, silver hake, smelt, sand lance, squid, crabs, and lobsters.

5.4.5 Black Sea Bass

Black sea bass prey includes crustaceans, fish, mollusks, and worms (Bigelow and Schroeder 2002). Crustaceans are consumed by black sea bass of all sizes and are the dominant prey for sea bass <20cm (Bowman et al. 2000). Fish become the dominant prey for black sea bass >40cm, accounting for 69% of prey consumed. Specific species of fish prey are anchovies, herring, seahorse, pipefish, cusk-eel, scup, sand lance, and windowpane flounder (Bigelow and Schroeder 2002).

5.4.6 Atlantic Salmon

The diet of Atlantic salmon includes invertebrates, amphipods, euphausiids, terrestrial insects, gammarids, and fishes. The importance of fish to the diet increases as salmon grow. Specific species of fish prey include Atlantic herring, sand lance, alewife, haddock, rainbow smelt, capelin, mummichog, small sculpins, small Atlantic mackerel, and flatfishes (Bigelow and Schroeder 2002).

5.5 SHARKS AND SKATES

Small elasmobranchs such as spiny dogfish and skates have become dominant components of total biomass in the northwestern Atlantic (Link et al. 2002a). In contrast, the total biomass of groundfish stocks has decreased. It has been hypothesized that the increase in elasmobranch biomass may be a limiting factor to groundfish recovery. In Link et al. (2002a), two hypotheses were suggested as to how elasmobranchs may inhibit groundfish recovery: (1) the effects of direct predation on groundfish by elasmobranchs, and (2) elasmobranchs inhibit groundfish recovery through competition. The first hypothesis was examined in the Link et al. (2002a). Researchers examined the amount of groundfish in the diet of several small elasmobranch species. Research suggested that groundfish, with the exception of silver hake, were not commonly found in the diet of small sharks and skates, occurring in less than 0.2% of the stomachs sampled. Silver hake was more commonly found in the diet of small sharks and skates, but still only occurred in less than 1% of the stomachs sampled (Link et al. 2002a). The major components of the elasmobranch diet were pelagic fish and crustaceans. Researchers concluded that predation on groundfish by elasmobranchs was not strong and thus not a limiting factor to groundfish recovery.

Fogarty and Murawski (1998) also investigated the apparent shift in biomass dominance from finfish to elasmobranchs in the northeast region. In this study, the authors examined the potential of predation by groundfish in regulating elasmobranch biomass. If groundfish are significant consumers of elasmobranchs, then a decrease in groundfish biomass would cause a decrease in predation on elasmobranchs and thus an increase in elasmobranch biomass. The results of the study suggested that this was not the case. In fact, there was no significant predation by groundfish on small elasmobranchs. The authors concluded that the switch in species dominance was not due to direct predation, but by a decrease in competition with groundfish for prey. Groundfish and elasmobranchs are both significant consumers of pelagic fish. With the decline in groundfish biomass there was less competition for prey and thus more resources available for elasmobranchs.

5.5.1 Porbeagle Shark

The diet of porbeagle sharks in the Gulf of Maine consists of mackerel, herring, other sharks, other small fish and squids (Bigelow and Schroeder 2002). Bowman et al. (2000) reported that cephalopods (illex squid) were the most dominant prey, found in 99% of the stomachs sampled.

5.5.2 Thresher Shark

Thresher sharks prey mainly on schooling fishes like herring, menhaden, bluefish, Atlantic saury, sand lance, and mackerel, as well as squids (Bigelow and Schroeder 2002). Bowman et al. (2000) report that bony fish comprised 97% of the diet. Sand lance and bluefish were seen as the dominant prey species.

5.5.3 Blue Shark

Fish constitute the majority of the diet of blue sharks, with bluefish and gadids being the dominant fish prey species. Other fish prey include mackerel, herring, and lancetfish. Cephalopods are another major prey group, representing 1/3 of the diet of blue sharks (Bowman et al. 2000).

5.5.4 Smooth Hammerhead Shark

Fish comprise 97-100% of the diet of smooth hammerhead sharks. Dolphin fish and Atlantic herring were the two most dominant species, accounting for 64% and 17% of the diet respectively. Butterfish and sea robins were also major prey species (Bowman et al. 2000).

5.5.5 Dusky Shark

Fish were the major prey species of the dusky shark, followed by elasmobranches, crustaceans, and squids. Specific fish prey include herring, menhaden, eels, anchovies, monkfish, hakes, black sea bass, scup, sand lance, bluefish, croaker, mackerel, tuna, and flat fishes (Bowman et al. 2000).

5.5.6 Barndoor Skate

Barndoor skates are benthic feeders and prey on invertebrates and fish. Invertebrate prey include polychaetes, bivalves, mollusks, gastropods, squids, and crustaceans. Fish prey include Atlantic herring, spiny dogfish, alewife, menhaden, hakes, sculpins, cunner, sand lance, and butterfish. The diet also varies according to the size of the barndoor skate. Smaller individuals feed mainly on benthic invertebrates while larger individuals feed on larger prey such as clams, squids, crabs, and fish (Packer et al. 2003). Bowman et al. (2000) describe a different diet for barndoor skates. This report suggested that barndoor skates feed almost exclusively in decapod crustaceans.

5.5.7 Thorny Skate

The diet of the thorny skate changes with size. The diets of thorny skates <60cm consists mainly of invertebrates such as annelids, euphausiids, decapods, amphipods, and polychaetes (Bigelow and Schroeder 2002; Bowman et al. 2000). The diet of thorny skates >60cm is comprised mainly of fish and squid species. Bowman et al. (2000) report that Atlantic herring and other clupea species are major prey species. In addition, sand lance and wrymouth are also considered important prey species. Bigelow and Schroeder (2002) add that mackerel, wolffish, flounders, sculpins, and redfish, are also preyed upon by thorny skates (Bowman et al. 2000).

5.5.8 Little Skate

The diet of little skates less than 30 cm consists mainly of invertebrates such as decapod crustaceans and amphipods (Bowman et al. 2000). The diet of adult little skates (>30 cm) include larger prey like fish, shrimp, crabs, and squids. Fish prey species includes sand lance, Atlantic herring, alewives, cunner, silver hake, tomcod, and silversides (Bowman et al. 2000; Packer et al. 2003).

5.5.9 Winter Skate

The most frequently-consumed prey of winter skates are amphipods and polychaetes, followed by decapods, isopods, bivalves, and fishes (Packer et al. 2003). By total weight of prey ingested, amphipods, decapods, and fish are the most important prey, with fish being especially important in large winter skates (Packer et al. 2003). Winter skates feed on a wide variety of fish such as Atlantic herring, alewives, blueback herring, smaller skates, eels, menhaden, sand lance, mackerel, butterfish, silver hake, cunner, sculpins, and tomcod (Bigelow and Schroeder 2002; Packer et al. 2003).

Link et al. (2002a) modeled the consumption of prey by winter skates in 1998. Table 10 describes the findings of the study and provides estimates of the amount and numbers consumed for several prey species.

Prey species	Mean weight consumed (tons)	Estimated number consumed
Haddock	0.2	NA
Atlantic herring	928	9,220,000
Atlantic cod	0.2	NA
Yellowtail flounder	0.3	NA
Atlantic mackerel	340	3,130,000
Silver hake	188	5,830,000
Summer flounder	79	1,240,000
American plaice	14	2,990,000

Table 10 Mean Annual Consumption and Mean Estimate of Number Consumed by Winter Skates (Link et al. 2002a)

5.6 INVERTEBRATES AND MISCELLANEOUS FISH SPECIES

5.6.1 Short-Finned Squid (Illex)

A dietary study was conducted based on otoliths found in the stomach of short-finned squid. The results only characterize the amount of fish prey ingested, as fish would be the only species to leave otoliths. Based on the results, Atlantic cod comprised the majority (61%) of otoliths found in the stomachs of squid. Sand lance accounted for 16% the otoliths. Arctic cod represented 8% of the otoliths. Various hake species totaled 5% of the otoliths found. Capelin and Atlantic herring both accounted for 3% of the otoliths found in the diet of short-finned squid (Dawe et al. 1997).

Cargnelli et al. (1999) described the diet of short-finned squid in the essential fish habitat source document. The report suggests that short-finned squid feed mainly on fish, other squids, and crustaceans. Fish prey described in the report include Atlantic cod, Arctic cod, red fish, sand lance, Atlantic herring, Atlantic mackerel, haddock, sculpins, capelin, and smelt. It should be noted that the fish species consumed were in their early life stages.

5.6.2 Long-Finned Squid (Loligo)

In the essential fish habitat source document for long-finned squid, Cargnelli et al. (1999) state that the diet of long-finned squid changes with size. Smaller squid feed mainly on plankton. Larger individuals feed primarily on crustaceans and fish. Typical prey of adult long-finned squid include crabs, shrimp, squid, silver hake, mackerel, herring, sand lance, menhaden, weakfish, and silversides.

