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Population Consumption of Fish and Invertebrate Prey by Striped Bass (*Morone saxatilis*) from Coastal Waters of Northern Massachusetts, USA

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Abstract

Seasonal, age-class, and population-level changes in diet and consumption demand of prey by striped bass residing in coastal waters of northern Massachusetts were investigated to determine their potential predatory impact on ecologically- and economically-important prey species. Most consumption by individual striped bass of ages 3–8 came from crustaceans and fish. More crustaceans (50–78% of total consumption) than fish were consumed during June–July, while more fish (52–88% of total consumption) than crustaceans were consumed during August–September. Rock crabs *Cancer irroratus* and American lobsters *Homarus americanus* became more important to the production of striped bass as bass aged, but Atlantic menhaden *Brevoortia tyrannus* became less important. Together, the biomass of prey consumed by all age-classes in 2000 totaled over 5 575 t. Atlantic menhaden accounted for 29% of the total biomass consumed, followed by rock crabs (18%), American lobster (11%), and Atlantic herring *Clupea harengus* (3%). On a numerical basis, striped bass consumed seasonally over 3, 1 940, and 965 times the numbers of lobsters, rock crabs, and menhaden, respectively, taken annually by regional and statewide fisheries, suggesting striped bass may exert considerable predation pressure on these prey populations.

Key words: *Morone saxatilis*, predation, prey consumption

Introduction

The striped bass *Morone saxatilis* is a recreationally- and commercially-important anadromous fish species found along the United States Atlantic coast from Florida to Maine (Setzler *et al*., 1980). As a result of over-exploitation of the adult spawning stock, striped bass abundance reached alarmingly low levels in the early 1980s which prompted interstate management regulations that severely restricted fishing (Richards and Rago, 1999). After several years of stringent regulations, the Atlantic States Marine Fisheries Commission declared in 1995 that the Atlantic coast striped bass population had recovered (Field 1997; Richards and Rago 1999). Estimated stock abundance had increased from 5 million in 1982 to around 50 million by the mid-1990s (Anon., 2004).

Despite this remarkable recovery, there is concern over the health of the striped bass population, and their predatory impacts on key prey species. In the northeastern United States, the angling public has expressed concern that the weight of large fish has decreased over the last two decades (Peros, 1999), suggesting that the striped bass population may be experiencing food limitation. Given that some important prey species of striped bass (e.g. young-of-the-year Atlantic menhaden *Brevoortia tyrannus* are declining (Anon., 2003), such limitation may be a plausible hypothesis. If food is limited for striped bass, they may exert high predation pressure on prey species that are of economical and cultural interest to humans. Thus, recovered striped bass may be in direct and significant competition with humans for potentially limited resources.

In Massachusetts waters, predation impact of striped bass may be substantial. With recent recreational striped bass catches being the largest observed in any coastal Atlantic state (Anon., 2004), a large proportion of the Atlantic population is believed to temporarily reside in Massachusetts waters during summer. While in Massachusetts waters, striped bass eat fish (e.g. sand

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lance *Ammodytes* sp., Atlantic herring *Clupea harengus* and Atlantic menhaden) that are important to other fishes, marine mammals, seabirds, and humans (Bowman and Michaels, 1981; Powers and Brown, 1987; Chase, 2002; Nelson *et al*., 2003). They also eat the decapod crustacean American lobster *Homarus americanus* which supports a multi-million dollar commercial fishery in Massachusetts (Estrella and McKiernan, 1989; Nelson *et al*., 2003).

Given the record high levels of striped bass abundance, it is possible that striped bass are exerting considerable predation pressure on prey populations important to both the local ecosystem and to the economy of Massachusetts. However, there are no estimates of prey consumption by the striped bass population. This current study was conducted to develop estimates of total biomass and numbers of prey consumed by striped bass and to describe seasonal and age-class changes in diet and consumption demand during their summer residence.

Materials and Methods

Individual Cumulative Consumption

The algorithms of Fish Bioenergetics 3.0 (Hanson *et al*., 1997) were used to estimate individual consumption of prey (g/fish/day) by striped bass inhabiting nearshore (estuarine and rocky shoreline) waters of the northern Massachusetts (Fig. 1; Nelson *et al*., 2003). The algorithms were programmed in SAS (SAS Institute, 2000) to duplicate the bioenergetics model (BEM) for striped bass. The bioenergetics model is based on a balanced energetics equation (Kitchell *et al*., 1977). It estimates daily consumption of prey given species- and age-specific physiological parameters relating fish body size and temperature to metabolic costs, temperature in the environment occupied by the fish, the energy densities of predator and prey, the diet proportions of each prey species, and growth of the predator (Hanson *et al*., 1997). All physiological equations and parameters for striped bass required by the BEMs were taken from Hartman and Brandt (1995a). An oxycalorific value of 13.6 joules per mg O_2 consumed (Priede, 1985) was used to convert respiration values to joule energy equivalents.

Based on the results of Nelson *et al*. (2003), daily consumption rates were estimated for individual striped bass of ages 3–8 during two time periods: 1 June–31 July (days 152–212 from 1 January) and 1 August–30 September (days 213–273). For each age and time period, consumption was estimated on a daily time step. Daily water temperature came from a calibrated data logger stationed in Beverly Harbor, MA at an average depth of 8 m during 1997–2000 (Fig. 2). We considered these temperatures to be representative of the nearshore thermal environment experienced by striped bass. Energy densities (joules per gram of wet weight) of striped bass and their prey (Table 1) were obtained from Thayer *et al*. (1973) and Steimle and Terranova (1985), or were estimated from generic models of fish energy densities (Hartman and Brandt, 1995b) using seasonal means of percent dry weight derived in this study.

Food habits data from Nelson *et al*. (2003) were used to estimate prey diet proportions for each age of striped bass. Diet weights were reconstructed by using various length (total, fork, standard, and backbone length (mm) for fish; carapace width for crabs; carapace length for lobsters) and weight (g) relationships derived in this study, by Wigley *et al*. (2003), and by Ferry (2003). It was assumed that the diet proportions represented what an "average bass" from each age-class would eat on a daily basis throughout each time period. Only stomachs with prey were used in the calculation of prey proportions (Table 1).

Growth was estimated from weight (g) and age data of individuals collected by Nelson *et al*. (2003). Age, designated with a decimal extension reflecting the date of capture in days from 1 January, was determined from scale impressions by an experienced scale reader for striped bass. Due to small sample sizes in some months, mean weight-at-age at the beginning and end of each time period was estimated from a power regression model that appropriately characterized the relationship between weight (w) and age (A) for ages 2–10 (asymptotic standard errors are in parentheses):

$$w = 57.36\ (2.63) * A^{2.11(0.02)};\ \left[r^2 = 0.83, n = 3\,113\right]$$

The cumulative consumption of prey by an individual striped bass during a time period was calculated by summing daily consumption rates over the number of days modelled in each BEM. We calculated cumulative consumption for all prey combined, five major taxa groups, and four prey species (American lobster, rock crab *Cancer irroratus*, Atlantic herring, and menhaden) deemed ecologically-important to striped bass or economically-important to Massachusetts.

Measures of uncertainty for consumption estimates were derived using a mixture of bootstrap (Efron and Tibshirani, 1998) and Monte Carlo (Haddon, 2001) resampling methods. Incorporated sources were errors in 1) diet proportions, 2) starting and ending weights-at-age, 3) parameters *CA* and *CB* of maximum consumption equation (C_{max} in Hartman and Brandt, 1995a), and 4) parameters *RA*, *RB*, *RQ*, and *ACT* of the metabolism equation (*R* in Hartman and Brandt, 1995a).

