

Effects of Age-1 Striped Bass Predation on Juvenile Fish in Western Albemarle Sound

JACK E. TUOMIKOSKI,*¹ PAUL J. RUDERSHAUSEN, AND JEFFREY A. BUCKEL

Department of Zoology, Center for Marine Sciences and Technology, North Carolina State University,
303 College Circle, Morehead City, North Carolina 28557, USA

JOSEPH E. HIGHTOWER

U.S. Geological Survey, North Carolina Cooperative Fish and Wildlife Research Unit, Department of
Zoology, North Carolina State University, Campus Box 7617, Raleigh, North Carolina 27695-7617, USA

Abstract.—Historically, the fisheries for adult river herring (i.e., alewife *Alosa pseudoharengus* and blueback herring *A. aestivalis*) and American shad *A. sapidissima* were economically important in Albemarle Sound, North Carolina. Stocks of these species are in decline, while stocks of striped bass *Morone saxatilis* have increased roughly 10-fold in the Albemarle Sound–Roanoke River since the early 1990s. The goal of this study was to quantify the predatory impact of age-1 striped bass on age-0 prey fishes by estimating striped bass consumption rates and comparing loss rates from predation with total prey loss rates using catch curves. Age-1 striped bass and their potential prey were collected with beach and purse seines from western Albemarle Sound from spring to fall, 2002 and 2003. Commercially and ecologically important prey in one or both years included river herring, American shad, Atlantic menhaden *Brevoortia tyrannus*, and yellow perch *Perca flavescens*. Predation by age-1 striped bass had a marked effect on juvenile American shad densities in 2002 but little effect in 2003. Conversely, predation by age-1 striped bass explained none of the loss in juvenile yellow perch in 2002 but accounted for nearly all of the loss early in 2003. In most cases, predation by age-1 striped bass did not greatly influence juvenile alewife numbers. Juvenile blueback herring were preyed on during late summer and fall, but the predatory impact could not be confirmed because of apparent downstream emigration into the study area. Thus, for some species, these predator–prey linkages are important in determining year-class strength and should be incorporated into multispecies population models.

Predation can be a major source of mortality of prey fishes (Bax 1998). Predator–prey interactions have received considerable attention in freshwater ecosystems (e.g., Tonn et al. 1992) but have been studied less in coastal systems (Hartman and Brandt 1995a) despite the likely importance of predation in regulating abundance of species that use estuaries as nurseries (Sheaves 2001). Research identifying predator–prey relationships and quantifying the effects of these relationships will improve our understanding of the factors influencing recruitment and guide ecosystem-based fisheries management (Latour et al. 2003).

Historically, the fisheries for river herring (i.e., alewife *Alosa pseudoharengus* and blueback herring *A. aestivalis*) and American shad *A. sapidissima* were economically important in coastal North Carolina, including Albemarle Sound (Hightower et al. 1996). The dramatic decline of these fish stocks in North Carolina and other Atlantic coastal states is probably

due to overfishing and loss of habitat (Crecco and Gibson 1990; Rulifson 1994). It was estimated that the Albemarle Sound river herring fishery would increase 10-fold in value if the population could rebuild to support the average annual catch from 1880 to 1970 (Hightower et al. 1996). The juvenile abundance index for Albemarle Sound blueback herring has been low since the mid 1980s and recruitment will have to improve before the river herring stock can recover (Carmichael 2003).

Predation by striped bass *Morone saxatilis* could influence year-class strength in *Alosa* spp. Savoy and Crecco (2004) provide evidence that striped bass predation on juvenile and adult blueback herring and American shad may have caused an otherwise unexplained decline in their abundance since the early 1990s. The U.S. East Coast striped bass population may currently be at record levels after a moratorium in the 1980s (Hartman and Margraf 2003). In Albemarle Sound, the number of striped bass age 4 and older has increased by an order of magnitude since the early 1990s (Grist 2004). The influence of increased striped bass biomass on their prey has been shown to be significant in Chesapeake Bay and Hudson River, New York (Hartman and Brandt 1995a; Hartman 2003;

* Corresponding author: jtuomikoski@yahoo.com

¹ Present address: Fish Passage Center, 1827 NE 44th Avenue, Suite 240, Portland, Oregon 97213, USA.

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Overton 2003; Uphoff 2003) but has not been quantified in Albemarle Sound.

Age-1 striped bass and juvenile *Alosa* spp. interact in Albemarle Sound. A study by Manooch (1973) and a companion study to this paper (Rudershausen et al. 2005) found *Alosa* spp. in age-1 striped bass diets in western Albemarle Sound; this area has the highest summer abundance of juvenile *Alosa* spp. based on 15 years of North Carolina Division of Marine Fisheries monitoring programs (NCDMF, unpublished data). We focused on age-1 striped bass as predators because *Alosa* spp. were never a dominant prey of age-2 and older striped bass (Rudershausen et al. 2005) and the density of larger striped bass is lower and more difficult to quantify. Studies in other systems found that younger striped bass (ages 1–3) dominate the population-level consumption of biomass (Hartman and Brandt 1995a; Cyterski et al. 2002; Overton 2003).

Age-1 striped bass may affect fish prey other than *Alosa* spp. Atlantic menhaden *Brevoortia tyrannus* are known as a striped bass diet item (Hartman 2003; Walter et al. 2003) and are a common prey of striped bass in Albemarle Sound (Manooch 1973; Rudershausen et al. 2005). Yellow perch *Perca flavescens*, a common diet item of age-1 striped bass in Albemarle Sound in 2003 (Rudershausen et al. 2005), have an expanding commercial fishery in North Carolina. Due to interest in their management, these two prey species were included in this study.

The focus of this study was on the early juvenile stages of prey during summer to determine whether age-1 striped bass predation had the potential to influence year-class strength. The objectives of this study were to (1) estimate the consumption rates of age-1 striped bass with a bioenergetics model and a field gastric evacuation approach; (2) calculate total loss rates for several juvenile fishes using catch curves; and (3) determine the predatory effect of striped bass by comparing the predation mortality rates with the total loss rates of prey fishes. Estimates of numbers of prey eaten were compared with numbers of prey present when total loss rates could not be estimated.

Methods

Study area.—Albemarle Sound is a submerged river bottom oligohaline estuary supplied with saltwater through Oregon Inlet and freshwater from the Chowan and Roanoke rivers; salinity is inversely related to river flow and stratification is disrupted by high winds (Bowden and Hobbie 1977). There is little tide, but easterly winds can cause waters to rise 0.3–0.6 m (Heath 1983). The study area consists of two depth zones. Shoals are 0–4 m deep and extend up to 1,400 m between beach and channel areas. Channels are

approximately 6 m deep. The area sampled in western Albemarle Sound was 32 km long and at most 13 km wide (see Figure 1 in Rudershausen et al. 2005).

Field sampling.—Striped bass and potential prey were sampled by beach seines in shoal areas and purse seines in channel areas. Biweekly seining in 2002 was exploratory, as well as functional, whereas sampling in 2003 was at fixed sites. In 2002 and 2003, both shoal and channel areas were sampled biweekly from May through August and once every 3 weeks in September and October. However, we did not sample during the period September 5–30, 2003, owing to safety issues caused by debris from Hurricane Isabel. Temperature, salinity and dissolved oxygen concentration were recorded at the surface at beach seine sites and at the surface and bottom at purse seine sites.

Shoals were sampled during the day with a 61-m × 3-m (~500 m²) beach seine (6.4-mm-bar mesh wings and 4.8-mm-bar mesh bag) set by boat. Shoals were not sampled at night due to snags and other hazards involved in setting and retrieving beach seines after dark. Beach seines of this type have been used to quantify age-0 fish densities in other estuaries (McBride et al. 1995; Buckel et al. 1999). Each biweekly beach seine trip consisted of one haul at a minimum of 18 stations in 2002 and 18 fixed stations in 2003.