5.6.3 Miscellaneous Fish

Several other fish were identified as consumers of Atlantic herring in Bigelow and Schroeder (2002). Descriptions of each diet are mainly anecdotal with Atlantic herring comprising only a small portion of the diet. The diet of tilefish is mainly comprised of invertebrates such as shrimp, crabs, mollusks, brittle stars, sea cucumber, polychaetes, urchins, anemones, and tunicates. Fish, including Atlantic herring, are an occasional component of the diet and include Atlantic herring.

Alewife are particulate feeders that mainly consume zooplankton. They also prey on small fish such as Atlantic herring, eel, sand lance, cunner, and other alewife. Hickory shad is a piscivorous fish that feeds on other smaller fish including sand lance, herring, anchovies, cunner, and scup. They also consume squids, fish eggs, pelagic crustaceans, and small crabs. Atlantic tomcod feed primarily on small crustaceans such as squids and mollusks. They also consume the larvae of fish like alewife, herring, menhaden, sand lance, anchovies, smelt, mummichog, cunner, and winter flounder.

5.7 MARINE MAMMALS

Marine mammals are known to consume significant amounts of prey in the northwest Atlantic. Kenney et al. (1997) estimated the amount of prey consumed by marine mammals in the northeast continental shelf. Consumption was estimated based on known metabolic requirements and seasonal cetacean abundances. Prey was grouped into three categories: fish, squid, and zooplankton. Overall, cetaceans were estimated to consume 1.9 million tons of prey annually. This includes 1.3 million tons of fish, 337,000 tons of squid, and 244,000 tons of zooplankton (Kenney et al. 1997). This level of consumption was suggested to be greater than removals from commercial fisheries and thus shows that marine mammals are important consumers in the ecosystem.

Diet composition was examined for 18 different marine mammal species in four regions (Gulf of Maine, Georges Bank, southern New England, and Mid-Atlantic Bight). Table 11 illustrates the percent composition of each of the three prey groups for each marine mammal species modeled. Table 12 provides the estimated amount consumed broken down by region and season.

	Diet composition (%)		
Predator	**Fish**	**Squid**	**Zooplankton**
Right whale	0	0	100
Fin whale	90	0	10
Sei whales	0	0	100
Minke whale	95	0	5
Humpback whale	95	0	5
Sperm whale	20	80	0
Bottlenose whale	5	95	0
Goose-beaked whale	0	100	0
Beaked whale	0	100	0
Pilot whale	10	90	0
Risso’s dolphin	0	100	0
Bottlenose dolphin	100	0	0
White-sided dolphin	90	10	0
Common dolphin	85	15	0
Striped dolphin	40	60	0
Spotted dolphin	20	80	0
Spinner dolphin	20	80	0
Harbor porpoise	95	5	0

Table 11 Cetacean Species of the USA Northeast Shelf with Estimated Dietary Composition (Kenney et al. 1997)

Region	Season	Fish	Squid	Zooplankton	Total
Gulf of Maine	Winter	5,808	767	0	6,575
	Spring	156,780	3,081	33,382	193,243
	Summer	265,988	2,771	39,534	308,293
	Autumn	118,249	3,001	8,428	129,678
	Total	546,825	9,620	81,344	637,789
Georges Bank	Winter	35,077	10,627	17,694	63,398
	Spring	191,002	33,991	78,912	303,905
	Summer	65,013	40,981	13,318	119,312
	Autumn	40,485	14,475	16,969	81,929
	Total	331,577	100,074	126,893	558,544
Southern New England	Winter	42,658	7,760	3,275	53,693
	Spring	94,703	25,595	8,833	129,131
	Summer	93,998	34,300	9,611	137,909
	Autumn	24,406	9,909	2,038	36,353
	Total	255,765	77,564	23,757	357,086
Mid-Atlantic Bight	Winter	30,774	20,280	2,468	53,522
	Spring	71,360	57,417	5,952	134,729
	Summer	24,761	32,950	1,170	58,881
	Autumn	27,718	39,580	1,956	69,254
	Total	154,613	150,227	11,546	316,389
	Total	1,288,780	337,485	243,540	1,869,805

Table 12 Estimated Consumption of Prey (tons) by Cetaceans in Four Regions of the USA Northeastern Shelf (Kenney et al. 1997)

5.7.1 Marine Mammals in the Gulf of Maine (GOM)

5.7.1.1 Harbor Seals

Illex squid were found to be the primary prey species of harbor seals in southern New England. Illex squid was found in 58.4% of all harbor seal stomachs sampled. Haddock, silver hake, and winter flounder were the second most common species, occurring in 5.6% of the stomachs sampled. Loligo squid, sand lance, limpets, and mussels each occurred in 3.7% of the stomachs sampled. Additionally, Atlantic herring and pollock were found to comprise a minor portion of the diet, occurring in 1.8% of the stomachs sampled (Selzer et al. 1986).

5.7.1.2 Harbor Porpoises

Harbor porpoises are considered to comprise a single stock in the northwest Atlantic. In the spring and summer, harbor porpoises feed in the waters of the Bay of Fundy. In the fall, they move south to feed in the Gulf of Maine. The Gulf of Maine diet study was conducted by sampling 95 porpoises taken by gillnets during the fall of 1989 and 1991-1994. Diet was analyzed by sex, maturity stage, and reproductive condition of the animal at the time of capture (Gannon et al. 1997).

Overall, in non-calf porpoises, Atlantic herring was found to be the most dominant prey, occurring in 78% of the stomachs sampled and accounting for 44% of the total mass of prey ingested. Silver hake was the second most common species, occurring in 68% of the stomachs sampled and the third most abundant, accounting for 22% of the total mass ingested. White hake was the fourth most common, occurring on 29% of the samples, and the second most abundant species in the diet, accounting for 26% of the total mass of prey ingested. Pearlsides were very common in the diet (38% occurrence), but accounted for only 3% of the total mass ingested. Illex squid, northern krill, butterfish, and redfish were also all common prey species found in the diet of harbor porpoises (Gannon et al. 1997).

In calves, pearlsides, krill, and silver hake were the most common prey found in the diet, each occurring in 54% of the stomachs sampled. Of these three species, pearlsides were the most abundant in the diet, accounting for 53% of the total mass ingested. Atlantic herring, butterfish, redfish, and white hake were the second most common group of species found in the diet, along with milk, each occurring in between 15-23% of the stomachs sampled. Of these, herring was the most abundant by mass, accounting for 11% of the total mass ingested (Gannon et al. 1997).

5.7.1.3 Pilot Whales

Overholtz and Waring (1991) reported on the diet composition of pilot whales in the Mid-Atlantic Bight in the spring of 1989. It was reported that pilot whales feed primarily on Atlantic mackerel and long-finned squid. Various hake species were also found in the diet. However, they are either of little importance, or may be consumed as a secondary prey species. A secondary prey species is a species found in the diet that was initially consumed by another species also found in the diet.

Gannon et al. (1997a and 1997b) also conducted studies examining the diet of pilot whales. These studies differ than the previous study in that they account for partially digested prey material. In the first study (1997a), 30 pilot whale stomachs were sampled. Based on the composition from intact prey, it was suggested that the main prey was Atlantic mackerel, followed by long-finned squid, Atlantic herring, silver hake, and short-finned squid. When partially digested material was taken into account, squids were seen as the dominant prey species, followed by mackerel, herring, silver hake, dogfish, and lanternfish.

In the second study (Gannon et al. 1997b), eight pilot whales were sampled from the Mid-Atlantic region. Based on both intact and partially digested material, squids (both long-finned and short-finned) were seen as the dominant prey. Additionally, herring, mackerel, dogfish, white hake, and silver hake were also consumed.

5.7.2 Marine Mammals in Canadian Waters

Hammill and Stenson (2000) estimated the consumption rates for four pinniped species in Canadian waters. The specific rates of consumption for each species are provided in the next four sub-sections. The population size was estimated for each species from 1990 to 1996 and is provided in Table 13. Consumption of Atlantic herring was also estimated by size group, results are provided in Table 14. In addition, prey consumption was estimated for all four species combined for the same time period. A list of each prey species and the amount of consumed is provided in Table 15.