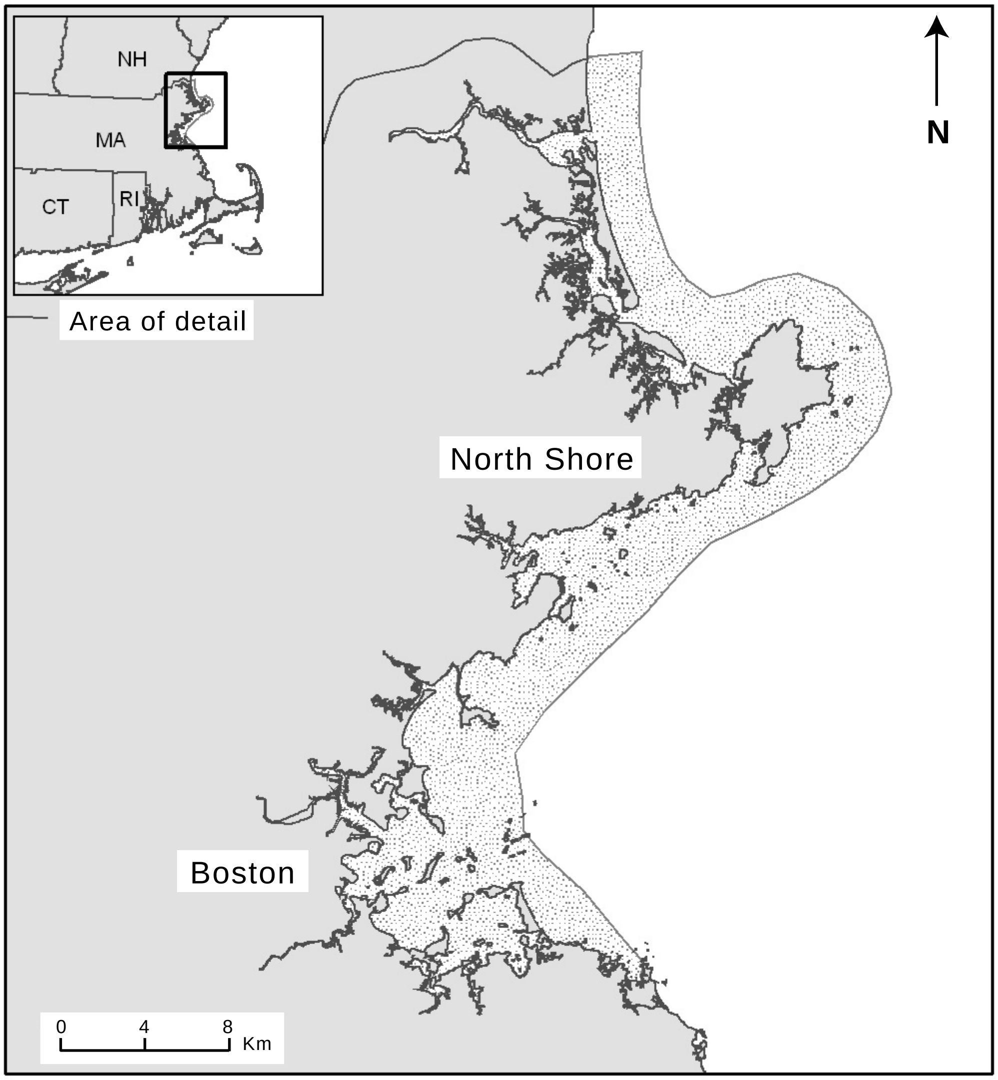

Fig. 1. Map showing boundaries of the North Shore region of Massachusetts.

Bootstrapping was used to resample diet data, while Monte Carlo sampling was used to randomly pick parameters for the maximum consumption, metabolism, and growth equations from normal distributions characterized with the original parameter estimates and associated standard errors. Standard errors were calculated from 95% confidence intervals and sample sizes given in Table 1 and figures of Hartman and Brandt (1995a). A run for each age and time period consisted of calculating the new diet proportions from a bootstrap sample, substituting the new physiological and growth parameters into the appropriate equations, and then estimating daily consumption. For each period and age combination, 1000 runs were made and the mean and standard error of cumulative consumption (q) were calculated from all runs. As a comparison to Hartman and Brandt (1995c), seasonal growth conversion efficiency for each age was calculated by dividing cumulative growth by the total consumption over the two periods.

Age-class and Population Consumption

The seasonal consumption of prey consumed by age-class and the entire population (ages 3–8) was calculated from estimates of average abundance of striped bass and cumulative individual consumption during the two time periods as follows:

$$\hat{Q}_{a,i} = \sum_{j} \hat{\bar{N}}_{a,j} \cdot \hat{q}_{a,i,j}$$

where $\hat{Q}_{a,i}$ is the total biomass (g) of prey i consumed by age-class a, $\hat{\bar{N}}_{a,j}$ is the average abundance of age a

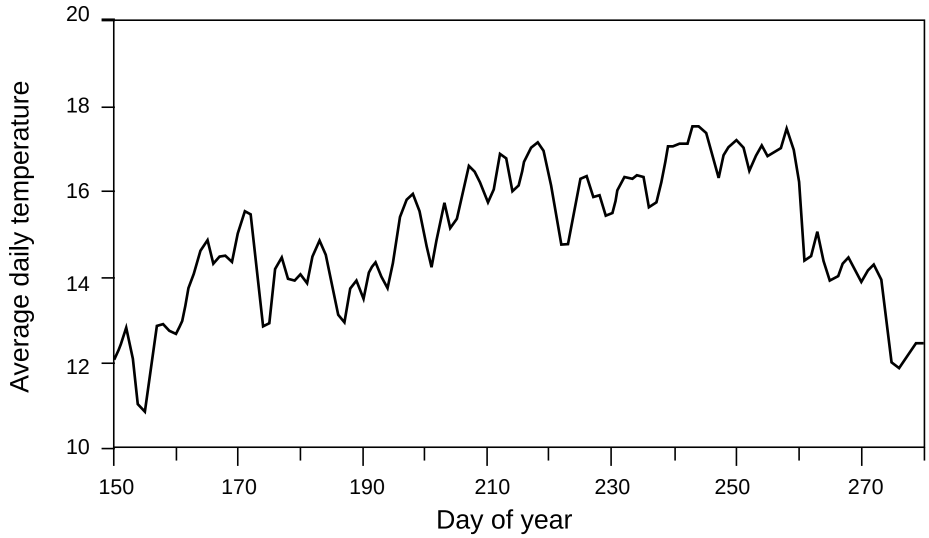

Fig. 2. Average daily water temperatures used in the bioenergetics models. Data were collected using a calibrated temperature data-logger during 1997–2000 at a depth of 8 m in Beverly Harbor, MA.

striped bass during period j, and $q_{a,i,j}$ is the cumulative individual consumption (g/fish) of prey i during period j by age a striped bass. The variance (SE^2) of $\hat{Q}_{a,i}$ was estimated from the product of two independent, random variables (Mood *et al.*, 1974):

$$SE^2(\hat{Q}_{a,i}) = \sum_j \hat{q}^2_{a,i,j} \cdot SE^2(\hat{\hat{N}}_{a,j}) + \hat{\hat{N}}^2_{a,j} \cdot SE^2(\hat{q}_{a,i,j}) + SE^2(\hat{\hat{N}}_{a,j})SE^2(\hat{q}_{a,i,j})$$