The channel was sampled at night with a purse seine set by boat. The purse seine was 6.1 m × 76.2 m (7.6-mm-bar mesh, 462 m² in area). Purse seines of this type have effectively quantified pelagic juvenile fish densities in other studies (Tischler et al. 2000) and give similar density estimates of fish as horizontal acoustics (Yule 2000). We sampled with the purse seine at night because *Alosa* spp. migrate vertically towards the surface after dark (Dixon 1996) and reduced schooling behavior of fish at night reduces variance in purse seine catches (Tischler et al. 2000). The purse seine fished the entire water column because the depth of the net was greater than the water depth. A set of purse seine samples consisted of one seine haul from at least 7 stations in 2002 and 12 fixed stations in 2003. Only 4 sites were sampled during August 11–17, 2002, and 10 sites during June 1–6, 2003, due to adverse weather.

Sampling of shoal or channel areas took place over two to four consecutive days because all sample sites could not be visited in a single day. The mean catch per unit effort (CPUE) was assigned to the first of two consecutive sample days; however, if sampling occurred over more than 2 d, the midpoint date was used as the date of collection. Density estimates for age-1 striped bass and prey needed for calculations of

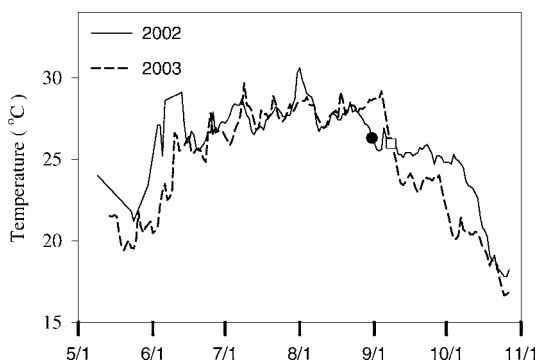


FIGURE 1.—Mean temperatures used in the striped bass bioenergetics model in 2002 and 2003, by date. The circle and square at about September 1 denote the first late-summer mean temperature of 26°C for 2002 and 2003, respectively.

predation effects (see below) used the gear areas (m^2) and assumed 100% capture efficiency.

Additional age-1 and older striped bass were collected in the sampling area by means of angling, boat electrofishing, gill netting, and trawling to supplement predator diet and growth data. Gill nets (bar mesh sizes of 13, 25, 38, 51, 64, and 76 mm) were soaked for less than 1 h to minimize the regurgitation and digestion of stomach contents (Sutton et al. 2004). Samples were also used from 24-h trips (see the section on gastric evacuation model estimates of consumption rate).

Upon capture, striped bass and prey fish were identified and measured. Age-1 and older striped bass were preserved in 10% formalin for later diet analysis (Rudershausen et al. 2005). *Alosa* spp. were preserved in ethanol and measured (total length [TL]; mm) and weighed (0.01 g) in the laboratory; large catches were volumetrically subsampled first. Other fishes were measured, counted, and returned to the sound. In 2003, subsamples of age-1 striped bass and potential prey fishes were frozen in water for later determination of seasonal energy content.

Bioenergetics model estimates of consumption rate.—Bioenergetics models have been developed for many fish species and are often used to predict consumption. We used the Kitchell et al. (1977) version of the mass-balanced bioenergetics models to estimate the daily ration of age-1 striped bass. This model has the general form

$$C = (R + A + SDA) + (F + U) + \Delta B,$$

where C is the specific rate of food consumption, R is resting metabolism, A is active metabolism, SDA is specific dynamic action, F is egestion, U is excretion, and ΔB is somatic growth. Each factor is expressed in

joules of energy while fitting daily consumption to costs and growth; consumption (C) is then converted back to a rate of biomass eaten by fish ($g \cdot g^{-1} \cdot d^{-1}$). The model was programmed into MATLAB (Mathworks 2002) and run with the physiological parameters for age-1 striped bass (Hartman and Brandt 1995b) for all simulations. Daily consumption rates were estimated with the model from May 9 to October 31, 2002, and from May 13 to October 31, 2003. Input requirements for the model include daily estimates of temperature, predator diet, predator growth, and energy content of both predator and prey; estimates for each input were specific to the study area.

Temperature was measured in both years by hourly temperature loggers placed 1 m below the surface in channel and shoal areas. Biweekly seining trips gave point estimates of shoal surface temperatures, and channel surface and bottom temperatures, respectively. A temperature datum for one model-day was a mean of all available mean temperatures; the most comprehensive example would be the mean of mean shoal logger, mean channel logger, mean beach seine, and mean purse seine temperatures (Figure 1). We linearly interpolated between point measurements of temperature on certain dates of 2002 (May 9, May 23, May 30, June 6, and June 13) because the temperature loggers were not yet installed. Water temperatures for the rest of 2002 included logger and point measurements. In 2003, temperature measurements were unrecoverable from the shoal temperature logger, but beach seine point measurements of temperature were available for this habitat.

Age-1 striped bass diet data were taken from Rudershausen et al. (2005). They computed mean monthly diet values with variance estimates for 2002 ($n = 411$) and 2003 ($n = 267$) using cluster estimators (see Buckel et al. [1999] for a description of cluster estimation.) Monthly cluster estimators of food biomass may not add up to 100% and were normalized to 100% for bioenergetics modeling. For each year, May diet values were assigned to the first model-day and June–August values were assigned to the mid-point of each month. Because Rudershausen et al. (2005) grouped yearly September and October diet values into one category, these values were assigned to September 15 onward. The model linearly interpolated between all monthly estimates to arrive at daily values.

The seasonal energy content of striped bass and prey was estimated by applying relationships between percent dry weight and whole body energy content (Tuomikoski 2004). We used published models (Rippetoe 1993; Hartman and Brandt 1995c) from data sets that included or were exclusively used for similar aged fish (e.g., age-1 striped bass, age-0

Atlantic menhaden). In the case of age-0 yellow perch, a linear model was created using data from Lantry (1997) and Kelso (1973). A linear silverside model was created using data supplied by Eric Schultz (University of Connecticut, personal communication; see Tuomikoski 2004 for equations). In the laboratory, fish were thawed, patted dry, weighed (0.001 g), and dried at 70°C until weights were stable to determine percent dry weight. The bioenergetics model linearly interpolated between all estimates of energy content. Where estimates of energy content were not available on the first model day, the closest temporal estimate was used. Energy values for invertebrates were means of static values from Cummins and Wuycheck (1971), Schindler et al. (1971), Thayer et al. (1972), Driver et al. (1974), and Steimle and Terravona (1985).

Observed growth of the predator over the period of interest is required by the bioenergetics model. To estimate size of an average predator at even temporal intervals, a logistic growth curve (Williams et al. 2001) was fit to predator weight data. The logistic curve equation was

$$W_{SB} = \beta / (1 + k \cdot e^{-\lambda t}),$$

where W_{SB} is the weight of an age-1 striped bass (g), t is the day of the year and β , k , and λ are parameters. This was fit for each field season with the SAS NLIN procedure (SAS 2001). Each year's growth curve (Figure 2) was used to generate input weights for the model in 14-d increments as these short time periods more accurately predict consumption (Rice and Cochran 1984).