Year	Harp seal	Hooded seal	Grey seal	Harbor seal
1990	4,193,200	469,900	96,900	22,800
1991	4,355,000	493,000	106,600	24,100
1992	4,556,200	517,200	117,400	25,500
1993	4,694,200	542,700	129,000	27,000
1994	4,915,800	569,400	142,400	28,500
1995	5,075,600	597,300	156,100	30,100
1996	5,236,800	626,700	173,500	31,900

Table 13 Estimated Population Abundance (Number of Animals) of Harp, Hooded, Grey, and Harbor Seals in Atlantic Canada Between 1990-1996 (Hammill and Stenson 2000)

	<30 cm		>30 cm		Total	
Seal species	**tons**	**% of total**	**tons**	**% of total**	**tons**	**% of total**
Harp	16,984	95	894	5	17,878	64.3
Hooded	901	72	351	28	1,252	4.5
Grey	6,938	84	1,322	16	8,260	29.7
Harbor	268	62.9	158	37.1	426	1.5
Total	25,091	90.2	2,725	9.8	27,816	100

Table 14 Consumption (tons) of Atlantic Herring by Seals in 1996 in the Northern Gulf of St. Lawrence by Size Group of Prey (Hammill and Stenson 2000)

	Year						
Prey species	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**
Capelin	825,560	866,841	894,200	924,671	968,402	1,001,626	1,037,741
Sand lance	352,640	371,153	392,630	411,984	437,481	459,436	484,764
Pleuronectidae	211,743	222,973	231,051	240,167	252,380	262,489	273,548
Greenland halibut	158,737	165,878	173,812	181,266	190,037	198,197	206,895
Atlantic cod	132,426	140,858	147,349	155,258	164,753	173,731	183,740
Arctic cod	146,104	151,665	158,514	163,630	171,306	177,115	183,049
Redfish	105,279	112,491	114,041	118,552	124,266	129,175	134,489
Atlantic herring	60,320	64,108	67,147	70,704	75,093	79,177	83,688
Witch flounder	42,540	44,632	46,826	49,129	51,545	54,079	56,738
Grenadier	19,557	20,732	21,980	23,330	24,781	26,325	28,005
American plaice	13,260	13,798	14,451	14,967	15,710	16,290	16,905
Sculpin	12,931	13,597	14,016	14,506	15,200	15,742	16,321
Blue hake	11,524	12,090	12,684	13,308	13,962	14,648	15,368
Mackerel	8,842	9,607	10,410	11,340	12,369	13,445	14,706
Silver hake	8,076	8,889	9,580	10,462	11,468	12,543	13,761
Windowpane	10,654	11,029	11,480	11,915	12,478	12,949	13,458
Gadus sp.	5,902	6,204	6,349	6,554	6,843	7,094	7,356
Lumpfish	3,812	4,111	4,417	4,775	5,168	5,568	6,044
Lancetfish	4,390	4,606	4,832	5,070	5,319	5,580	5,855
Wolffish	3,754	4,029	4,306	4,632	4,988	5,343	5,770
White hake	4,363	4,549	4,742	4,905	5,141	5,317	5,512
Pollock	2,313	2,538	2,785	3,062	3,371	3,709	4,091
Haddock	2,766	2,979	3,009	3,140	3,304	3,446	3,605
Atlantic salmon	2,467	2,652	2,688	2,807	2,955	3,084	3,229
Ocean pout	1,649	1,770	1,891	2,033	2,189	2,345	2,531
Eelpout	1,139	1,196	1,256	1,319	1,385	1,454	1,528
Yellowtail flounder	956	1,027	1,098	1,182	1,274	1,365	1,475
Alewife	687	735	779	832	891	948	1,019
Skates	554	595	637	686	739	793	857
Rainbow smelt	189	200	204	212	222	230	238
Winter flounder	110	117	125	133	142	151	162
Cunner	52	56	59	64	68	73	78
Other fish	225,327	234,624	244,421	252,558	264,405	273,650	283,132
Total fish	2,380,623	2,502,329	2,603,769	2,709,153	2,849,635	2,967,117	3,095,658
Shrimp	421,680	437,879	457,158	471,688	493,761	510,215	527,202
Squid	56,823	59,963	62,937	66,186	69,842	73,510	77,442
Euphausiis	4,761	4,943	5,166	5,331	5,582	5,768	5,957
Other invertebrates	239,262	249,449	259,317	267,755	280,324	289,602	299,585
Total invertebrates	722,526	752,234	784,578	810,960	849,509	879,095	910,186
Total Prey	3,103,149	3,254,563	3,388,347	3,520,113	3,699,144	3,846,212	4,005,844

Table 15 Estimated Prey Consumption (tons) by Harp, Hooded, Grey, and Harbor Seals in Atlantic Canada, 1990-1996 (Hammill and Stenson 2000)

5.7.2.1 Harp Seals

Modeling consumption was utilized to quantify the amount and type of prey consumed by several pinniped species in the Atlantic waters off of Canada. Hammill and Stenson (2000) used information on energy requirements, population size, diet composition, and seasonal changes in distribution to generate these estimates. A complete list of prey species consumed by harp seals, hooded seals, grey seals, and harbor seals, is provided in Table 15. This section addresses the major prey consumed by harp seals only. Table 16 provides the estimated tons consumed in 1996 for the major prey species of harp seals in Canadian waters.

Prey Species	Amount Consumed (tons)
Capelin	1,023,060
Arctic cod	176,833
Sand Lance	351,300
Greenland halibut	72,996
Atlantic cod	90,924
Atlantic herring	48,858
Redfish	111,785
Total	1,875,756

Table 16 Estimated Consumption of Some of the Important Prey Items Consumed by Harp Seals in 1996 (Hammill and Stenson 2000)

5.7.2.2 Hooded Seals

Modeling consumption was utilized to quantify the amount and type of prey consumed by several pinniped species in the Atlantic waters off of Canada. Hammill and Stenson (2000) used information on energy requirements, population size, diet composition, and seasonal changes in distribution to generate these estimates. A complete list of prey species consumed by harp seals, hooded seals, grey seals, and harbor seals, is provided in Table 15. This section addresses the major prey consumed by hooded seals only. Table 17 provides the estimated tons consumed in 1996 for the major prey species of hooded seals in Canadian waters.

Prey Species	Amount Consumed (tons)
Capelin	3,423
Arctic cod	6,217
Sand Lance	0
Greenland halibut	133,723
Atlantic cod	37,472
Atlantic herring	6,003
Redfish	20,908
Total	207,746

Table 17 Estimated Consumption of Some of the Important Prey Items Consumed by Hooded Seals in 1996 (Hammill and Stenson 2000)

5.7.2.3 Grey Seals

Modeling consumption was utilized to quantify the amount and type of prey consumed by several pinniped species in the Atlantic waters off of Canada. Hammill and Stenson (2000) used information on energy requirements, population size, diet composition, and seasonal changes in distribution to generate these estimates. A complete list of prey species consumed by harp seals, hooded seals, grey seals, and harbor seals, is provided in Table 15. This section addresses the major prey consumed by grey seals only. Table 18 provides the estimated tons consumed in 1996 for the major prey species of grey seals in Canadian waters.

Prey Species	Amount Consumed (tons)
Capelin	10,900
Arctic cod	0
Sand Lance	133,464
Greenland halibut	176
Atlantic cod	54,971
Atlantic herring	27,228
Redfish	1,768
Total	228,507

Table 18 Estimated Consumption of Some of the Important Prey Items Consumed by Grey Seals in 1996 (Hammill and Stenson 2000)

In addition to modeling the consumption rates of grey seals, diet analysis was conducted on 528 stomachs collected on the Scotian Shelf (Bowen et al. 1993). From this analysis, 22 different species were identified from 143 stomachs that contained food. The majority of the prey was herring, cod, sand lance, silver hake, and squid. Together, this group made up 88% of the estimated weight of prey consumed (Bowen et al. 1993). Atlantic herring was the most abundant of these species (38.5% by weight), followed by cod (19.2%) then sand lance (12.8%). Other species found in the diet in lesser amounts included mackerel, haddock, pollock, winter flounder, yellowtail flounder, ocean pout, cunner, cusk, butterfish, skate, and sea raven (Bowen et al. 1993).

5.7.2.4 Harbor Seals

Modeling consumption was utilized to quantify the amount and type of prey consumed by several pinniped species in the Atlantic waters off of Canada. Hammill and Stenson (2000) used information on energy requirements, population size, diet composition, and seasonal changes in distribution to generate these estimates. A complete list of prey species consumed by harp seals, hooded seals, grey seals, and harbor seals, is provided in Table 15. This section addresses the major prey consumed by harp seals only. Table 19 provides the estimated tons consumed in 1996 for the major prey species of harp seals in Canadian waters.

Prey Species	Amount Consumed (tons)
Capelin	361
Arctic cod	0
Sand Lance	0
Greenland halibut	0
Atlantic cod	374
Atlantic herring	1,599
Redfish	26
Total	2,360

Table 19 Estimated Consumption of Some of the Important Prey Items Consumed by Harbor Seals in 1996 (Hammill and Stenson 2000)

5.7.2.5 Harbor Porpoises

Harbor porpoises inhabit the waters of the Bay of Fundy in the spring and summer and move into the Gulf of Maine in the fall. As stated previously, harbor porpoises are thought to comprise a single stock in the northwest Atlantic. Summertime feeding was analyzed from 160 porpoises, which were caught in gillnets from June to September 1985-1987. Eleven prey species were obtained from the 127 stomachs that contained food. Atlantic herring was the most dominant prey species in the diet of harbor porpoises, accounting for 64% of the total mass ingested. Atlantic cod and silver hake were the second dominant species, accounting for 13.7% and 18.6% of the total mass ingested respectively. Mackerel, alewife, white hake, winter flounder, and squid also made up a portion, although minor, of the diet.