$\hat{\hat{N}}_{a,j}$ was calculated from a combined form of the exponential cohort survival model and Baranov's catch equation (Ricker, 1975; Quinn and Deriso, 1999):

$$\hat{\hat{N}}_{a,j} = \frac{1-e^{-Z_j}}{Z_j} \cdot \frac{\hat{L}_a}{\mu_a} \cdot e^{-p_{t-1} \cdot M - \theta_{t-1} \cdot F_a}$$

where L_a is the number of age a fish killed annually, μ_a is the annual exploitation rate of age a, t is the beginning month of period j, ρ_{t-1} and θ_{t-1} are the fractions of natural (M) and fishing (F) mortality, respectively, experienced by age a through month t-1, and Z_j is the total instantaneous mortality rate during period j. This model estimates the hypothetical numbers-at-age that had to be present at 1 January, even though striped bass are not present in Massachusetts waters during this time, given L_a, M, and F_a, and then decrements those numbers over time given bi-monthly estimates of F and Z. A full F was derived by subtracting M for the coastwide stock (0.15) (Anon., 2004) from an estimate of Z (0.50) derived using total catch-at-age (Nelson *et al.*, 2001) and the Chapman-Robson survival estimator (Chapman and Robson, 1960). Full F was then apportioned to each age using the partial recruitment vector calculated for the coastal migratory population of striped bass in 2000 (Anon., 2004). F-at-age was then distributed equally across May–October, the months when striped bass fisheries in Massachusetts occur; therefore, θ_{t-1} was 0 for $t \leq 5$, (t-5)/6 for $6 \leq t \leq 11$, and 1 otherwise. We distributed natural mortality equally across all months so that ρ_{t-1} was calculated as (t-1)/12. Assuming constant mortality rates for each age, an estimator for the variance of $\hat{\hat{N}}_{a,j}$ is

$$SE^2(\hat{\hat{N}}_{a,j}) = \left(\frac{1-e^{-Z_j}}{Z_j} \frac{e^{-p_{t-1}M - \theta_{t-1}F_a}}{\mu_a} \right)^2 SE^2(\hat{L}_a)$$

To estimate L_a for each age, we first post-stratified the National Marine Fisheries Service's Marine Recreational Fisheries Statistics Survey (MRFSS) estimates for Massachusetts by two-month wave, county and fishing mode (i.e. shore *versus* boat fishing). The harvest and release estimates from Essex, Suffolk, and Norfolk counties for anglers fishing in estuaries (all modes) and those fishing in the ocean from shore were selected as representing the numbers harvested and released for the nearshore region of northern Massachusetts. The MRFSS estimates were then summed across all waves to get annual harvest ($\hat{C}$) and releases ($\hat{E}$). We then apportioned the MRFSS numbers into age-classes by using estimates of proportions-at-age. The proportion of age a that was

TABLE 1. Energy densities of prey and predator (joules per gram wet weight), reconstructed diet composition (percent biomass), total number of stomachs, number of stomachs with prey, average stomach weight (g), and average body weight (g) of striped bass during June–July (JJ: days 152–212) and August–September (AS: days 213–273).

			Percent Biomass											
	Energy Density		Age 3		Age 4		Age 5		Age 6		Age 7		Age 8	
Category	JJ	AS	JJ	AS	JJ	AS	JJ	AS	JJ	AS	JJ	AS	JJ	AS
Prey														
Polychaetes[a]	4 200	4 200	8.8	0.3	2.4	0.2	1.3	–	0.7	0.3	–	–	0.3	–
Molluscs[a]	5 283	5 283	<0.1	0.2	5.0	4.5	1.1	0.9	0.8	0.1	3.0	<0.1	<0.1	2.2
Sand shrimp[b]	3 700	3 700	9.5	0.3	1.5	0.5	<0.1	0.3	0.2	0.2	0.3	–	<0.1	–
American lobster[b]	4 800	4 800	0.1	0.3	12.3	2.0	12.6	2.0	4.4	2.1	27.7	17.2	51.2	17.4
Rock crab[b]	3 700	3 700	10.7	7.2	29.2	8.4	35.5	9.7	22.8	7.8	16.5	7.3	5.3	44.4
Green crab[c]	3 700	3 700	5.2	1.8	7.8	0.8	5.5	0.9	2.8	2.2	3.4	6.8	–	5.1
Mysids[d]	5 265	5 265	0.5	<0.1	1.0	0.1	0.3	–	0.1	–	–	–	<0.1	–
Isopods[d]	3 400	3 400	–	–	–	–	<0.1	–	–	–	–	–	–	–
Amphipods[a]	3 400	3 400	10.5	0.8	6.8	0.1	1.3	0.3	0.3	–	<0.1	0.2	–	–
Other small crustacea[e]	6 038	6 038	–	–	–	–	<0.1	–	<0.1	–	–	0.4	–	–
Other large crustacea[e]	4 169	4 169	1.1	–	9.8	1.7	9.0	5.0	5.0	3.4	–	6.5	2.9	18.4
Unidentifiable crustacea[e]	4 819	4 819	2.6	0.9	10.2	1.8	7.9	1.3	11.4	8.3	2.2	5.8	1.0	3.4
Misc. invertebraes[e]	3 203	3 203	0.2	–	–	–	0.9	<0.1	–	–	0.4	0.8	1.0	–
Blueback/Alewife herring[f]	5 817	5 412	10.3	–	0.5	–	<0.1	–	7.3	–	0.6	–	–	–
Menhaden[f]	4 038	4 038	–	81.7	–	73.0	<0.1	73.7	–	55.0	–	31.9	–	–
Atlantic herring[f]	8 188	6 010	30.8	–	2.9	–	<0.1	–	8.2	–	8.5	–	14.5	0.6
Unidentifiable herring[a]	7 540	7 540	–	–	–	–	0.2	–	–	–	–	–	–	–
Atlantic silverside[b]	7 300	7 300	–	0.6	1.1	0.4	<0.1	0.1	–	–	–	–	–	–
Rock gunnel[a]	5 058	5 058	3.4	–	5.0	1.7	5.6	0.4	0.7	2.3	0.1	2.6	0.7	–
Sand lance[f]	6 896	6 270	2.4	1.5	1.2	0.3	0.5	–	–	–	0.7	–	0.4	–
Other fish[a]	5 168	5 170	3.8	4.4	3.4	4.5	18.3	5.4	35.3	18.3	36.5	20.5	22.8	8.5
Predator														
Striped bass[f]	6 395	6 395												
Total stomachs			85	115	167	214	96	120	106	110	102	78	56	53
Stomachs with prey			70	70	112	140	65	70	56	57	40	40	31	17
Ave. stomach weight(g)			6.2	9.8	7.4	14.9	13.0	17.9	10.1	12.6	13.6	14.5	31.7	12.2
$SE_{\text{stomach weight}}$			0.95	1.61	1.08	1.75	2.00	2.87	2.19	2.18	3.26	3.52	7.61	4.69
Ave. bass weight (g)			946	999	1 417	1 472	2 093	1 992	2 873	2 977	4 157	4 290	5 135	4 948
$SE_{\text{bass weight}}$			33.4	25.4	34.2	27.4	69.9	66.6	115.2	97.8	110.9	154.4	180.3	221.1

[a] average taxa values in Steimle and Terranova (1985).
[b] Steimle and Terranova (1985).
[c] energy density of rock crab.
[d] Euphausidacea in Steimle and Terranova (1985).
[e] average taxa values in Steimle and Terranova (1985) and Thayer *et al.* (1973).
[f] derived from generic models of fish energy density (Hartman and Brandt, 1995b) and seasonal means of percent dry weight (this study).