Gastric evacuation model estimates of consumption rate.—The gastric evacuation model estimates of the consumption rate were used to corroborate predictions from the bioenergetics model. This method of estimating daily ration requires data on stomach fullness over 24 h and gastric evacuation rate estimates at temperatures similar to field conditions. Collection areas were selected to minimize gear issues (i.e., with few snags and safely navigable at night), and based on previous high catches of age-1 striped bass. Collections were made every 4 h on June 11, 2002, July 11, 2002, July 10, 2003, August 5, 2003, and September 8, 2003. Striped bass were collected with the beach seine in 2002. In 2003, gill nets and electrofishing were used because striped bass were not dense at beach seine areas. The results of 24 h sampling were entered into the Eggers equation (Eggers 1977), presented here as

$$C = 24 \cdot \bar{S} \cdot G_e,$$

where C is the daily consumption rate (g prey \cdot g predator⁻¹ \cdot d⁻¹), G_e is the instantaneous rate of gastric

evacuation, and \bar{S} is mean stomach fullness (g/g) of all 4-h estimates of stomach fullness in a 24-h period. The instantaneous gastric evacuation rate, G_e , was estimated by fitting an exponential model to decreasing stomach fullness with the SAS NLIN procedure (SAS 2001). The equation used to estimate G_e was

$$S_t = S_0 \cdot e^{-G_e \cdot t},$$

where S_t is the mean stomach fullness at time t , S_0 is the mean stomach fullness at time zero (peak gut fullness level), and t is the elapsed time in hours. Feeding is assumed to be zero over periods where G_e is estimated from the loss in stomach contents. In 2002, G_e was estimated from 1600 to 0800 hours in July 2002 and from 0800 to 1600 hours in July 2003. Changes in G_e are linked with water temperature (He and Wurtsbaugh 1993). The daily mean temperature varied by less than 0.5°C for the two 2002 collections and by less than 1°C for the two successful 24-h collections in 2003. Therefore, each year's G_e estimate was used for both ration computations within that year. Standard errors for field estimates of consumption rates were computed by means of the delta method (Williams et al. 2001:736–737).

Prey loss due to predation.—Daily prey loss rates from predation were calculated separately for channel and shoal samples. The biomass of the predator within the area of a seine haul on a given date was calculated as

$$B_{SB} = D_{SB} \cdot W_{SB},$$

where B_{SB} is the biomass of predators (g/seine haul), D_{SB} is the density of striped bass (individuals/seine haul), and W_{SB} is the estimated weight of an average predator (g). Then biomass eaten was calculated as

$$B_{PREY} = B_{SB} \cdot C \cdot P_{PREY},$$

where B_{PREY} is the biomass of a particular prey type eaten (g), C is the consumption rate from the bioenergetics model, and P_{PREY} is percent biomass of a particular prey in the diet.

To convert the biomass of prey eaten (B_{PREY}) to the number of individuals eaten, we combined a species-specific relationship of prey lengths in the diet versus the day of the year and a species and year-specific length-weight relationship (Tuomikoski 2004). This equation was of the form

$$W_{PREY} = \alpha(b + m \cdot \text{day of year})^\beta,$$

where W_{PREY} is the weight of an individual that was eaten (g), α and β are constants from the length-weight regression, and m and b are the slope and intercept of the linear relationship between prey length eaten and day of the year.

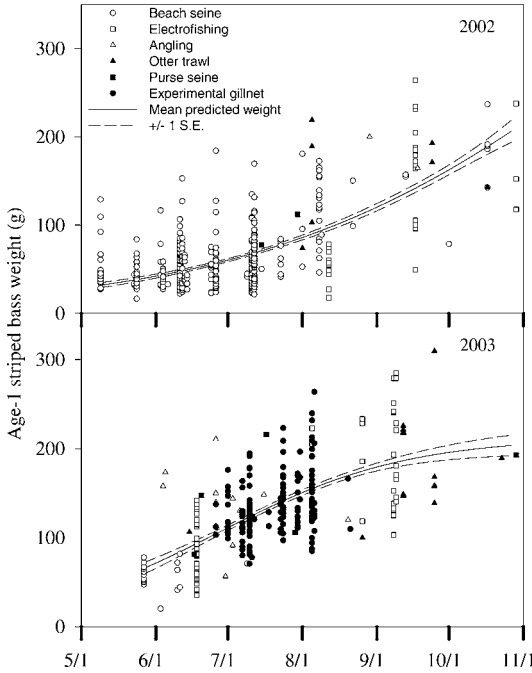


FIGURE 2.—Age-1 striped bass weights in 2002 and 2003, by date and method of capture. The solid line shows the predicted means from the logistic model, the dashed lines the corresponding SEs.

Finally, the number of individual prey items eaten within the area of a seine haul (I_{PREY}) was calculated as

$$I_{PREY} = \sum (B_{PREY}/W_{PREY})$$

over the period of interest. Calculations of I_{PREY} were made at estimated mean values and at one standard error from the mean; standard errors for number of prey eaten were estimated using the delta method (Williams et al. 2001:736–737). The bioenergetics model estimate of consumption rate (C) does not provide a standard error and the predicted value was used in all calculations. The estimate of the instantaneous loss rate of a particular prey type due to predation (M_{PRED}) was then

$$M_{PRED} = (I_{PREY}/D_{PREY})/\text{number of days,}$$

where D_{PREY} is the geometric mean density of prey during the period of interest.

The daily loss rate due to predation was calculated as $1 - e^{-M_{PRED}}$. Total loss rates from catch curves were calculated and compared with loss due to predation for American shad on the shoals in each year, yellow perch and alewives on the shoals in 2003, and alewives in the channels in each year.

Prey total loss rates and predatory impact.—Catch curve analysis was used to estimate total loss rates,

where the instantaneous total loss rate of prey items (Z) was computed as the slope of the decreasing $\log_e(\text{CPUE})$ over time (Ricker 1975). The catch curve analysis was done separately for beach and purse seine density estimates.

Total loss is mortality plus the sum of immigration and emigration; we assumed 100% efficiency and that immigration and emigration were negligible. To reduce bias, loss rates were estimated over times where fish movement was assumed to be low. For yellow perch, emigration due to increasing salinity was assumed not to be a factor because observed salinities did not influence the congener, Eurasian perch *Perca fluviatilis* (Lozys 2004). For juvenile *Alosa* spp., migrations out of the primary nursery habitat typically occur in late summer or early fall (Bozeman and Van Den Avyle 1989). Cues to fall migrations include decreasing daylight and water temperatures, increasing rainfall, rising water levels, and increasing flow rates (Leggett 1976; Marcy 1976; O’Leary and Kynard 1986; Bozeman and Van Den Avyle 1989). Because several of these cues are associated with declining water temperature, water temperature was used as an indicator of fall emigration. Water temperatures of 18–26°C have been reported to cue mass fall emigrations of juvenile *Alosa* spp. in other east coast estuaries (Leggett 1976; Marcy 1976; O’Leary and Kynard 1986). To minimize the error in total loss estimates, we used 26°C to terminate catch-curve analysis. So, catch curve analysis was applied from the period where fish are completely recruited to the gear, or the peak catch, and ceased before the first mean water temperature of 26°C after mid-July (Figure 1). To further remove bias from movement of juvenile cohorts, catch curve analysis was only performed when monthly length-frequency distributions were consecutively unimodal (see Tuomikoski 2004 for length-frequency distributions).

Daily total loss rates were computed as $1 - e^{-Z}$. These were compared with daily loss rates from predation (see above) over the same time interval to determine how important striped bass predation was to the apparent total loss rate of a particular prey fish.

For those species, gear, and year combinations for which the data did not meet the criteria for catch curve analysis (ascending and descending limbs and unimodal size distribution through time), estimates of I_{PREY} were compared with prey fish densities (number per seine haul or CPUE). Prey fish densities were estimated from a particular sampling date; I_{PREY} was estimated from the preceding midpoint to the following midpoint of sampling dates to bracket the estimate of density.