5.7.3 Modeling Marine Mammal Consumption

Overholtz et al. (1991) used diet information and predator and prey abundance to estimate the amount consumed of the major prey species by several key predators in the northwest Atlantic. Values presented in Table 20 are estimates of average consumption (tons) between 1988-1992.

	Predator										
Prey	Humpback	Finback	Minke	Pilot	Grampus	Bottle-nose dolphin	White-sided dolphin	Harbor porpoise	Common dolphin	Harbor seal	Total
Sand Lance	9,907	37,932	607	2,834	0	0	428	470	633	2,952	55,763
Mackerel	2,423	9,995	110	13,413	311	336	560	111	8,855	450	36,264
Herring	2,586	9,959	366	2,803	0	0	1,487	684	0	1,433	19,318
Whiting (north)	0	0	0	0	0	0	1,984	954	0	449	3,387
Whiting (south)	0	0	0	3,130	333	190	0	0	1,798	0	5,451
Total	14,915	57,886	1,082	22,180	664	527	4,459	2,218	10,986	5,284	120,182

Table 20 Average Consumption (tons) By Marine Mammals on the Five Prey Species in the Pelagic Ecosystem for 1988-1992 (Overholtz et al. 1991)

5.8 MARINE BIRDS

Little is known about what effect predation by marine birds has on the marine environment. References on the subject have been mainly qualitative, with no specific consumption rates provided (Axelsen et al. 2001; Bigelow and Schroeder 2002; Hislop and MacDonald 1989; Reid et al. 1999). Overholtz et al. (1991) estimated the amount of prey consumed by seabirds by taking into account seasonal estimates of seabird abundance and daily consumption rates for the different bird species between 1988-1992. The model looked at three groups of seabirds (northern gannet, shearwater, and black-legged kittiwakes) and four prey species (sandeel, Atlantic mackerel, Atlantic herring, and silver hake). Silver hake are separated into northern and southern stocks. The estimates are listed in Table 21 in average tons consumed.

Prey	Predator			Total
	Northern gannet	Shearwater	Black-legged kittiwake	
Sandeel	0	992	3,332	4,324
Atlantic mackerel	10,328	90	26	10,433
Atlantic herring	2,827	247	0	3,074
Silver hake (north)	0	0	83	83
Silver hake (south)	1,443	0	0	1,443
Total consumption	14,597	1,329	3,439	19,365

Table 21 Average Consumption (tons) by Seabirds on the Five Prey Species in the Pelagic Ecosystem for 1988-1992 (Overholtz et al. 1991)

6.0 ATLANTIC HERRING AS A PREDATOR

Atlantic herring are zooplanktivorous filter feeders whose diet varies according to fish size, season, and geographic region (Bigelow and Schroeder 2002; Reid et al. 1999). Early life stages of herring feed on nauplii, copepods, copepod eggs, mollusk larvae, diatoms, and other algae (Bigelow and Schroeder 2002). Juvenile Atlantic herring feed mainly on large copepods, but also feed opportunistically on a wide variety of organisms including amphipods, euphausiids, mysids, cladocerans, larvae of barnacles, bivalves, and crustaceans, arrow worms, ctenophores, and pteropods (Bigelow and Schroeder 2002; Bowman et al. 2000).

Sherman and Perkins (1971) examined the diet of juvenile herring in the waters of coastal Maine. Sampling was conducted on 256 juvenile fish throughout all seasons of the year. Fifteen zooplankton groups were found in the stomachs of juvenile herring. However, only five of the groups occurred in greater than 20% of the samples - copepods, larval decapods, larval cirripeds, larval pelecypods, and cladocerans. The occurrence of these groups also varied seasonally. Copepods were common in the herring diet year-round. Larval decapods were mainly consumed in the spring. Larval cirripeds were dominant in the spring and summer. Larval pelecypods were common in the summer. Finally, cladocerans mainly occurred in the herring diet during the summer and autumn (Sherman and Perkins 1971).

There appears to be a shift in the diet of Atlantic herring from age 2 to age 3. During this time, herring shift from a predominantly copepod diet to predominantly euphausiid diet. This marks a change to an adult diet that consists mainly of euphausiids. In addition, adult herring also consume chaetognaths, molluscan larvae, fish eggs, and annelids (Bigelow and Schroeder 2002; Reid et al. 1999).

Garrison et al. (2000) examine the possibility that both Atlantic herring and Atlantic mackerel may impact the survival of larval gadids on the southern flank of Georges Bank. Data is based on the possibility of spatial and temporal overlap between pelagic fish species and larval gadids and not on any empirical data. Researchers suggest that the only possibility of spatial and temporal overlap occurs between herring and larval haddock. Mackerel does not overlap spatially and temporally with any larval gadid and other than haddock, herring does not overlap either. Due to the spatial and temporal overlap between herring and larval haddock, the possibility of predation was suggested. However, no data exist to support this.

7.0 SUMMARY AND CONCLUSIONS

The ecosystem in the northwest Atlantic has changed in terms of species dominance over the last four decades. During this time, important commercial groundfish species declined in biomass, being replaced by elasmobranches and pelagic fish. The increase in Atlantic herring biomass was attributed, in part, to a decrease in predation from declining fish species (Overholtz et al. 2000). As fish stocks like groundfish continue to rebound, there is potential for increased predation pressure on herring. Understanding the importance of Atlantic herring to the diet of other commercially-important fish species, as well as other predators, is necessary to determine the impacts of future predation on Atlantic herring.

This paper confirms that Atlantic herring is an important prey species for many species of fish, marine mammals, and marine birds. However, the degree of predation by these species on herring varies significantly, and it is difficult to accurately quantify predation. Major fish predators of Atlantic herring include Atlantic cod, silver hake, spiny dogfish, bluefin tuna, bluefish, striped bass, and large winter skates. Predation on herring also occurs by other fish species including haddock, American plaice, summer flounder, Atlantic halibut, monkfish, swordfish, pollock, and several species of sharks and skates. Major marine mammal predators of herring include harbor porpoises, fin back whales, humpback whales, and pilot whales. Additionally, several species of seals have also been documented to be significant predators of Atlantic herring. While little data exist, marine birds are known to consume large amounts of Atlantic herring. Marine bird predators include northern gannet and shearwater gulls.

Table 22 summarizes available quantitative estimates of herring consumption by important predators based on all of the literature that was reviewed during the preparation of this paper. While this is not an exhaustive list of predator species, it represents a summary of available quantitative data regarding the importance of herring as a forage species in the northwest Atlantic ecosystem. As indicated in Table 22, several estimates exist for some predator species; these estimates result from different approaches to modeling the predators' behavior and sampling the predators' diet. The data presented in Table 22 are not intended to represent absolute amounts of herring consumed by the predator species, but instead are intended to provide some perspective on how to quantify the importance of herring as a forage species based on available information. Note that the time periods associated with the estimates in Table 22 reflect when a particular study or modeling exercise was undertaken and what data may have been available at that time. As a result, some estimates only reflect one specific year (1996, for example).

Predator Species	**Herring Consumption Estimates**
Atlantic Cod	→173 tons Estimated from 1988-1992 (Overholtz et al. 1991) →12% by prey weight in the diet estimated from 1986-1990 (Link and Garrison 2002) →25% by weight of prey in the diet estimated from 1991-1998 (Link and Garrison 2002)
Silver Hake (N)	→457 tons Estimated from 1988-1992 (Overholtz et al. 1991)
Silver Hake (S)	→1013 tons Estimated from 1988-1992 (Overholtz et al. 1991)
Spiny Dogfish	→4,255 tons Estimated from 1988-1992 (Overholtz et al. 1991) →67,000 tons in 1998 (Link et al. 2002b)
Juvenile Haddock	→< 2% of the diet (Bowman 1981)
Adult Haddock	→No herring documented in the diet
Summer Flounder	→5.5% by weight for fish 41-45cm (Bowman et al. 2000) →13.4% by weight for fish 56-60cm (Bowman et al. 2000) →8% by weight over the last 10 years (Link et al. 2002a)
Atlantic Halibut	→11.1% of the diet for fish 41-50cm (Bowman et al. 2000) →<0.1% of the diet for fish 41-70cm (Bowman et al. 2000) →4% of the total diet (Link et al. 2002a)
Monkfish	>90cm: 0.8% of the diet (Bowman et al. 2000)
Bluefin Tuna	Sampling from 1988-1992: (Chase 2002) →Jefferies Ledge: 87.2% by weight of the diet, →Stellwagen Bank: 27.3% by weight →Great South Channel: 48.4% by weight →Cape Cod Bay: 2.1% by weight →Martha's Vineyard: 2.5% by weight
Swordfish	→0.2% by weight of the diet (Bowman et al. 2000)
Bluefish	Adult Bluefish (Buckel et al. 1999) →1994: 11.3% by weight →1995: 17.6% by weight
Striped Bass	1997-2000: (Nelson et al. 2003) →North shore: 5.8% by weight →Cape Cod Bay: 0.1% by weight →Nantucket Sound: 0% by weight