harvested or released and its variance was estimated from length frequency and age-length keys developed for striped bass from Massachusetts waters using a two-stage random sampling estimator (Quinn and Deriso, 1999, pp. 303–306):

$$\hat{p}_a = \sum_{k=1}^{m} \hat{a}_k \cdot \hat{p}_{k,a}$$

with

$$SE^2(\hat{p}_a) = \sum_{k=1}^{m} \frac{\hat{a}_k^2 \cdot \hat{p}_{k,a} \cdot (1-\hat{p}_{k,a})}{A_k - 1} + \sum_{k=1}^{m} \frac{\hat{a}_k \cdot (\hat{p}_{k,a} - \hat{p}_a)}{T}$$

where m is the total number of length intervals, $\hat{a}_k$ is the estimated proportion of lengths in interval $k, \hat{p}_{k,a}$ is the proportion of age a in interval k, A_k is the total number of age samples in interval k, and T is the total number of length samples. The total number of harvested fish of age a ($\hat{C}_a$) was calculated as

$$C_a = \hat{C} \cdot \hat{p}_{c,a}$$

The variance estimate of $\hat{C}_a$ was derived as

$$SE^2(\hat{C}_a) = \hat{p}_{c,a}^2 \cdot SE^2(\hat{C}) + \hat{C}^2 \cdot SE^2(\hat{p}_{c,a})$$
$$+ SE^2(\hat{C}) \cdot SE^2(\hat{p}_{c,a})$$

Similarly, the total number of bass of age a that died due to hooking and handling stress ($\hat{H}_a$) was derived as follows:

$$\hat{H}_a = \hat{h} \cdot \hat{E} \cdot \hat{p}_{E,a}$$

where $\hat{h}$ is the proportion of released bass that die (Diodati and Richards, 1996), $\hat{E}$ is the number of released fish, and $\hat{p}_{E,a}$ is the proportion of age a in the releases. Its variance is given by:

$$SE^2(\hat{H}_a) = SE^2(\hat{h}) \cdot \hat{E}^2 \cdot \hat{p}_{E,a}^2 + \hat{h}^2 \cdot \hat{p}_{E,a}^2 \cdot SE^2(\hat{E}) +$$
$$\hat{h}^2 \cdot \hat{E}^2 \cdot SE^2(\hat{p}_{E,a}) + \hat{h}^2 \cdot SE^2(\hat{E}) \cdot SE^2(\hat{p}_{E,a}) +$$
$$\hat{p}_{E,a}^2 \cdot SE^2(\hat{h}) \cdot SE^2(\hat{E}) + E^2 \cdot SE^2(\hat{h}) \cdot SE^2(\hat{p}_{E,a}) +$$
$$SE^2(\hat{E}) \cdot SE^2(\hat{p}_{E,a}) \cdot SE^2(\hat{h})$$

Finally, $\hat{L}_a$ was estimated as:

$$\hat{L}_a = \hat{C}_a + \hat{H}_a$$

with

$$SE^2(\hat{L}_a) = SE^2(\hat{C}_a) + SE^2(\hat{H}_a)$$

We used the MRFSS harvest and release numbers, length-frequency, and age data for striped bass collected in Massachusetts during 2000, a representative year during the 1997–2000 diet study, to calculate abundance for each age class. Estimates of harvested and released fish by commercial striped bass anglers were not included in the analyses because fishing generally occurs in more offshore waters, harvested fish are generally outside the age range studied here (>age 8), and commercial discards represent only a small fraction (<2%) of what dies after release in the recreational fishery. Recreational harvest and release numbers from boats fishing in waters other than estuaries were not included because no justifiable means of partitioning the numbers into nearshore and offshore strata were available.

The total number of prey consumed by an age class was estimated by

$$\hat{P}_{ai} = \frac{\hat{Q}_{a,i}}{\hat{\bar{w}}_{a,i}}$$

where $\hat{P}_{a,i}$ is the total number of prey i consumed by age-class $a, \hat{Q}_{a,i}$ is the total biomass consumed, and $\hat{\bar{w}}_{a,i}$ is the average back-calculated weight of individuals of prey i found in the stomachs of striped bass. The variance of $\hat{P}_{a,i}$ is given by:

$$SE^2(\hat{P}_{a,i}) = \hat{P}_{a,i}^2 \cdot \left(\frac{SE^2(\hat{Q}_{a,i})}{\hat{Q}_{a,i}^2} + \frac{SE^2(\hat{\bar{w}}_{a,i})}{\hat{\bar{w}}_{a,i}^2} \right)$$

assuming negligible covariance (Mood *et al*., 1974). The total biomass and numbers of prey consumed by the population of striped bass and their variances were calculated by summing total age-class consumption and variances over all ages.

Total biomass and numbers consumed by all age-classes were compared to the commercial landings of American lobster, rock crab, Atlantic herring and Atlantic menhaden from northern Massachusetts, when data could be partitioned into regions, or from the entire state in order to examine the gross magnitude of striped bass predation in relation to human harvesting. Landings data were collected by the Massachusetts Division of Marine Fisheries and the National Marine Fisheries Service through various required dealer and/or fishermen reporting systems. Such comparisons may suggest potential impacts on ecologically- and economically-important prey as well as indirect impacts on humans.

Results

Individual Cumulative Consumption

Estimates of cumulative consumption of all prey ranged from 695 and 1 134 g/fish at age 3 to 3 010 and 4 361g/fish at age 8 during June–July and August–September, respectively, and were generally higher dur-

TABLE 2. Mean BEM cumulative consumption (*q*: g/fish), standard error (*SE*), and proportional standard error (*PSE*) of general prey taxa for ages 3–8 striped bass during June–July and August–September.

		June–July			Aug–Sept		
Age	Prey	*q*	*SE*	*PSE*	*q*	*SE*	*PSE*
3	All Prey	695.4	93.33	0.13	1134.3	155.79	0.14
	Polychaetes	62.3	34.24	0.55	3.0	1.48	0.49
	Molluscs	0.1	0.04	0.40	2.7	1.34	0.50
	Crustaceans	283.0	50.16	0.18	130.0	36.58	0.28
	Am. Lobster	0.6	0.41	0.68	3.5	2.52	0.72
	Rock Crab	73.2	18.38	0.25	83.2	25.22	0.30
	Fish	348.5	56.76	0.16	998.6	140.48	0.14
	Atl. Herring	210.7	44.20	0.21	–	–	–
	Menhaden	–	–	–	924.4	133.60	0.14
	Other	1.6	1.20	0.75	0.1	0.06	0.60
4	All Prey	1285.4	172.53	0.13	1641.5	243.58	0.15
	Polychaetes	30.8	22.35	0.73	3.1	3.11	1.00
	Molluscs	65.9	45.77	0.69	75.6	59.80	0.79
	Crustaceans	1008.2	143.83	0.14	256.0	60.24	0.24
	Am. Lobster	153.9	53.69	0.35	3.5	1.29	0.37
	Rock Crab	376.7	70.11	0.19	139.5	34.62	0.25
	Fish	180.6	37.64	0.21	1306.7	219.86	0.17
	Atl. Herring	37.4	13.26	0.35	–	–	–
	Menhaden	–	–	–	1194.7	206.00	0.17
	Other	–	–	–	–	–	–
5	All Prey	1827.9	270.99	0.15	2259.9	341.69	0.15
	Polychaetes	23.4	14.65	0.63	0.1	0.13	1.30
	Molluscs	18.6	16.51	0.89	27.4	36.47	1.33
	Crustaceans	1315.8	234.09	0.18	487.7	211.61	0.43
	Am. Lobster	235.6	99.16	0.42	56.0	63.70	1.13
	Rock Crab	647.5	151.27	0.23	245.6	178.72	1.14
	Fish	454.2	115.82	0.25	1744.4	364.07	0.21
	Atl. Herring	–	–	–	–	–	–
	Menhaden	–	–	–	1603.9	368.58	0.23
	Other	15.8	9.51	0.60	0.3	0.41	1.37
6	All Prey	2107.9	387.89	0.18	2783.1	456.81	0.16
	Polychaetes	13.2	10.05	0.76	6.6	9.23	1.40
	Molluscs	19.1	27.36	1.43	2.2	2.95	1.34
	Crustaceans	1034.5	405.28	0.39	685.1	266.93	0.39
	Am. Lobster	105.5	115.73	1.10	59.3	29.15	0.49
	Rock Crab	511.2	265.37	0.52	219.3	133.54	0.61
	Fish	1040.7	291.17	0.28	2089.2	417.39	0.20
	Atl. Herring	144.7	194.40	1.34	–	–	–
	Menhaden	–	–	–	1526.0	394.11	0.26
	Other	0.2	0.26	1.30	–	–	–
7	All Prey	2590.8	472.50	0.18	3423.1	564.01	0.16
	Polychaetes	0.2	0.25	1.25	<0.1	<0.01	1.10
	Molluscs	99.2	144.07	1.45	0.4	0.59	1.48
	Crustaceans	1438.7	678.11	0.47	1615.4	595.32	0.37
	Am. Lobster	839.6	546.55	0.65	599.5	305.17	0.51
	Rock Crab	443.1	180.69	0.41	302.8	283.63	0.94
	Fish	1043.2	655.05	0.63	1768.8	645.09	0.36
	Atl. Herring	209.5	290.40	1.39	–	–	–
	Menhaden	–	–	–	1010.2	672.07	0.66
	Other	9.6	13.34	1.39	38.5	63.44	1.65