Results

Water Quality

Salinity and dissolved oxygen differed by year, but temperature did not (Tuomikoski 2004). Salinity ranged from below 1.0‰ to 8.4‰ in 2002 but was rarely above 0.5‰ in 2003. Monthly average bottom dissolved oxygen levels in the channel were below 4.1 mg/L in 4 of 5 months in 2002 but were always above 4.0 mg/L in 2003. Temperature ranged from 17.8 to 30.6°C in 2002 and from 16.6 to 29.7°C in 2003 (Figure 1).

CPUE of Age-1 Striped Bass and Prey

Catches of age-1 striped bass varied by year and gear. Age-1 striped bass were caught predominantly on shoals in 2002 and were largely unavailable in channels that year. In 2003, catches of these predators were reduced on shoals; electrofishing and gill netting at the break between shoals and the channels provided the majority of age-1 striped bass (Figure 2).

Catch curve analyses were based on beach seine catches of American shad and yellow perch, purse seine catches of alewives, and beach seine catches of alewives in 2003 (Figure 3). The \log_e transformed CPUE for these prey showed the ascending and descending limbs characteristic of a catch curve. Also, monthly length-frequency distributions were unimodal throughout the sampling period, which provided evidence that a single cohort was followed through time (Tuomikoski 2004). Loss rates could not be calculated for American shad in purse seines in either year because of low catches (<150 for both years combined; Tuomikoski 2004). Catches of blueback herring and Atlantic menhaden for all cases and for alewife catches from the 2002 beach seine did not meet the criteria for catch curve analysis and were examined for predatory effects by comparing numbers eaten and numbers available.

Estimates of Age-1 Striped Bass Consumption Rate

We estimated age-1 striped bass consumption rates on four of five 24-h trips (Figure 4; Table 1). The mean stomach fullness pattern for June 2002 was variable and generally low; all time-point values were less than 0.015 g/g. The July 2002 collection peaked at 1600 hours and decreased through the night. This decrease in stomach fullness yielded a gastric evacuation estimate of 0.148/h (used for both dates in 2002). Mean stomach fullness for the July 2003 collection was highest at both 0800 hours time points, with a lesser peak at 2000 hours; the decrease in stomach fullness through the day yielded an evacuation estimate of 0.147/h (used for both dates in 2003). The August 2003 collection peaked at 2000 hours, with lesser peaks at both 0800

and 1200 hours. Estimates of consumption were 0.025 and 0.078 $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ in 2002 and 0.054 and 0.075 $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ in 2003 (Table 1). The sample size of age-1 striped bass was too low ($n = 18$) for us to estimate a consumption rate in September 2003.

Bioenergetics modeling provided daily estimates of consumption rates from May through October each year (Figure 5). These estimates ranged from 0.04 to 0.12 $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ in 2002. Seasonally, the rate increased from May to mid-July and decreased through October. Bioenergetics modeling estimates of the consumption rate declined markedly for a short period around August 2, 2002; this drop coincided with temperatures near 30°C, close to the upper thermal limit allowed in the temperature-based consumption function. The bioenergetics model estimates of the consumption rate were within two standard errors of the July field estimate but much different from the June field estimate. In 2003, bioenergetics estimates of the consumption rate ranged from 0.03 to 0.09 $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$. Seasonally, estimates of the rate followed a pattern similar to that in 2002, when they climbed to a maximum around mid-July and then declined through October. When compared with field estimates in 2003, model estimates were within two standard errors of the July field estimate and matched well with that of the August. Theoretical maximum consumption rates are often examined to see how a bioenergetics model performs. The P -value is the percentage of this daily maximum consumption that the model calculates must have occurred to explain observed predator growth (Kitchell et al. 1977). These values increased from about 0.8 in May to maximum values of around 1 during midsummer, then decreased through October of each year (Figure 5). These values theoretically range from 0 to 1, but the estimated values exceeded 1 briefly in both years.

Prey Loss Rates Due to Predation

Losses from predation varied between years and among prey species (Table 2). In 2002, the average loss rate due to predation (with range) for American shad on the shoal was 4.21%/d (range, 0–11.40%); predation rates for alewives in the channel were lower, with an average of 0.28%/d (range, 0–0.61%). There was no evidence of predation by age-1 striped bass on juvenile yellow perch in 2002. In 2003, estimates of the mean predation mortality of American shad were never above 0.001%/d for any biweekly period (Table 2), while estimates for alewives in shoal and channel areas were 0.12% (range, 0–0.36%) and 0.13% (range, 0.02–0.23%), respectively; the estimate of predation mortality rate on yellow perch in shoal areas was 1.47%/d (range, 0.12–2.79%). Most yellow perch mortality occurred from May 26 to June 10, 2003.

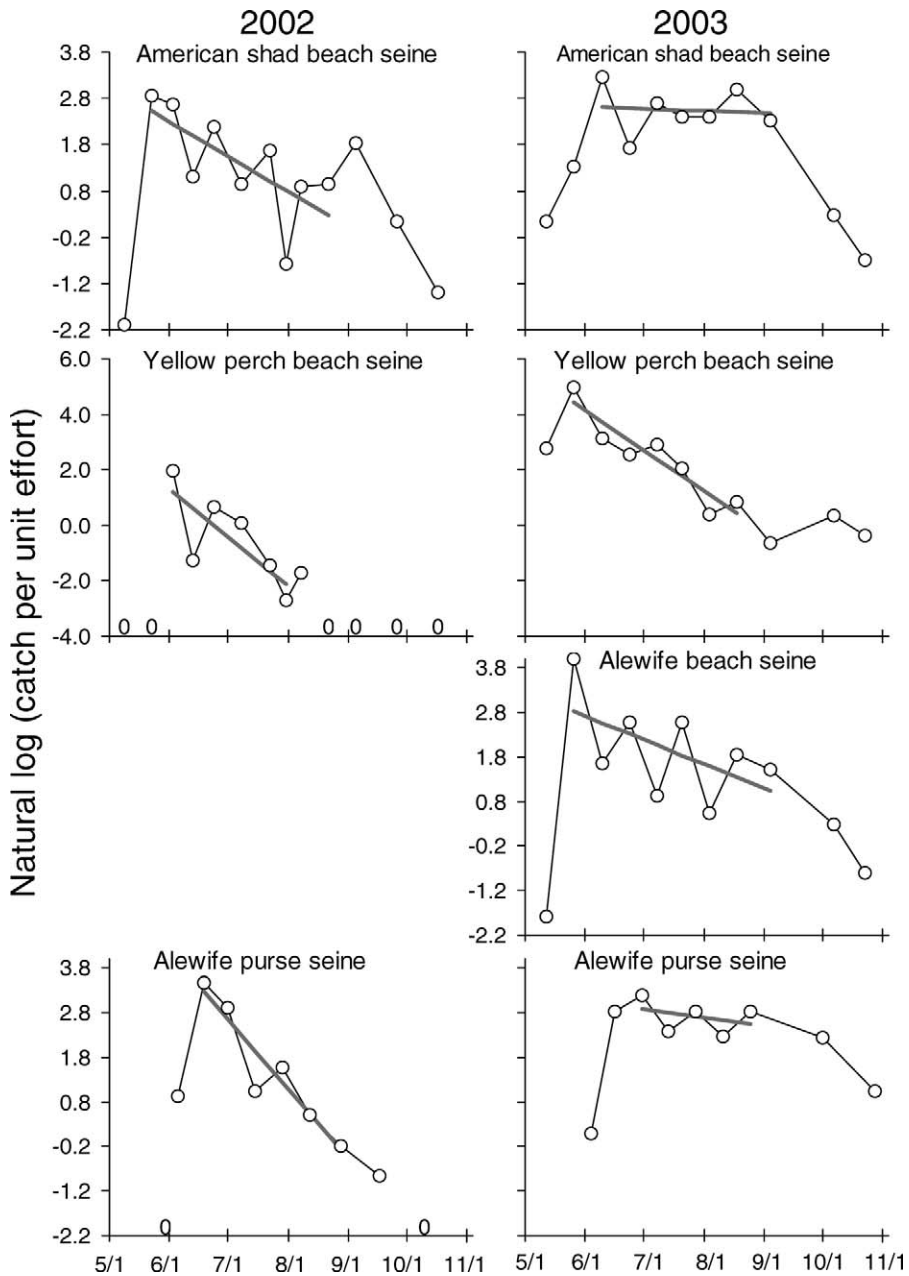


FIGURE 3.—Log_e(CPUE) versus date for American shad and yellow perch caught in beach seines in 2002 and 2003; alewives caught in beach seines in 2003; and alewives caught in purse seines in 2002 and 2003. The catch curve analysis is represented as linear regression fits. Zero catches are denoted by zeros above the x-axis on the dates they occurred; these data were not included in the regressions.