Table 22 Estimated Consumption Rates of Atlantic Herring by Several Known Predators in the Northwest Atlantic

Predator Species	Herring Consumption Estimates
Black Sea Bass	→2.3% by weight fir fish 21-25cm (Bowman et al. 2000)
Blue Shark	→0.4% by weight (Bowman et al. 2000)
Smooth Hammerhead	→17% by weight (Bowman et al. 2000)
Thorny Skate	→63.5% by weight for fish 61-70cm →20.8% by weight for fish >90cm (Bowman et al. 2000)
Winter Skate	→928 tons in 1998 (Link et al. (2002a)
Short-finned Squid	→3% of otoliths found in the stomachs (Dawe et al. 1997)
Harbor Seals	→Found in 1.8% of the stomachs sampled (Seltzer et al. 1986) →1,433 tons Average between 1988-1992 (Overholtz et al. 1991)
Harbor Porpoises (autumn distribution)	→44% by weight (Gannon et al. 1998) →684 tons Average between 1988-1992 (Overholtz et al. 1991)
Pilot Whales	→ 0% (Overholtz and Waring (1991) → Occurred in 12.5% of the samples (Gannon et al. 1997b) →Occurred in 18.2% of the samples (Gannon et al. 1997a) →2,803 tons Average between 1988-1992 (Overholtz et al. 1991)
Humpback Whales	→2,586 tons Average between 1988-1992 (Overholtz et al. 1991)
FinBack Whales	→9,959 tons Average between 1988-1992 (Overholtz et al. 1991)
Minke Whales	→366 tons Average between 1988-1992 (Overholtz et al. 1991)
White-Sided Dolphin	→1,487 tons Average between 1988-1992 (Overholtz et al. 1991)
Northern Gannet (Marine Birds)	→2827 tons Average between 1988-1992 (Overholtz et al. 1991)
Shearwater (Marine Birds)	→247 tons Average between 1988-1992 (Overholtz et al. 1991)

Table 22 Estimated Consumption Rates of Atlantic Herring by Several Known Predators in the Northwest Atlantic

Adult Atlantic herring diet consists mainly of euphausiids. In addition, herring also consume chaetognaths, mollusks larvae, fish eggs, and annelids. For further discussion of this issue, see Section 6.0.

Throughout available literature regarding the importance of herring as a forage species, several other species were identified as major prey species in the ecosystem. These included, but are not limited to, squid (illex and loligo), sand lance, silver hake, and mackerel. These prey species, in combination with Atlantic herring, compose the majority of prey for several key species such as cod, tuna, sharks, marine mammals, and birds. This suggests that prey dependence may not be limited to herring alone. Rather, many species make up the forage base in the northwest Atlantic.

Similarly, many major predators of herring are opportunistic and feed on many species of prey, depending on what is readily available. Table 7 summarizes available information about other prey species and their major predators. For example, monkfish is an important predator with a feeding behavior/pattern that is recognized as opportunistic. Monkfish prey on a combination of crustaceans, mollusks, and finfish, including dogfish, skates, eels, mackerel, menhaden, weakfish, smelt, cod, haddock, hake, etc. Monkfish diet also varies considerably by region, as do the diets of many predators.

Opportunistic feeding behaviors by some of these important predators correspond primarily to the distribution and resulting availability of particular prey species. For example, bluefin tuna sampled in the inshore Gulf of Maine (Jeffreys Ledge) were observed to ingest larger proportions of herring than those sampled in the southern New England region (south of Martha's Vineyard). This may reflect the distribution and availability of herring as a forage species more than a predator's dependence on or preference for a particular prey species.

This paper recognizes the importance of herring as a forage species in the northwest Atlantic ecosystem. It is not the role of herring as an individual species in the ecosystem that is most important to understand, however; the interactions of herring with its major predators and other prey species in the region should be considered critical components of successful long-term management of forage species and their associated predators. All species within the ecosystem are ecologically-linked and interact in numerous and complex ways. These interactions become especially difficult to identify and quantify in a system where both predator and prey species are targeted in commercial fisheries. A better understanding of the interactions between predator and prey species will ultimately lead to better management practices for the northwest Atlantic ecosystem as a whole.

8.0 ATLANTIC HERRING AND ECOSYSTEM-BASED MANAGEMENT

Interactions between predators and prey can potentially cause changes in the structure of the environment. Understanding these interactions is important for effective ecosystem management (Bax 1998). Atlantic herring in the northwest Atlantic ecosystem is a significant prey item for a wide variety of species including fish, marine mammals, and birds. The importance of herring to the diet of each species varies significantly. Because of this, each predator species would react differently to fluctuations in herring populations. Therefore understanding the specific interactions of Atlantic herring to each predatory species is critical in managing that species. For example, species that feed on a wide variety of prey (generalist predators) would be less affected by changes in one specific prey biomass. In contrast, species that feed exclusively on a specific prey (specialist predators) would be highly sensitive to changes in prey biomass (Bax 1998).

In addition to being a major prey species, Atlantic herring is itself a potentially significant predator on larval fish and invertebrates. Therefore, herring itself has the ability to impact the dynamics of the ecosystem through predation.

Because of its status as a keystone prey and predator species, understanding the role of Atlantic herring in the northwest Atlantic ecosystem may be critical to effective management of each individual component of the ecosystem. This makes Atlantic herring an excellent candidate for ecosystem-based management. An overview of the major elements of ecosystem-based management in provided in Section 1.0 of this document.

9.0 OTHER ECOSYSTEM-BASED MANAGEMENT APPROACHES

Ecosystem-based management approaches have become common in both research and management in the United States. An internet search on the subject yielded an extraordinary amount of links to programs all over the country ranging from marine ecosystems to terrestrial ecosystems.

Recognizing that the northwest Atlantic ecosystem is highly complex, the Northeast Fisheries Science Center in Woods Hole, Massachusetts has implemented a Food Web Dynamics Program. The program examines predator-prey and competitive interactions among species in the ecosystem and assesses what impact harvesting of these species has on there interactions. For example, research on the changing predator biomass will shed light on what effects it has on the recovery on important commercial fisheries.

The mission statements of the Food Web Dynamics Program can be obtained by accessing: (http://www.nefsc.noaa.gov/femad/pbio/fwdp/FWDP.htm).

The major elements of the mission statement include:

1. To assess predation mortality (relative to fishing mortality) of commercially important fishes.
2. To mechanistically and predicatively model species interactions that impact the status of these stocks, enhancing identification of critical life stages.
3. To relate changes in diet to changes in population level growth rates.
4. To understand the structure and dynamics of the northeast continental shelf ecosystem.

Similar programs have been implemented in the Pacific Northwest ecosystem. Alaska has a Forage Fish Management Plan to manage the commercial harvesting of forage fish species. The plan acknowledges that forage fish are an important component in marine ecosystems, and maintaining populations of forage fish is necessary to maintain healthy populations of other commercially important fish. The forage species included in the plan (as listen on the website) are as follows: capelin, eulachon, and other smelts, laternfishes, deep-sea smelt, Pacific sand lance, Pacific sandfish, gunnels, picklebacks, warbonnets, eelblennys, cockcombs, shannys, bristlemouths, lightfishes, anglemouths, krill.

Information on the plan can be obtained at: (http://touchngo.com/lglcntr/akstats/AAC/Title05/Chapter039/Section212.htm).

Additionally, in the Pacific Northwest, the state of Washington has its own Forage Fish Management Plan. The plan is intended to be used as a guide to resource management decisions and developing fishing regulations. The plan identifies forage fish as small schooling fish that are considered to be important prey for fish, birds, and marine mammals. Examples include herring, anchovies, sardines, and smelt. The plan proposes managing forage fish from an ecosystem-based approach rather than a single species approach and attempts to take a precautionary approach to management. Additional information, as well as the plan itself, can be found on the website: http://www.wa.gov/wdfw/fish/forage/manage/foragman.htm.

Ecosystem-based management is not limited to marine ecosystems. Minnesota's department of natural resources utilizes ecosystem-based management to its natural environment. This approach was implemented to address the problems of nonpoint source pollution, habitat alteration and destruction, toxic contamination of biota, and overall loss of biological diversity. The Minnesota DNR defines ecosystem-based management as "the collaborative process of sustaining the integrity of ecosystems through partnerships and interdisciplinary teamwork. The long-term goal is sustainability of Minnesota's ecosystems, the people who live in them, and the economies founded on them." Additional information can be found on: http://www.dnr.state.mn.us/ecological_services/ebm/index.html.