TABLE 2. (Cont'd). Mean BEM cumulative consumption (*q*: g/fish), standard error (*SE*), and proportional standard error (*PSE*) of general prey taxa for ages 3–8 striped bass during June–July and August–September.

Age	Prey	June–July			Aug–Sept		
		q	*SE*	*PSE*	*q*	*SE*	*PSE*
8	All Prey	3009.7	543.53	0.18	4361.1	725.53	0.17
	Polychaetes	12.1	17.60	1.45	<0.1	<0.01	1.00
	Molluscs	0.4	0.59	1.48	117.4	131.65	1.12
	Crustaceans	1740.6	579.05	0.33	3843.7	733.46	0.19
	Am. Lobster	1448.4	501.99	0.35	824.4	851.00	1.03
	Rock Crab	166.4	96.19	0.58	1871.5	824.38	0.44
	Fish	1222.9	505.31	0.41	399.9	321.69	0.80
	Atl. Herring	360.5	297.75	0.83	37.6	48.42	1.29
	Menhaden	–	–	–	–	–	–
	Other	33.7	36.10	1.07	–	–	–

ing the latter period (Table 2). Striped bass consumed mostly crustaceans and fish, but more crustaceans (50–78% of total consumption) than fish were consumed by individuals of ages 4–8 bass during June–July, while more fish (52–88% of total consumption) than crustaceans were consumed by individuals of ages 3–7 during August–September (Fig. 3). In addition, the percentage of crustaceans and fish consumed during August–September increased and declined, respectively, as striped bass age increased (Fig. 3). Cumulative consumption of polychaetes, molluscs, and "other" prey per individual was low (<117 g/fish) during both time periods (Table 2; Fig. 3). Growth conversion efficiency was 0.09 for age 3, 0.07 for ages 4–6, and 0.06 for ages 7 and 8 striped bass.

Lobster consumption accounted for <12% of total consumption by ages 3–6 striped bass during June–July and August–September, but >17% of total consumption by ages 7 and 8 during both time periods (Table 2; Fig. 4). Consumption of rock crabs was generally highest during June–July, contributing up to 35% of the total consumption (Fig. 4), peaked at age 5, and generally declined as age of bass increased (the exception being age 8 in August–September) (Table 2). Estimates of Atlantic herring consumption (most had low precision) represented 0–30% of total cumulative consumption for ages 3–8 striped bass during June–July, but it contributed little to total consumption in August–September (Table 2; Fig. 4). No menhaden were consumed in June–July, but they became the dominant prey in August–September, contributing 29–81% of total consumption for ages 3–7 striped bass (Table 2; Fig. 4).

Estimates of Abundance

The total number of harvested ($\hat{C}$) and released ($\hat{E}$) striped bass estimated by the MRFSS in 2000 was 40 267 and 3.5 million fish, respectively (Table 3). Age-specific estimates of harvest ($\hat{C}_a$) ranged from 403 fish at age 5 to 8 456 fish at age 8, and estimates of bass that died due to handling and hooking ($\hat{H}_a$) ranged from 16 113 fish at age 3 to 93 455 fish at age 4 (Table 3). Combined losses-at-age (L_a) were highest at age 4 and declined as age increased (Table 4). Estimates of average abundance ranged from 88 906 fish at age 8 to 544 518 fish at age 4 during June–July, and from 77 679 fish at age 8 to 500 147 fish at age 4 during August–September (Table 4), indicating that about 1.3 million striped bass of ages 3–8 were present in nearshore waters of northern Massachusetts during summer of 2000. The large number of age 4 striped bass reflected the strong 1996 year-class spawned in Chesapeake Bay (Anon., 2004).

Age-class and Population Consumption

Age-class consumption of all prey ranged from 369 (metric tons) at age 3 to 1 521 t at age 4, and peaked at ages 4 and 6 (Table 5). Highest consumption of polychaetes, molluscs, crustaceans and fish was imposed by age 4 bass, but secondary peaks in consumption of crustaceans and fish occurred at ages 7 and 6, respectively (Table 5). Age 4 striped bass consumed the most rock crabs and menhaden, ages 7 and 8 striped bass consumed the most lobsters, and age 3 striped bass consumed the most Atlantic herring (Table 6). Together,