Prey Total Loss Rates and Predatory Impact

Total loss rates varied by year, prey species, and area sampled. Catch curve estimates of instantaneous loss rates (Z ; Figure 3; Table 2) were converted into conditional total loss rates for American shad,

alewives, and yellow perch. In 2002 the total loss rate in shoal areas was 2.45%/d for American shad and 5.52%/d for yellow perch; alewife catches in the channel declined at 4.93%/d. In 2002 predation by age-1 striped bass accounted for more than all of the

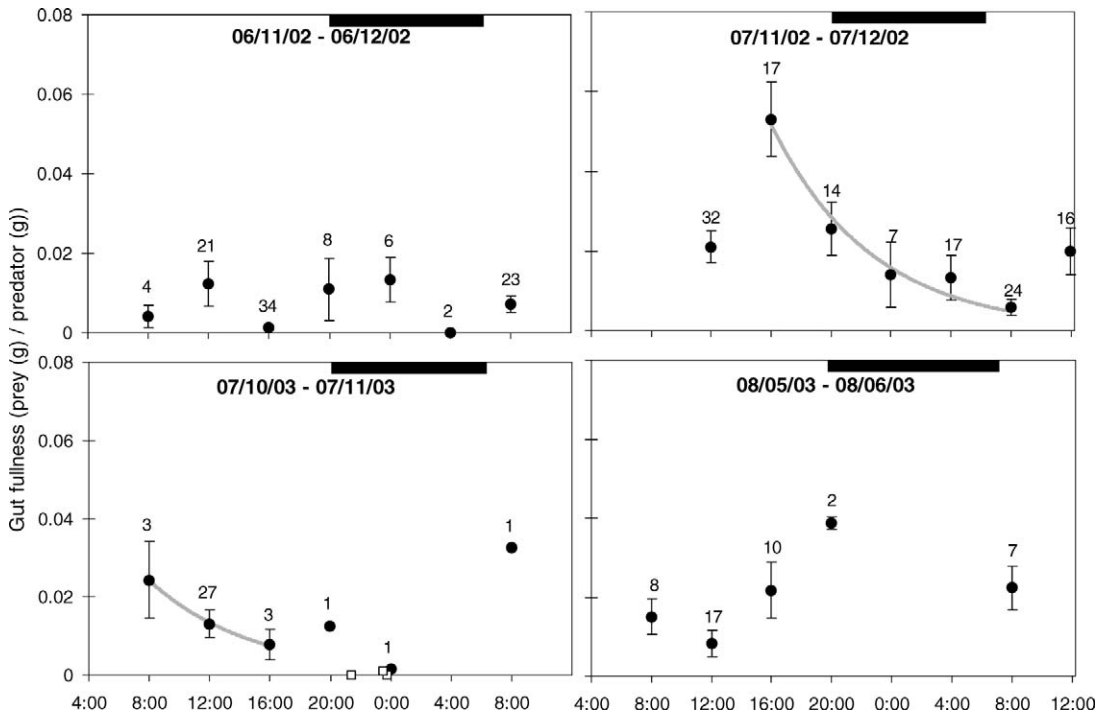


FIGURE 4.—Mean \pm SE gut fullness values of age-1 striped bass versus time of capture during 24-h collections on selected dates in 2002 and 2003. The numbers shown above the data points are sample sizes. The dark horizontal bar at the top of each panel denotes the period from sunset to sunrise. Fitted gastric evacuation rate functions are represented by gray lines in the panels for July 11–12, 2002, and July 10–11, 2003. The squares in the panel for July 10–11, 2003, represent gut fullness values for individual striped bass captured by purse seine during July 2003 and not used in the estimation of gastric evacuation or consumption rates.

apparent loss of American shad in shoal areas, 6% of total loss of alewives in channels, and none of the total loss of yellow perch. In 2003 the American shad loss rate was 0.15%/d and yellow perch 4.61%/d on shoals. The alewife loss rate was 1.75%/d on shoals and 0.61%/d in channels. In 2003 age-1 striped bass predation on American shad was essentially zero but accounted for 7% and 21% of total loss rates of alewives on shoals and in the channel, respectively. The larger predation effects on alewives in 2003 were due to lower total loss rates whereas the predation loss

rate estimates for alewives were similar between years. Striped bass predation on juvenile yellow perch accounted for 32% of the total loss rate in 2003, but most of the loss of juvenile yellow perch occurred from May 26 to June 10, 2003; striped bass predation mortality was 4.93% and accounted for all of the loss during that period.

For prey species for which catch curves were not considered valid, the numbers of prey consumed by striped bass were compared with estimates of the numbers of prey available to gain insight into predation

TABLE 1.—Field estimates and SEs of parameters used to estimate daily ration of age-1 striped bass. The instantaneous rate of gastric evacuation (G_e) was estimated over periods in which feeding was assumed to be zero. Stomach fullness (S ; g prey/g predator) is the mean of time point means over a 24-h period. Daily ration is expressed in grams of prey per gram of predator per day. See text for details on calculations. The sample size (n) is the number of striped bass collected over each 24-h period.

Date	Mean temperature (°C)	G_e		S		Daily ration		n
		Mean	SE	Mean	SE	Mean	SE	
Jun 11, 2002	25.8			0.007	0.002	0.025	0.008	98
Jul 11, 2002	26.1	0.148	0.018	0.022	0.006	0.078	0.023	127
Jul 10, 2003	28.8	0.147	0.008	0.015	0.005	0.054	0.017	36
Aug 5, 2003	28.1			0.021	0.005	0.075	0.018	44