10.0 RECOMMENDATIONS FOR FUTURE RESEARCH

While much research has been conducted on the subject of Atlantic herring predation, more information needs to be obtained. Low sample sizes due to the rarity of specimens has attributed to the lack of information for marine birds, marine mammals, large pelagic fish, and large elasmobranchs. While sufficient information exists for certain species within each group, there are also several species for which information is not yet available. Because of this, there is a need for additional research on predation on herring by these species.

Regional differences were also observed for species such as cod (Section 4.1.1), bluefin tuna (Section 4.4.1), and striped bass (Section 4.4.4). These species illustrate the importance of examining the regional differences in prey preference as these differences may alter the ecosystem in different ways. This may have implications for designing an ecosystem-based management plan if large regional variations in predation exist.

Many of the models summarized in this paper used estimates of both predator and prey biomass. It is important that this information be as accurate as possible as these variables significantly impact estimates of consumption. Therefore, additional work may be needed to examine the changing biomass levels for the key species in the region.

Competition for resources between species that occupy similar niches (for example spiny dogfish and Atlantic cod) can have an impact on the prey species in the region. Changing the biomass of one species may alter the feeding habits of another. This in turn, may alter the food web of the system. Thus, it is important to identify species which may be competing for a resource as well as the level of that competition.

Establishing a timeline for incorporating predator/prey information into an ecosystem-based approach to management may be necessary for successful implementation. Establishing a timeline may make clear the steps needed for this approach. A timeline may also be used to set short-term goals to meet the overall goal of establishing an ecosystem-based plan.

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Predator-prey interactions between Atlantic puffins and Atlantic herring were observed using multibeam sonar. This technique allowed for observation of prey responses to predator attacks. The study only documents behavior and does not document any predation rates.

Bax N.J. 1998. The significance and prediction of predation in marine fisheries. ICES Journal of Marine Science. 55: 997-1030.

This paper summarizes the findings of several other papers on the subject of predation in the marine environment. The paper examines predation by fish, marine mammals, birds, and squid and describes their impact on marine ecosystems. The paper stresses the importance of examining the interactions between predator and prey for effective management of marine resources.

Bowman R.E. 1981. Food of 10 species of northwest Atlantic juvenile groundfish. Fishery Bulletin. 79(1): 200-206.

The diet of 10 species of juvenile groundfish was examined through stomach content analysis. Stomachs were collected from 1953 to 1976. Specific diet information is given for each individual species sampled as percent of the total weight of the diet for each prey species.

Bowman, R., R. Eppi, and M. Grosslein. 1984. Diet and consumption of Spiny dogfish in the northwest Atlantic. ICES Council Meeting 1984 (collected papers) Demersal Fish Comm., Pelagic Fish Comm., ICES, Copenhagen (Denmark), 1984. 16 pp.

The diet of spiny dogfish was examined through stomach content analysis between 1963-1983 in the northwest Atlantic. Fish was determined to be the major prey item for spiny dogfish. Of these, herring and mackerel were observed to be the dominant fish prey in the diet. The study also documents changes in diet over the time series of the study.

Bowman R.E. 1984. Food of Silver Hake (*Merluccius bilinearis*). National Marine Fisheries Service Laboratory Reference Document. No. 80-31.

The stomachs of 2,622 silver hake were collected for diet analysis from 1973 to 1976. Data was analyzed seasonally as well as between age classes and sexes. Diet analysis demonstrate that prey preference is highly variable and may be dependent on prey availability in a given area.

Bowman R.E., C.E. Stillwell, W.L. Michaels, and M.D. Grosslein. 2000. Food of Northwest Atlantic Fishes and Two Common Species of Squid. NOAA Technical Memorandum NMFS-NE-155. 149pp.

This report is a highly detailed analysis on the diet of several species of bony fish, elasmobranches, and squid. Diet analysis is provided in frequency of prey occurrence and/or the percent biomass in the diet. Data are analyzed according to length of predator and area of sampling. Sampling for the study was conducted over a long time series allowing for a comprehensive species specific analysis of diet.

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.

Grey seal populations have increased on the Scotian Shelf over the last 20 years. As a result, predation by grey seals has also increased. To examine grey seal diet, 528 stomachs were collected between 1988 and 1990.From this data, it was determined that grey seals feed mainly on Atlantic herring, silver hake, cod, and squid.

Buckel, J.A., M.J. Fogarty, and D.O. Conover. 1999. Foraging habits of bluefish, *Pomatomus saltatrix*, on the U.S. east coast continental shelf. Fishery Bulletin. 97: 758-775.

Adult bluefish are found on the U.S. east coat continental shelf throughout the summer and fall. Bottom trawl surveys captured these fish for analysis in 1994 and 1995. Analysis of stomachs suggested a preference for species such as squid, butterfish, bay anchovies, and clupeids.

Cargnelli L.M., S.J. Griesbach, and W.W. Morse. 1999. Atlantic Halibut, *Hippoglossus hippoglossu*s, life History and Habitat Characteristics. Essential Fish Habitat Source Document. NOAA Technical Memorandum NMFS-NE-125. 26pp.

This is the National Marine Fisheries Service's "Essential Fish Habitat Source Document" for Atlantic halibut. The report gives a basic summary of the life history characteristics, habitat requirements, feeding behavior, and breeding behavior of the species. The report also summarizes historical fisheries information as well as current management strategies for the species.

Cargnelli L.M., S.J. Griesbach, D.B. Packer, P.L. Berrien, D.L. Johnson, and W.W. Morse. 1999. Pollock, *Pollachius viren*s, Life History and Habitat Characteristics. Essential

Fish Habitat Source Document. NOAA Technical Memorandum NMFS-NE-131. 38pp.

This is the National Marine Fisheries Service's "Essential Fish Habitat Source Document" for Pollock. The report gives a basic summary of the life history characteristics, habitat requirements, feeding behavior, and breeding behavior of the species. The report also summarizes historical fisheries information as well as current management strategies for the species.

Cargnelli L.M., S.J. Griesbach, C. McBride, C.A. Zetlin, and W.W. Morse. 1999. Longfin Inshore Squid, *Loligo pealei*i, Life History and Habitat Characteristics. Essential Fish Habitat Source Document. NOAA Technical Memorandum NMFS-NE-146. 36pp.

This is the National Marine Fisheries Service's "Essential Fish Habitat Source Document" for Longfin squid. The report gives a basic summary of the life history characteristics, habitat requirements, feeding behavior, and breeding behavior of the species. The report also summarizes historical fisheries information as well as current management strategies for the species.

Chase, B.C. 2002. Differences in diet of Atlantic bluefin tuna (*Thunnus thynnus*) at five seasonal feeding grounds on the New England continental shelf. Fishery Bulletin. 100: 168-180.

The diet of Atlantic bluefin tuna was examined at five known seasonal feeding grounds in New England waters. The stomachs of 819 Atlantic bluefin tuna were examined from 1988-1992. Stomach content analysis showed there to be regional differences in prey preference. There preferences may reflect prey availability in the area.

Collette B.B., and G. Klein-MacPhee. Bigelow and Schroeder's Fishes of the Gulf of Maine. Third Edition. Smithsonian Institution Press. Washington.

A revised edition to Bigelow and Schroeder's original "Fishes of the Gulf of Maine." The book gives species specific information about life histories, ecology, and reproductive behavior for fish found in the Gulf of Maine.

Dawe, E.G., E.L. Dalley, and W.W. Lidster. 1997. Fish prey spectrum of short-finned squid (*Illex illecebrosus*) at Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences. 54(Suppl. 1): 200-208.

Fish prey of short-finned squid were examined by collecting the otolith remains from 17,729 squid stomachs from 1980-1993. Analysis was conducted by area sampled as well as over the entire time series of collection. Data suggest that Atlantic cod is the main fish prey of short-finned squid. In addition to Atlantic cod, Atlantic herring, capelin, sand lance, and red fish were also consumed.

Fahay M.P., P.L. Berrien, D.L. Johnson, and W.W. Morse. 1999. Atlantic Cod, *Gadus morhu*a, Life History and Habitat Characteristics. Essential Fish Habitat Source Document. NOAA Technical Memorandum NMFS-NE-124. 50pp.

This is the National Marine Fisheries Service's "Essential Fish Habitat Source Document" for Atlantic cod. The report gives a basic summary of the life history characteristics, habitat requirements, feeding behavior, and breeding behavior of the species. The report also summarizes historical fisheries information as well as current management strategies for the species.

Fogarty, M.J. and S.A. Murawski. 1998. Large scale disturbance and the structure of Marine systems: Fishery impacts on Georges Bank. Ecological Applications. 8(1): S6-S22.