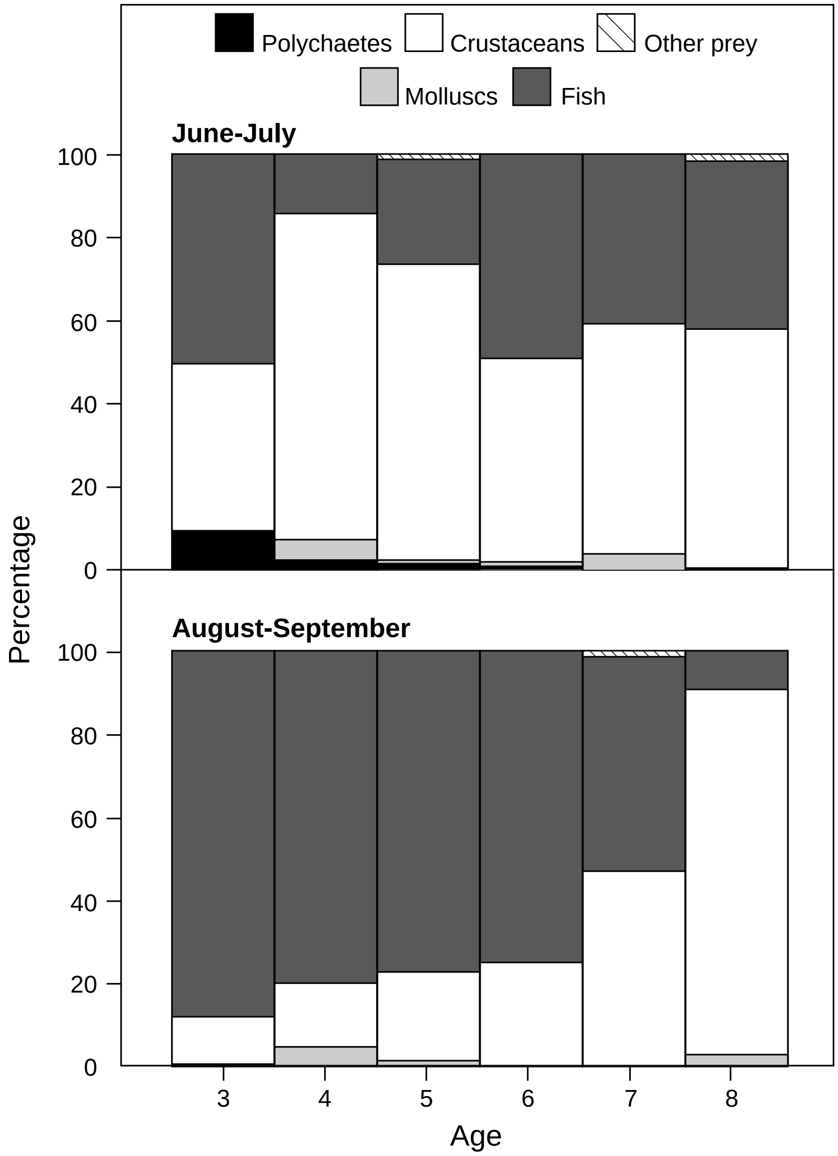

Fig. 3. General prey composition (percentage of total consumption (g)) of ages 3–8 striped bass during June–July and August–September in northern Massachusetts.

prey consumption by all ages totaled over 5 575 t. Atlantic menhaden accounted for 29% of the total biomass consumed seasonally by ages 3–8 striped bass in 2000, followed by rock crabs (18%), American lobster (11%), and Atlantic herring (3%).

The seasonal biomass consumption of lobsters by striped bass was much lower than the annual commercial landings of northern Massachusetts in 2000, while the consumption of rock crab was much higher (Table 7). Striped bass consumed more menhaden biomass, but less herring biomass, than were landed statewide (Table 7). On a numerical basis, however, striped bass consumed seasonally over 3, 1 940, and 965 times the numbers of lobsters, rock crabs, and menhaden, respectively, taken annually by regional and statewide fisheries due to the small sizes of prey eaten (Table 7).

Discussion

Individual Cumulative Consumption

We believe that the estimates of individual cumulative consumption produced by the BEMs are reasonably accurate for several reasons. First, the efficacy of this modeling approach has been corroborated for many fish

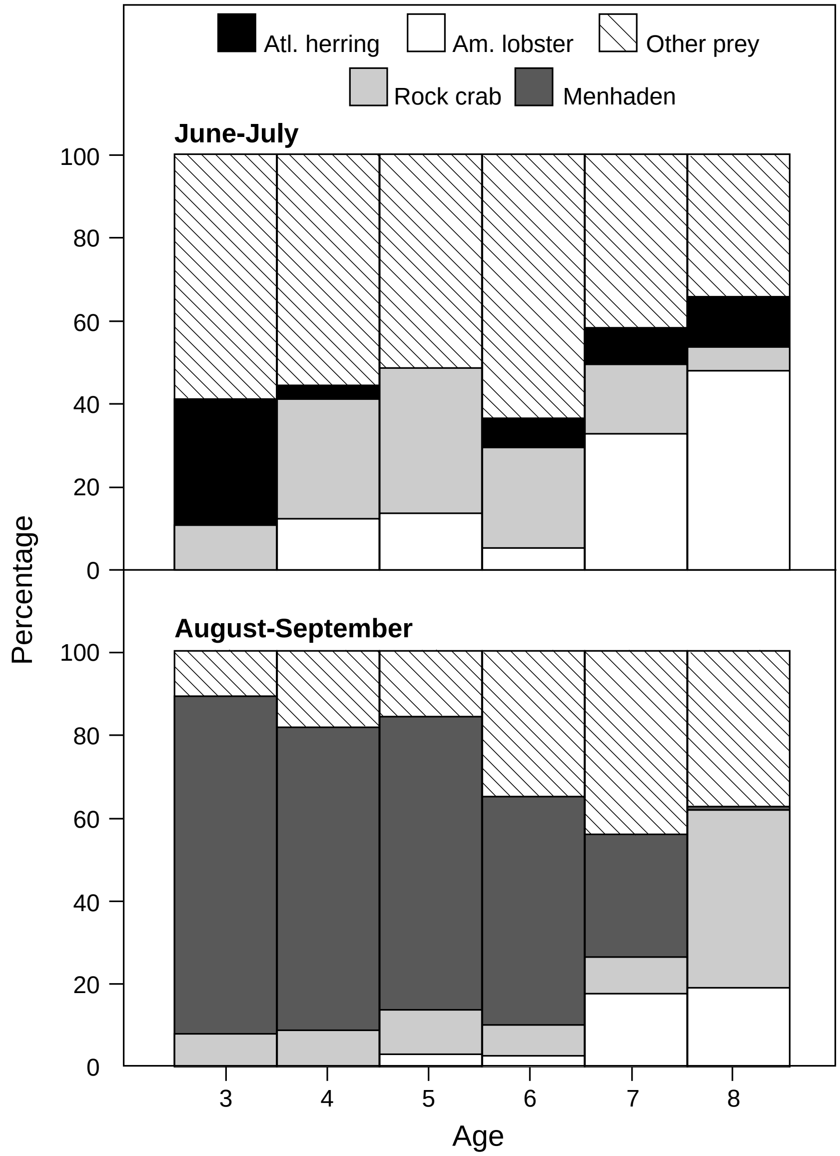

Fig. 4. Selected-prey composition (percentage of total consumption (g)) of ages 3–8 striped bass during June–July and August–September in northern Massachusetts.

species (e.g., Beauchamp *et al.*, 1989; Huuskonen *et al.*, 1998) including age 0 striped bass (Hartman and Brandt, 1993; Hartman, 2000a). Second, the model parameters for the consumption and respiration equations, the most important contributors to prediction errors (Bartell *et al.*, 1986), were well-estimated by Hartman and Brandt (1995a). Lastly, the diet data reflected average composition over each period (Nelson *et al.*, 2003) and therefore assuming it reflected the daily composition is not unreasonable. Similarly, the exponential model should give accurate predictions of average growth given that the sample size was large, and declines in growth during warm months were not expected because water temperatures in northern Massachusetts never approach critical temperatures (>30°C) (DMF daily temperature records from 1997–2005).

Our results showed that the contribution of specific prey to the production of striped bass varied over time. Most consumption came from benthic crustaceans during June and July, and from pelagic fish during August–September. Rock crabs and lobsters became more

TABLE 3. Estimates of parameters and standard errors (*SE*) used to calculate abundance of ages 3–8 striped bass in coastal waters of northern Massachusetts in 2000. $\hat{C}$ and $\hat{E}$ are estimated harvest and release numbers, respectively, $\hat{h}$ is the proportion of released bass that die, $\hat{p}_{c,a}$ and $\hat{p}_{E,a}$ are proportions of age *a* in the harvest and releases, and $\hat{C}_a$ and $\hat{H}_a$ are the estimated numbers-at-age of harvest and releases that die.