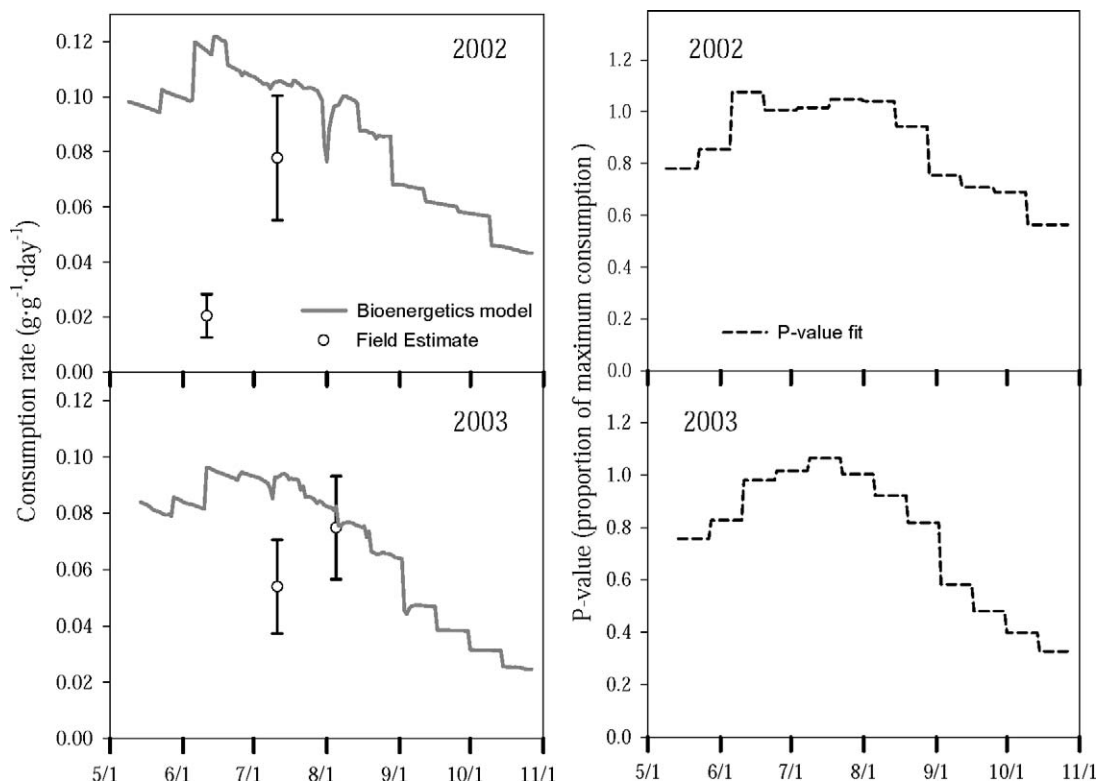


FIGURE 5.—Bioenergetics model estimates of consumption rates for age-1 striped bass in western Albemarle Sound and model *P*-value (proportion of maximum consumption) fits for 2002 and 2003, by date. The model was fit to age-1 striped bass growth in 14-d increments. Field estimates of consumption rates (mean \pm SE) are also shown.

effects (Figure 6). For blueback herring, predation varied in importance through time on shoals and was relatively unimportant in the channel. In 2002 the estimated numbers of blueback herring juveniles eaten by age-1 striped bass on shoals increased gradually until late June then dropped off quickly; this was followed by increases in number eaten in late August and reached high levels in October. The estimated numbers of blueback herring eaten from May to late June and in October exceeded available density in that year. In 2002 the purse seine estimates of age-1 striped bass densities were low and the number of blueback herring lost to predation was near zero and minimal compared with available density. Early in 2003 the estimated numbers of blueback herring consumed on shoals were similar in timing and magnitude to 2002. However, there was no fall peak in the consumption of blueback herring in 2003. Estimated numbers of blueback herring eaten in June 2003 using striped bass densities in the channel exceeded the available density for only one period.

Predation on alewives on shoals in 2002 was comparable in magnitude to the density available for

predation during most time periods during May–August, but the numbers of alewives eaten dropped to zero afterward. The estimated numbers of juvenile Atlantic menhaden consumed on shoals early in 2002 were much higher than the estimates of Atlantic menhaden present. However, this is the only year–area combination for which the estimates of the numbers eaten suggested a predatory effect; the estimates of the numbers of Atlantic menhaden consumed are an order of magnitude or more lower than estimates of densities seen for shoals in 2003 and in the channel in both years.

Discussion

With the resurgence of striped bass populations on the U.S. Atlantic coast, interest in their predatory effects on prey fishes has increased. For example, a multispecies virtual population analysis is being developed by the Atlantic States Fisheries Management Commission with striped bass as a modeled predator (Garrison and Link 2003). In our study, age-1 striped bass predation accounted for a considerable fraction of the total mortality of American shad in 2002 and

TABLE 2.—Effects of predation by age-1 striped bass on their prey in 2002 and 2003. The geometric mean prey density per seine haul, number of days per period, and number of prey consumed were used to calculate daily instantaneous predation mortality (M_{PRED} ; see text for equations), which is presented here as a conditional rate, $(1 - e^{-M_{\text{PRED}}}) \cdot 100$. Striped bass predatory effects were determined by comparing M_{PRED} with the total instantaneous loss rate (Z) to obtain the percent of total loss explained by striped bass predation (M_{PRED}/Z). Instantaneous total mortality rates are presented here as conditional rates, $(1 - e^{-Z}) \cdot 100$. Conditional predation mortality estimates are bounded by the SEs of the numbers of prey consumed; when mortality would be negative, a zero is reported. The weighted means of M_{PRED} using the number of days in the time period as a weighting factor are also presented as conditional rates.

Year	Period	Geometric mean	Days	Prey consumed (\pm SE)	Predation mortality (%/d) (\pm SE)	Total loss explained (%) (\pm SE)
American shad, shoal (total loss = 2.45%)						
2002	May 23–Jun 3	15.76	12	0.87 (0–2.65)	0.46 (0–1.39)	19 (0–57)
	Jun 3–Jun 13	6.64	11	0.45 (0–1.34)	0.61 (0–0.81)	25 (0–74)
	Jun 13–Jun 24	5.22	12	2.91 (0–8.39)	4.55 (0–2.53)	186 (0–512)
	Jun 24–Jul 8	4.77	15	6.83 (0–19.51)	9.11 (0–3.89)	372 (0–975)
	Jul 8–Jul 23	3.68	16	2.60 (0–7.50)	4.32 (0–1.96)	177 (0–488)
	Jul 23–Jul 31	1.58	9	0.87 (0–2.52)	5.93 (0–6.27)	242 (0–664)
	Jul 31–Aug 8	1.08	9	0.81 (0–2.32)	7.98 (0–1.27)	326 (0–868)
	Aug 8–Aug 22	2.53	15	0.49 (0–1.4)	1.28 (0–3.62)	52 (0–148)
	Weighted mean				4.21 (0–11.40)	176 (0–506)
Alewife, channel (total loss = 4.93%)						
	Jun 19–Jul 1	24.24	13	0	0	0
	Jul 1–Jul 15	7.20	15	0.11 (0–0.25)	0.10 (0–0.23)	2 (0–5)
	Jul 15–Jul 29	3.69	15	0.38 (0–0.78)	0.68 (0.01–1.40)	13 (0–28)
	Jul 29–Aug 12	2.85	15	0.27 (0–0.61)	0.62 (0–1.42)	12 (0–28)
	Aug 12–Aug 28	1.18	17	0	0	0
	Weighted mean				0.28 (0–0.61)	6 (0–12)
	American shad, shoal (total loss = 0.15%)					
2003	Jun 10–Jun 24	12.12	15	0	0	0
	Jun 24–Jul 8	9.07	15	0	0	0
	Jul 8–Jul 21	12.80	14	0.001 (0–0.003)	0.001 (0–0.002)	0.35 (0–1.11)
	Jul 21–Aug 04	11.14	15	0	0	0
	Aug 4–Aug 18	14.94	15	0	0	0
	Aug 18–Sep 4	14.33	18	0	0	0
	Weighted mean				0	0
Alewife, shoal (total loss = 1.75%)						
	May 26–Jun 10	16.91	16	1.91 (0–5.8)	0.7 (0–2.12)	40 (0–121)
	Jun 10–Jun 24	8.26	15	0.08 (0–0.24)	0.07 (0–0.19)	4 (0–11)
	Jun 24–Jul 8	5.78	15	0.02 (0–0.05)	0.03 (0–0.06)	1 (0–3)
	Jul 8–Jul 21	5.81	14	0.03 (0–0.07)	0.04 (0–0.09)	2 (0–5)
	Jul 21–Aug 4	4.77	15	0	0	0
	Aug 4–Aug 18	3.29	15	0	0	0
	Aug 18–Sep 4	5.35	18	0	0	0
	Weighted mean				0.12 (0–0.36)	7 (0–21)
Yellow perch, shoal (total loss = 4.61%)						
	May 26–Jun 10	57.16	16	46.26 (3.6–89.48)	4.93 (0.39–9.32)	107 (8–207)
	Jun 10–Jun 24	17.09	15	8.23 (0.72–15.74)	3.16 (0.28–5.96)	68 (6–130)
	Jun 24–Jul 8	15.23	15	0.57 (0–1.23)	0.25 (0–0.54)	5 (0–11)
	Jul 8–Jul 21	11.90	14	0.27 (0–0.58)	0.16 (0–0.35)	3 (0–7)
	Jul 21–Aug 04	3.45	15	0	0	0
	Aug 4–Aug 18	1.87	15	0	0	0
	Weighted mean				1.47 (0.12–2.79)	32 (2–62)
Alewife, channel (total loss = 0.61%)						
	Jun 30–Jul 14	16.17	15	0.05 (0–0.11)	0.02 (0–0.04)	3 (0–7)
	Jul 14–Jul 28	13.47	15	0.44 (0.1–0.78)	0.22 (0.05–0.39)	36 (8–63)
	Jul 28–Aug 11	12.82	15	0.52 (0.09–0.94)	0.27 (0.05–0.49)	44 (8–80)
	Aug 11–Aug 25	12.72	15	0	0	0 (0–0)
	Weighted mean				0.13 (0.02–0.23)	21 (4–38)