A shift in the food web was detected in the Georges Bank region and attributed to overfishing. Species dominance shifted from valuable groundfish species to non-valuable small elasmobranch species. This increase in elasmobranch abundance may be a potential limiting factor in groundfish recovery. An ecosystem-based management approach is suggested to examine possible mechanisms for groundfish recovery.

Gannon, D.P., A.J. Read, J.E. Craddock, and J.G. Mead. 1997b. Stomach contents of long-finned pilot whales (*Globicephala melas*) stranded on the U.S. mid-Atlantic coast. Marine Mammal Science. 13(3): 405-418.

Eight long-finned pilot whale stomachs were sampled from standings along the U.S. Mid-Atlantic coast. Results indicated that 10 taxa were found in the diet of long-finned pilot whales. Of these taxa, squid were seen ad the dominant prey species.

Gannon, D.P., A.J. Read, J.E. Craddock, K.M. Fristrup, and J.R. Nicolas. 1997a. Feeding ecology of long-finner pilot whales *Globicephala melas* in the western North Atlantic. Marine ecology Progress Series. 148: 1-10.

Stomach content analysis was conducted on 30 long-finned pilot whales taken in the distant-water mackerel fishery. Results considered both partially digested prey and whole prey found in the stomachs. Results indicated that squid dominated the diet of long-finned pilot whales.

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

The autumn diet of harbor porpoises was examined through the stomach remains of 95 porpoises caught in gillnets between 1989-1994 in the Gulf of Maine. This population of harbor porpoises is identical to the spring/summer distribution in the Bay of Fundy. Analysis of prey remains suggests that Atlantic herring is the main prey species of harbor porpoises.

Garrison, L.P., W. Michaels, J.S. Link, and M.J. Fogarty. 2000a. Predation risk on larval gadids by pelagic fish in the Georges Bank ecosystem. I. Spatial overlap associated with hydrographic features. Canadian Journal of Fisheries and Aquatic Sciences. 57: 2455-2469.

The potential for predation on larval gadids by pelagic fish was determined by examining the degree of spatial overlap between the species. The larval gadids studied were Atlantic cod and haddock. The pelagic predators were Atlantic mackerel and Atlantic herring. The only overlap

observed was between Atlantic herring and juvenile haddock. This suggests only the possibility of predation between the two groups as no direct predation was observed.

Garrison, L.P., and J.S. Link. 2000b. Diets of five hake species in the northeast United States continental shelf ecosystem. Marine Ecology Progress Series. 2040: 243-255.

Five hake species were examined for prey preference along the northeast continental shelf. Stomach analysis illustrated a preference for pelagic invertebrates and pelagic fish. Analysis also shows regional and seasonal differences in prey preference.

Hammill, M.O., C. Lydersen, K.M. Kovacs, and B. Sjare. 1997. Estimated fish consumption by Hooded seals (*Cystophora cristata*), in the Gulf of St. Lawrence. Journal of Northwest Atlantic Fishery Science. 22: 249-257.

Fish consumption by hooded seals was estimated by using information on energy requirements, population size, and diet composition. In addition to fish consumption, modeling also estimates pup production from 1991-1995.

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 Harbour seals (*Phoca vitulina*) in Atlantic Canada. Journal of Northwest Atlantic Fishery Science. 26: 1-23.

Consumption by the four seal species was estimated from 1990-1996 in Atlantic Canadian waters. Information for the model was derived from energy requirements, population size, and diet composition for each individual species. The model showed that total annual consumption for the four species increased from 3.1 million to 4 million tons over the period of the study. The results give species-by-species and area-by-area consumption rates.

Hanson, J.M., and G.A. Chouinard. 2002. Diet of Atlantic cod in the southern Gulf of St. Lawrence as an index of ecosystem change, 1959-2000. Journal of Fish Biology. 60: 902-922.

The change in Atlantic cod diet from 1959-2000 was examined through stomach sampling. Sampling was conducted on the Gulf of St. Lawrence population of Atlantic cod. Analysis was broken down by size classes of Atlantic cod and diet was examined for each group.

Hislop, J.R.G., and W.S. MacDonald. 1989. Damage to fish by seabirds in the Moray Firth. Scottish Birds. 15: 151-155.

Fish caught during trawl surveys were examined for instances of attacks by predators. Herring were one of three fish species observed to have these marks. These marks were attributed to attempted predation by marine birds based on matching teeth patterns of the birds to the marks on the fish.

Johnson D.L., P.L. Berrien, W.W. Morse, and J.J. Vitaliano. 1999. American Plaice, *Hippoglossoides platessoide*s, Life History and Habitat Characteristics. essential Fish Habitat Source Document. NOAA Technical Memorandum NMFS-NE-123. 40pp.

This is the National Marine Fisheries Service's "Essential Fish Habitat Source Document" for American plaice. The report gives a basic summary of the life history characteristics, habitat requirements, feeding behavior, and breeding behavior of the species. The report also summarizes historical fisheries information as well as current management strategies for the species.

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.

Cetaceans were suggested to be significant consumers in the marine environment. Consumption of squid, zooplankton, and finfish was estimated for 18 species of whales, dolphins, and porpoises in four areas of the northeast continental shelf. Estimates were based on seasonal abundances of each species in each area, as well as on known dietary requirements.

Langton. R.W. 1982. Diet overlap between Atlantic cod, *Gadus morhua,* silver hake, *Merluccius bilinearis,* and fifteen other northwest Atlantic finfish. Fishery Bulletin. 80: 745-759.

Diet overlap was examined for Atlantic cod and silver hake with fifteen other finfish species in the northwest Atlantic. Diet overlap described how similar the diets were between species with inferences for trophic linkages between the species. The study was conducted between 1973-1976.

Link, J.S., and L.P. Garrison. 2002. Trophic ecology of Atlantic cod *Gadus morhua* on the northeast US continental shelf. Marine Ecology Progress Series. 227: 109-123.

The trophic ecology of Atlantic cod was examined using a 25-year time series of food habit data from bottom trawl surveys. In all, 15,000 stomachs were sampled. Results illustrated that the diet of cod changed in correlation with changes in forage species abundance and distribution.

Link J.S., L.P. Garrison, and F.P. Almeida. 2002a. Ecological interactions between elasmobranchs and groundfish species on the northeastern U.S. continental shelf. I. Evaluating predation. North American Journal of Fisheries Management. 22: 550-562.

The increase biomass of small elasmobranches like skates and spiny dogfish was hypothesized to be a limiting factor to groundfish recovery. To examine this hypothesis predation by elasmobranches on groundfish was examined. The stomachs spiny dogfish, smooth dogfish, little skate, winter skate, and thorny skate were analyzed for groundfish remains. Results showed that, with the exception of silver hake, groundfish predation was minimal.

Link J.S., K. Bolles, and C.G. Milliken. 2002b. The feeding ecology of flatfish in the northwest Atlantic. Journal of Northwest Atlantic Fishery Science. 30: 1-17.

The diet of several flatfish species was examined with 25 years of data collected from bottom trawl surveys. Data was used to determine if changes in the diet occurred over the time series as a result of fishing. Results are given for each individual species and show specific prey preference.

McMillan D.G. and W.W. Morse. 1999. Spiny Dogfish, *Squalus acanthia*s, Life History and Habitat Characteristics. Essential Fish Habitat Source Document. NOAA Technical Memorandum NMFS-NE-150. 28pp.

This is the National Marine Fisheries Service's "Essential Fish Habitat Source Document" for Spiny dogfish. The report gives a basic summary of the life history characteristics, habitat requirements, feeding behavior, and breeding behavior of the species. The report also summarizes historical fisheries information as well as current management strategies for the species.

Nelson G.A., B.C. Chase, and J. Stockwell. 2003. Food habits of striped bass (*Morone saxatilis*) in coastal waters of Massachusetts. Journal of Northwest Atlantic Fishery Science. 32: 1-25.

Stomachs of striped bass from three locations off of Massachusetts were collected for analysis. Samples were taken between June and September 1997-2000, a time when striped bass are present in the area. Results showed that diet varied between areas, suggesting regional differences in prey preference.

NMFS Ecosystem Principles Advisory Panel. 1999. Ecosystem-Based Fishery Management.

A report to congress on the implementation of ecosystem-based management to current fishery management plans. The report outlined several steps and goals that should be used to apply these ecosystem-based strategies.

Overholtz, W.J., S.A. Murawski, and K.L. Foster. 1991. Impact of predatory fish, marine mammals, and seabirds on the pelagic fish ecosystem of the northeastern USA. ICES Marine Science Symposium. 193: 198-208.

Modeling was used to examine the impacts of several predator species on the pelagic fish community in the northeastern USA. The model estimated average consumption (tons) between 1988-1992 for these predator species by considering predator/prey abundances and consumption rates. Results may be used in management to consider ecosystem impacts of harvesting these predator and prey species.

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.