$\hat{C}$	$SE(\hat{C})$	$\hat{E}$	$SE(\hat{E})$	$\hat{h}$	$SE(\hat{h})$	*Age*	$p_{c,a}$	$SE(p_{c,a})$	$p_{E,a}$	$SE(p_{E,a})$	$\hat{C}_a$	$SE(\hat{C}_a)$	$\hat{H}_a$	$SE(\hat{H}_a)$
40 267	6 838.7	3 580 657	309 715	0.09	0.02	3	0.0	0.000	0.05	0.007	0	0.0	16 113	4 498.8
						4	0.0	0.000	0.29	0.016	0	0.0	93 455	22 977.8
						5	0.01	0.002	0.21	0.013	403	106.5	67 674	16 753.4
						6	0.05	0.011	0.20	0.012	2 013	564.6	64 452	15 923.6
						7	0.24	0.028	0.15	0.010	9 664	2 000.4	48 339	12 029.8
						8	0.21	0.022	0.06	0.006	8 456	1 694.1	19 336	5 034.9

TABLE 4. Estimates of annual losses (*L*) and average abundance (*N*) during the June–July and August–September periods in 2000 for ages 3–8 striped bass in coastal waters of northern Massachusetts. Parameters are defined in the text.

						June–July				August–September			
Age	L_a	$SE(L_a)$	μ_a	F_a	Z_j	ρ	θ	$\hat{\hat{N}}_a$	$SE(\hat{\hat{N}}_a)$	ρ	θ	$\hat{\hat{N}}_a$	$SE(\hat{\hat{N}}_a)$
3	16 113	4 498.8	0.07	0.08	0.052	0.417	0.167	207 957	58 062.2	0.583	0.500	197 485	55 138.5
4	93 455	22 977.8	0.15	0.18	0.085	0.417	0.167	544 518	133 880.8	0.583	0.500	500 147	122 971.1
5	68 077	16 753.7	0.22	0.27	0.115	0.417	0.167	262 518	64 605.4	0.583	0.500	233 999	57 587.0
6	66 465	15 933.6	0.23	0.28	0.118	0.417	0.167	244 350	58 577.8	0.583	0.500	217 081	52 040.5
7	58 003	12 195.0	0.28	0.35	0.142	0.417	0.167	171 166	35 987.1	0.583	0.500	148 556	31 233.6
8	27 792	5 312.3	0.26	0.33	0.135	0.417	0.167	88 906	16 994.0	0.583	0.500	77 679	14 847.9

TABLE 5. Seasonal (1 June–30 September) consumption ($\hat{Q}$) of prey in weight (metric tons) by striped bass of ages 3–8 in coastal waters of northern Massachusetts. Standard errors (*SE*) and prpoprtional standard errors (*PSE*) are shown.

Age	Statistic	Polychaetes	Molluscs	Crustaceans	Fish	Other	All Prey
3	$\hat{Q}$	13.5	0.6	84.5	269.7	0.3	368.6
	SE	8.23	0.31	22.25	66.49	0.31	83.48
	PSE	0.61	0.51	0.26	0.25	1.03	0.23
4	$\hat{Q}$	18.3	73.7	677.0	751.9		1 520.9
	SE	13.29	42.09	163.30	199.18		308.96
	PSE	0.72	0.57	0.24	0.26		0.20
5	$\hat{Q}$	6.2	11.3	459.5	527.4	4.2	1 008.7
	SE	4.24	10.05	120.92	140.11	9.43	207.44
	PSE	0.68	0.89	0.26	0.26	2.24	0.21
6	$\hat{Q}$	4.6	5.1	401.5	707.8	<0.1	1 119.2
	SE	3.37	7.00	137.35	171.96	0.07	236.89
	PSE	0.73	1.37	0.34	0.24	1.40	0.21
7	$\hat{Q}$	<0.1	17.0	486.2	441.3	7.4	952.0
	SE	0.04	25.44	165.71	164.86	9.99	185.16
	PSE	1.33	1.50	0.34	0.37	1.35	0.19
8	$\hat{Q}$	1.1	9.1	453.3	139.8	3.0	606.3
	SE	1.61	10.56	101.21	56.62	3.32	111.89
	PSE	1.46	1.16	0.22	0.40	1.11	0.18

important to striped bass when Atlantic menhaden were absent. Atlantic herring were important to age 3 striped bass during June–July only. These differences in consumption may be due, in part, to the temporal and spatial availability of prey to striped bass. High densities of lobsters and rock crabs are known to occur in the rocky and boulder-strewn areas that dominate northern Massachusetts coastlines (Bigford, 1979; MacKenzie and Moring, 1985; Chase *et al*., 2002). In regions where rocky areas are absent, these crustaceans comprise lower percentages of the diet of striped bass (Nelson *et al*, 2003). Juvenile Atlantic herring are abundant in the nearshore waters of the Gulf of Maine, including Massachusetts, during spring and early summer, but they move to deeper, offshore areas during summer and autumn (Stevenson and Scott, 2005); therefore, the near-absence of herring

TABLE 6. Seasonal consumption of selected prey in weight ($\hat{Q}$ in metric tons), mean weight (*g*) of individual prey ($\hat{\bar{w}}$), seasonal consumption in numbers ($\hat{P}$), and proportional standard errors (*PSE*). Standard errors are shown in parentheses.

Age	*Prey*	$\hat{Q}$	PSE_Q	$\hat{\bar{w}}$	PSE_w	$\hat{P}$	PSE_P
3	Am. Lobster	0.8 (0.54)	0.68	29.3 (12.17)	0.41	2.7×10^4 (2.16×10^4)	0.79
	Rock Crab	31.7 (8.86)	0.28	5.1 (1.38)	0.27	6.2×10^6 (2.42×10^6)	0.39
	Atl. Herring	43.8 (15.30)	0.35	5.0 (0.72)	0.14	8.8×10^6 (3.31×10^6)	0.38
	Menhaden	182.6 (57.40)	0.31	2.2 (0.13)	0.06	8.3×10^7 (2.66×10^7)	0.32
4	Am. Lobster	100.5 (38.60)	0.38	29.3 (12.17)	0.41	3.4×10^6 (1.94×10^6)	0.57
	Rock Crab	274.9 (67.78)	0.25	7.8 (0.47)	0.06	3.5×10^7 (8.95×10^6)	0.25
	Atl. Herring	20.4 (8.79)	0.43	5.0 (0.72)	0.02	4.1×10^6 (1.85×10^6)	0.45
	Menhaden	597.5 (179.4)	0.30	2.1 (0.07)	0.03	2.8×10^8 (8.61×10^7)	0.30
5	Am. Lobster	75.0 (33.79)	0.45	29.3 (12.17)	0.41	2.6×10^6 (1.57×10^6)	0.61
	Rock Crab	227.4 (72.63)	0.32	9.8 (0.74)	0.08	2.3×10^7 (7.62×10^6)	0.33
	Atl. Herring	–					
	Menhaden	375.3 (136.4)	0.34	2.7 (0.10)	0.04	1.4×10^8 (4.71×10^7)	0.34
6	Am. Lobster	38.6 (29.79)	0.77	29.3 (12.17)	0.41	1.3×10^6 (1.15×10^6)	0.88
	Rock Crab	172.5 (77.92)	0.45	5.8 (0.71)	0.12	3.0×10^7 (1.39×10^7)	0.47
	Atl. Herring	35.4 (48.25)	1.36	106.0 (39.73)	0.37	3.3×10^5 (4.72×10^5)	1.41
	Menhaden	331.3 (116.7)	0.35	2.5 (0.15)	0.06	1.3×10^8 (4.74×10^7)	0.36
7	Am. Lobster	232.8 (109.9)	0.47	79.7 (14.81)	0.18	2.9×10^6 (1.48×10^6)	0.51
	Rock Crab	120.8 (55.46)	0.46	10.2 (1.07)	0.10	1.2×10^7 (5.58×10^6)	0.47
	Atl. Herring	35.9 (50.28)	1.40	106.0 (39.73)	0.37	3.4×10^5 (4.91×10^5)	1.45
	Menhaden	150.1 (104.7)	0.70	4.1 (0.20)	0.05	3.7×10^7 (2.56×10^7)	0.70
8	Am. Lobster	192.8 (84.36)	0.44	79.7 (14.81)	0.18	2.4×10^6 (1.15×10^6)	0.48
	Rock Crab	160.2 (70.38)	0.44	11.1 (1.31)	0.12	1.4×10^7 (6.57×10^6)	0.45
	Atl. Herring	35.0 (27.44)	0.78	106.0 (39.73)	0.37	3.3×10^5 (2.87×10^5)	0.87
	Menhaden	–		–		–	
All	Am. Lobster	640.5 (150.7)	0.24			1.3×10^7 (3.33×10^6)	0.26
	Rock Crab	987.5 (155.1)	0.16			1.2×10^8 (2.03×10^7)	0.17
	Atl. Herring	170.5 (76.94)	0.45			1.4×10^7 (3.86×10^6)	0.28
	Menhaden	1 636.8 (280.5)	0.17			6.8×10^8 (1.15×10^8)	0.17