yellow perch in 2003. This study provides the first empirical evidence that striped bass predation in an estuarine environment can negatively affect the year-class strength of its prey.

Estimates of Age-1 Striped Bass Consumption Rates

Bioenergetics model estimates of the consumption rates of age-1 striped bass were similar in magnitude and pattern between years. Although striped bass

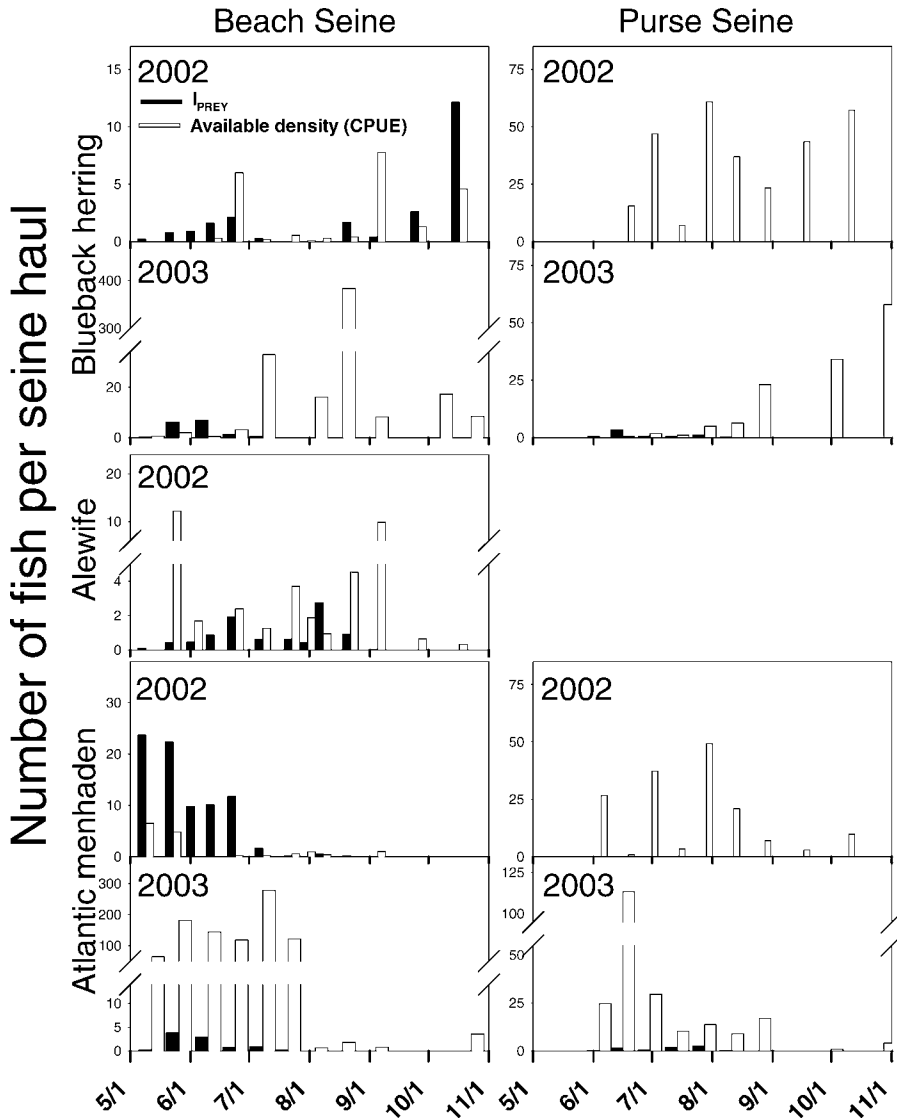


FIGURE 6.—Numbers of blueback herring, alewives, and Atlantic menhaden eaten by age-1 striped bass (I_{PREY} ; see text for calculation) and the available density of those prey fishes as determined by beach and purse seine CPUE in 2002–2003. Both the numbers eaten and the available densities are presented per area sampled by one unit of seine effort. The available prey densities were estimated on particular sampling dates; I_{PREY} was estimated from the preceding midpoint between successive sampling dates to the following midpoint in order to bracket the estimates of prey density.

growth was lower early in 2002, higher temperatures led to estimates of consumption rate comparable with 2003. The bioenergetics model consumption estimates were higher than field-derived estimates but within 2 standard errors on three of the four occasions. Because both methods have their own assumptions, either or both could be incorrect; potential problems with both methods are described below.

These are the first field estimates of age-1 striped

bass consumption rates and gastric evacuation rates during summer in an estuarine environment. Field estimates of G_e and the resulting consumption rate estimates would be biased downward if feeding occurred over periods where it was estimated. This could explain the discrepancy between the two estimates of consumption rate. Field and laboratory measurements of gastric evacuation rates at similar temperatures and fish sizes with no feeding are needed.

During 2003, age-1 striped bass could not be obtained at 0000 hours (August) or 0400 hours (July and August). This lack of data on stomach fullness may have biased estimates of consumption rate.

Ney (1993) described the potential for bioenergetics models to give erroneous output. The output of an age-0 striped bass model was most sensitive to parameters associated with consumption and metabolism; on the other hand, those tend to be the parameters most precisely estimated (Hartman and Brandt 1993). Overton (2003) conducted a sensitivity analysis of annual bioenergetics model runs using Chesapeake Bay data and physiological parameters of striped bass from Hartman and Brandt (1995b). He found that the model was very sensitive to prey energy densities, the metabolism-versus-weight parameter (RB), and the metabolism-versus-temperature parameter (RQ). These parameters were measured in the laboratory (Hartman and Brandt 1995b) and we assumed that they were valid for striped bass in Albemarle Sound. Additional field estimates of consumption are needed to evaluate the realism of the striped bass bioenergetics model.

Consumption rates from bioenergetics modeling and field estimates are not always similar. Rice and Cochran (1984) found that their field estimates for largemouth bass *Micropterus salmoides* consumption followed the same pattern as their bioenergetics estimates, but did not always correspond closely. However, because growth inputs to bioenergetics models integrate variable feeding rates over time, they concluded that bioenergetics estimates might be better than predictions based solely on field estimates. Given this, along with the fact that we cannot determine which of the consumption rate methods is erroneous with the data at hand and that bioenergetics models provide daily estimates of consumption rate throughout the summer, we chose to use the bioenergetics model for estimating the effect of age-1 striped bass on prey fishes.