Stomachs of pilot whales and common dolphins were sampled for prey composition. Samples were taken in the spring of 1989 in the Mid-Atlantic Bight. Results were separated by length and sex of the predator as well as the mean weight and length of the prey.

Overholtz, W.J., J.S. Link, and L.E. Suslowicz. 1999. Consumption and harvest of Pelagic fishes and squids in the Gulf of Maine-Georges Bank ecosystem. Ecosystem Approaches for Fisheries Management. 163-186. Lowell Wakefield Fisheries Symposium Series. no. 16.

This paper describes a shift in fish biomass to pelagic fish dominance in the Gulf of Maine-Georges Bank area. As pelagic fish biomass increases, so does predation by fish on them. The study estimates rates of consumption for 12 species of fish eating fish. Results show that consumption is comparable to landings in the ecosystem.

Overholtz, W.J., J.S. Link, and L.E. Suslowicz. 2000. Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. ICES Journal of Marine Science. 57: 1147-1159.

Estimates of consumption by 12 piscivorous fish were estimated for the northeastern USA shelf ecosystem. Results describe species specific consumption rates on several pelagic fish species. Analysis suggests that the abundance of prey in the diet reflects the abundance of prey in the environment.

Overholtz, W.J., and K.D. Friedland. 2002. Recovery of the Gulf of Maine-Georges Bank Atlantic herring (*Clupea harengus*) complex: perspectives based on bottom trawl survey data. Fishery Bulletin. 100: 593-608.

Changes in the distribution and abundance of Atlantic herring were examined from data collected from NMFS bottom trawl surveys. Surveys were conducted from 1963-1998 in the Gulf of Maine-Georges Bank region. Results show that Atlantic herring in the region have fully recovered since being overexploited in the 1960s and 1970s. Analysis also shows that the distribution has also shifted to a pre-exploited state.

Packer D.B., C.A. Zetlin, and J.J. Vitaliano. 2003. Little Skate, *Leucoraja erinace*a, Life History and Habitat Characteristics. Essential Fish Habitat Source Document. NOAA Technical Memorandum NMFS-NE-175. 76pp.

This is the National Marine Fisheries Service's "Essential Fish Habitat Source Document" for Little skate. The report gives a basic summary of the life history characteristics, habitat requirements, feeding behavior, and breeding behavior of the species. The report also summarizes historical fisheries information as well as current management strategies for the species.

Packer D.B, C.A. Zetlin, and J.J. Vitaliano. 2003. Winter Skate, *Leucoraja ocellat*a, Life History and Habitat Characteristics. Essential Fish Habitat Source Document. NOAA Technical Memorandum NMFS-NE-179. 68pp.

This is the National Marine Fisheries Service's "Essential Fish Habitat Source Document" for Winter skate. The report gives a basic summary of the life history characteristics, habitat requirements, feeding behavior, and breeding behavior of the species. The report also summarizes historical fisheries information as well as current management strategies for the species.

Recchia, C.A., and A.J. Read. 1989. Stomach contents of harbor porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. Canadian Journal of Zoology. 67: 2140-2146.

127 stomachs from harbor porpoises were collected from June-September 1985-1987 in the Bay of Fundy. This represents the spring/summer distribution of the species that migrated into the

Gulf of Maine in the fall. Relative prey importance was measured using both numeric and caloric values. Results illustrate that Atlantic herring is the dominant prey species in the diet of harbor porpoises.

Reid R.N., L.M. Cargnelli, S.J. Griesbach, D.B. Packer, D.L. Johnson, C.A. Zetlin, W.W. Morse, and P.L. Berrien. 1999. Atlantic Herring, *Clupea harengu*s, Life History and Habitat Characteristics. Essential Fish Habitat Source Document. NOAA Technical Memorandum NMFS-NE-126. 56pp.

This is the National Marine Fisheries Service's "Essential Fish Habitat Source Document" for Atlantic herring. The report gives a basic summary of the life history characteristics, habitat requirements, feeding behavior, and breeding behavior of the species. The report also summarizes historical fisheries information as well as current management strategies for the species.

Schwalme, K., and G.A. Chouinard. 1999. Seasonal dynamics in feeding, organ weights, and reproductive maturation of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. ICES Journal of Marine Science. 56: 303-319.

Atlantic cod in the Gulf of St. Lawrence were sampled for seasonal changes in diet composition between 1991-1993. Seasonal sampling illustrates how diet changes before, during, and after spawning occurs. In addition to stomach sampling, liver and gonads were also weighed to examine reproductive changes over time.

Selzer L.A., G. Early, P.M. Fiorelli, P.M. Payne, and R. Prescott. 1986. Stranded animals as indicators of prey utilization by harbor seals, *Phoca vitulina concoloe*, in southern New England. Fishery Bulletin. 84: 217-220.

The diet of harbor seals was examined in southern New England. In all, 63 stomachs were collected with 53 containing prey. Analysis showed that squid were the main prey species of harbor seals followed by haddock and silver hake.

Sherman, K., and H.C. Perkins. 1971. Seasonal variations in the food of Juvenile herring in coastal waters of Maine. Transactions of the American Fisheries Society. 100: 121-124.

The diet of Atlantic herring was examined in 256 juvenile individuals from the waters of coastal Maine. Diet was examined for seasonal differences in prey preference as well as changes in movement based in changes in prey availability.

Steimle F.W., W.W. Morse, and D.L. Johnson. 1999. Goosefish, *Lophius americanu*s, Life History and Habitat Characteristics. Essential Fish Habitat Source Document. NOAA Technical Memorandum NMFS-NE-127. 40pp.

This is the National Marine Fisheries Service's "Essential Fish Habitat Source Document" for Goosefish (monkfish). The report gives a basic summary of the life history characteristics, habitat requirements, feeding behavior, and breeding behavior of the species. The report also summarizes historical fisheries information as well as current management strategies for the species.

Steimle F.W., C.A. Zetlin, P.L. Berrien, D.L. Johnson, and S. Chang. 1999. Tilefish, *Lopholatilus chamaeleonticep*s, Life History and Habitat Characteristics. Essential Fish Habitat Source Document. NOAA Technical Memorandum NMFS-NE-152. 38pp.

This is the National Marine Fisheries Service's "Essential Fish Habitat Source Document" for Tilefish. The report gives a basic summary of the life history characteristics, habitat requirements, feeding behavior, and breeding behavior of the species. The report also summarizes historical fisheries information as well as current management strategies for the species.

Swain, D.P., and A.F. Sinclair. 2000. Pelagic fishes and the cod recruitment dilemma in the northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences. 57: 1321-1325.

The failure of groundfish recovery in Canadian waters was examined as a function of recruitment. Factors attributing to poor recruitment such as lack of prey, intense competition, and predation were hypothesized to be limiting factors in groundfish recovery. Pelagic fish species such as, herring and mackerel, were seen as possible species behind these limiting factors. It was hypothesized that there exists a negative relationship between pelagic fish biomass and recruitment of Atlantic cod.

Tsou, T.S., and J.S. Collie. 2001a. Predation-mediated recruitment in the Georges Bank fish community. ICES Journal of Marine Science. 58: 994-1001.

Using multi-species analysis, predation was examined as a possible mechanism to control recruitment in an ecosystem. Predation by eight species was modeled in the Georges Bank region. Results suggest that cod and silver hake were the most important predators with Atlantic herring being the most important prey.

Tsou, T.S., and J.S. Collie. 2001b. Estimating predation mortality in the Geoges Bank fish community. Canadian Journal of Fisheries and Aquatic Sciences. 58: 908-922.

Multispecies virtual population analysis was used to determine predation mortality, fishing mortality, and population abundances of several fish species on Georges Bank between 1978-1992.

Weinrich, M., M. Martin, R. Griffiths, J. Bove, and M. Schilling. 1997. A shift in dristribution of humpback whales, *Megaptera novaeangliae*, in response to prey in the southern Gulf of Maine. Fishery Bulletin. 95: 826-836.

The change in the distribution of humpback whales in the Gulf of Maine was examined from the mid-1970s to the mid-1990s. Results were based on observations of humpback whales in each area over time. Observations suggested a change in distribution from Stellwagen Bank to Jefferies Ledge. The change was attributed to a shift in prey preference from sand lance, which is dominant on Stellwagen Bank, to herring, which are dominant on Jefferies Ledge.

Witherell D., C. Pautzke, and D. Fluharty. 2000. An ecosystem-based approach for Alaska groundfish fisheries. ICES Journal of Maine Science. 57: 771-777.

This paper describes the ecosystem-based approach, which is being taken to manage groundfish fisheries in the north Pacific Alaskan waters. The approach involves public and scientific input on such issues as bycatch, setting conservative catch quotas, gear restrictions, and monitoring and enforcement. Ecosystem-based management has been seen as a possible means of taking a precautionary approach to management and maintaining the health of the ecosystem.