in the diets during August–September may reflect this migratory pattern. Atlantic menhaden young-of-the-year migrate from local estuaries to nearshore waters during August–September (Munroe 2002; Chase *et al*., 2002), and become more available to striped bass in nearshore waters. The importance of menhaden to the production of striped bass has been reported in other studies (Hartman and Brandt, 1995c; Uphoff, 2003).

Our results also showed that the contribution of specific prey to the production of striped bass varied with the age of striped bass. Rock crabs and lobsters became more important to striped bass as bass aged, but Atlantic menhaden became less important. The increase in rock crab and lobster importance may reflect increases in predator morphology related to ingestion (e.g. gape height and throat width) as bass grow in size (e.g. Chervinski *et al*., 1989; Hartman, 2000b). The decline in menhaden importance with age during August–September may reflect the absence of large, adult schools from nearshore waters in the past decade that seem to be optimal sizes for older (and larger) bass (Overton, 2002).

Seasonal growth conversion efficiencies of striped bass from northern Massachusetts were equal to or higher than annual growth conversion efficiencies of striped bass from Chesapeake Bass (Hartman and Brandt, 1995c). Although difficult to interpret because of the differences in the duration over which the conversion efficiencies were calculated, the results may suggest that bass foraging in

TABLE 7. Comparison of striped bass consumption and fishery landings characteristics from northern Massachusetts in 2000. 95% confidence intervals are shown in parentheses.

Prey	Unit	Striped Bass Consumption		Fishery Landings
Am. Lobster	Biomass (t)	640.5	(345.1–935.8)	2 253
	Number (millions)	12.7	(3.3–19.2)	3.9
	Mean Carapace Length (mm)	36		88
Rock Crab	Biomass (t)	987.5	(683.5–1291.4)	12.0
	Number (millions)	120.7	(80.9–160.9)	<0.1
	Mean Carapace Width (mm)	30		140
Atlantic Herring	Biomass (t)	170.5	(31.4–309.5)	4 361[1]
	Number (millions)	13.8	(6.3–21.4)	23.1
	Mean Total Length (mm)	84		280
Menhaden	Biomass (t)	1636.8	(1 096.2–2 177.4)	136[1]
	Number (millions)	675.6	(450.2–910.0)	0.7
	Mean Total Length (mm)	62		242

[1] represents landings from all Massachusetts waters

northern Massachusetts waters experience during their summer residence a slight growth advantage over resident Chesapeake Bay fish perhaps due to a larger scope for growth at more optimum temperatures and/or higher, consistent prey availability (Brandt, 1993). Our estimates of seasonal age-specific individual consumption for ages 3–6 represent about 21–30% of the annual individual consumption for resident striped bass of age 3–6 in Chesapeake Bay (Hartman and Brandt, 1995c).

Estimates of Abundance

The accuracy of the estimates of average abundance is entirely dependent on the mortality parameters and catch data included in the cohort survival-catch equation model. Many simplifications were made because of lack of data. A constant natural mortality rate was used for all ages because only one estimate is available (Anon., 2004), but in reality it is likely higher for the younger ages (Quinn and Deriso, 1999). Higher natural mortality rates would increase the estimates of average abundance produced in this study. The 2000 F estimate used is reasonable given that it is similar to the 2000 F estimate for the coast-wide striped bass population (Anon., 2004); however, average abundance estimates would change slightly if the full F was distributed differently across months. If MRFSS data could be partitioned into finer spatial scales, boat catches from nearshore water could be incorporated into the model which would add harvest and release to the model, ultimately increasing the estimates of average abundance. Given current data limitation and knowledge of striped bass population and fishery dynamics, the abundance estimates are the best available for northern Massachusetts.

Age-class and Population Consumption

Striped bass appear to consume substantial amounts of prey during their seasonal residence in nearshore waters of northern Massachusetts. The striped bass population of ages 3–8 consumed over 5 500 t of prey (mostly crustaceans and fish) and, compared to the results of Hartman (2003), the estimate represents about 4% of the total consumption for the Atlantic coast striped bass population. Striped bass consumption of Atlantic menhaden and herring from northern Massachusetts in 2000 represented about 0.4% of the Atlantic coast abundance of ages 0 and 1 menhaden (Anon., 2003) and it represented about 0.3% of the Georges Bank/Gulf of Maine population of age 0 (back-calculated from age 1 recruitment in 2001 and M = 0.5) and age 1 Atlantic herring (Overholtz *et al*., 2004). In 2000, age 4 striped bass, the large 1996 year-class from Chesapeake Bay, had the highest contribution to total biomass consumption suggesting that if striped bass are capable of exerting significant predation pressure on prey, it will vary, in part, with striped bass year-class strength. Similar conclusions have been reached for coastal bluefish (Buckel *et al*., 1999) and

Chesapeake Bay resident striped bass (Hartman and Brandt, 1995c).

Striped bass could have local influence on population dynamics of rock crabs, menhaden, and lobsters in Massachusetts because striped bass consumption exceeded the statewide and regional fisheries landings in biomass and/or numbers for these species. However, the true strength of their impact will depend on the population sizes of the prey. If consumption of prey by striped bass reaches levels that impact prey abundances, the influence will be likely on recruitment of individuals to the local and coastal fisheries because striped bass consumed mostly pre-recruits (YOY and age 1). Given that striped bass abundance has increased dramatically since the late 1980s, their predatory impact has probably increased as well. Uphoff (2003) suggested that increased predation by the recovered striped bass population was responsible for declines in Atlantic menhaden population in Chesapeake Bay and possibly coast-wide. In Massachusetts, lobster recruitment to the inshore Gulf of Maine area has been declining (Anon., 2006) concurrent to increases in recreational catches (a reasonable proxy for striped bass abundance), suggesting potential impact by striped bass predation. Although cause and effect can not be insinuated from this comparison, it does suggest that further quantification of striped bass and prey population dynamics, particularly predation mortality, is warranted. Currently, there are no estimates of local prey abundances from which the direct impact of striped bass predation on prey could be quantified. This should be the next step in the investigations to understand the impacts of striped bass predation in Massachusetts.

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