The model results indicated that age-1 striped bass in Albemarle Sound were maximizing their growth potential during midsummer. Observed growth was sufficiently high so that the bioenergetics model predicted consumption rates at or greater than the expected maximum consumption rates for those temperatures. These high estimated *P*-values may result from high prey abundance or problems with the model. Similar to our study, Hartman and Brandt (1995a) found that age-1 striped bass in Chesapeake Bay were prey limited until June but had adequate prey and optimized their growth potential (i.e., *P*-values were at or near 1) until September, after which time they became prey limited again.

Effects of Age-1 Striped Bass Predation

Striped bass affect juvenile fishes in other systems. Age-1 striped bass were a large contributor to the annual consumption of clupeids in Smith Mountain Lake (Cyterski et al. 2002). Hartman (2003) found that predatory demand of striped bass on clupeids at Atlantic coast-wide (Atlantic menhaden) and estuarine scales (Hudson River and *Alosa* spp.) was exceedingly high. These studies described impacts with annual time steps, or summarized annual influences of striped bass predation by using models with daily time steps. We estimated predatory impacts over shorter time intervals in this study to determine whether age-1 striped bass were a significant source of daily mortality during the potentially critical early juvenile stage of several fishes in their nursery habitat. Of the predator-prey interactions that we examined, age-1 striped bass predation explained a large fraction of total mortality of American shad in 2002 and yellow perch in 2003. Our estimates of total loss rates for juvenile American shad, alewives, and yellow perch (mean = 2.42%/d, range = 0.15–4.93) are similar to other studies. A daily loss rate of 2.9% was found for juvenile largemouth bass (Timmons et al. 1981), 0.5% for age-0 striped bass (Dey 1981), 0.8–3.7% for Atlantic croaker *Micropogonias undulatus*, and 3.6–6.4% for spot *Leiostomus xanthurus* (Ross 2002). The estimated juvenile American shad daily loss rate in 2002 (2.45%) was similar to loss rates in the Connecticut (Crecco and Savoy 1987) and Hudson rivers (Limburg 1996).

The direct impacts of predators on prey require that predator and prey overlap in time and space and that prey be available for capture during that time (Bax 1998). In Albemarle Sound American shad appear to occupy shoal areas almost exclusively; this is similar to spatial distributions of shad in the Hudson River (Limburg 1996). Thus, the impact of age-1 striped bass on American shad will be primarily limited to shoals and will depend on predator-prey overlap there. In 2002 age-1 striped bass were relatively abundant on shoals and accounted for over 100% of the total loss rate of American shad. In 2003 age-1 striped bass were far less abundant on shoals and estimated predation loss rate was zero for American shad. Striped bass may have used shoal habitat as a refuge from hypoxic waters in 2002 (Tuomikoski 2004).

The year-class strength of American shad in the Connecticut River may be established before the juvenile stage such that juvenile abundance indices are qualitative predictors of adult recruitment (Crecco et al. 1983; Crecco and Savoy 1984). However, the variable predatory impact of age-1 striped bass on juvenile American shad between years in this study

indicates the importance of quantifying mortality in the juvenile stage. This has implications for the timing of surveys used to develop juvenile abundance indices. Beach seine catches of juvenile American shad differed markedly from early to late summer 2002. Future work should determine whether mid- to late-summer collections of juvenile American shad most accurately predict recruitment.

The predatory impacts of age-1 striped bass on yellow perch also differed by year. Yellow perch were not a prey of age-1 striped bass in 2002, so estimated predation mortality was 0.0% and total loss rate 5.5%. While declines in yellow perch abundance in 2002 could be due to the same factors as for alewives (see below), the absolute loss of yellow perch in 2002 was not great. Densities of yellow perch in 2002 decreased from 5.7 to 0.2 fish/seine haul. In 2003 the absolute decline in yellow perch (from 153.2 to 3.1 fish/seine haul) was much greater. Age-1 striped bass predation accounted for over 32% of the yellow perch total mortality in 2003. Further, from late May to mid-June 2003, age-1 striped bass predation accounted for nearly all yellow perch mortality. Predatory impacts on yellow perch juveniles have been observed in freshwater systems (Nielsen 1980) but, to our knowledge, this is the first example in an estuary.

Age-1 striped bass predation appeared to have little effect on juvenile alewives. Relatively little of the decline in alewife abundance could be attributed to age-1 striped bass predation. Although predation estimates by age-1 striped bass were a larger percentage of the estimated total loss of alewives in 2003, most of the total loss rate in both years is unaccounted for. Sources of loss other than age-1 striped bass could include older striped bass, other piscivorous fish and birds, and emigration. Rudershausen et al. (2005) found that older striped bass during the same period had few *Alosa* spp. in their stomachs. Other piscivores in this system include southern flounder *Paralichthys lethostigma* and white perch *Morone americana*, but in fewer numbers than age-1 striped bass.

When comparing estimates of the numbers of blueback herring eaten in shoal areas with available densities in 2002, we found that early and late predation events exceeded apparent available densities; this was also observed for blueback herring in early 2003 for both shoal and channel areas. This nonintuitive finding may result from blueback herring immigrating into the sampling area (e.g., a continual input or throughput of prey) that manifests itself in density estimates lower than the actual numbers available for predation. The low density of age-1 striped bass in the channel in 2002 may mean that this habitat was a refuge from predation by age-1 striped

bass for much of that summer. Although blueback herring were found in the diet of age-1 striped bass in late summer and early fall 2003, we did not collect any striped bass in our seines; thus, estimates of predation during this period for these two areas are zero. This is obviously an erroneous result and the true estimate for predation on blueback herring in 2003 (and for all prey not solely associated with the shoal habitats) would require estimates of age-1 striped bass densities throughout Albemarle Sound.

Atlantic menhaden are a common prey of age-1 and older striped bass (Walter et al. 2003). In this study, age-1 striped bass had varying effects on juvenile Atlantic menhaden. The greatest potential impact occurred when high densities of age-1 striped bass were on the shoals in 2002. Other estimates of the predatory effects on Atlantic menhaden were relatively low. The lack of evidence for age-1 striped bass influencing Atlantic menhaden biomass in 2003 is due to predators being less abundant in shoal areas and lower selectivity on menhaden early in 2003 (Rudershausen et al. 2005).

Potential Sources of Error

The catch curve estimates of total loss rates assumed that immigration and emigration were negligible. We attempted to reduce this uncertainty by restricting their use to cases in which patterns in catch rates and length distributions suggested that we were tracking a single cohort. Nevertheless, immigration and emigration cannot be ruled out and would bias loss rates downward and upward, respectively. A better understanding of juvenile *Alosa* spp. summer movements in the sound would help determine the severity of these potential biases.

We also assumed 100% capture efficiency of both gears used. If beach and purse seine efficiencies decreased as prey fishes grew, the catch curves would overestimate total mortality and the calculated predatory effects would be conservative (i.e., predation mortality would explain a lower amount of the biased total mortality estimate). The capture efficiencies of beach seines on pelagic fishes have been found to be relatively high (Pierce et al. 1990). Tischler et al. (2000) found that Eurasian perch of roughly 30–70 mm TL could not escape a purse seine similar to that used in this study and attributed declining catches to migration and mortality. Efficiencies less than 100% on age-1 striped bass would lead to a conservative estimate of impact because estimates of predation mortality would be biased downward.

Management Implications and Future Work

Understanding the effects of resurgent predator populations on prey fishes at low populations is vital

to successful management (Link 2002). Interannual differences in predation mortality may lead to concurrent variability in recruitment. The finding of an influence of age-1 striped bass on juvenile American shad numbers will be useful to management agencies charged with establishing stocking schedules for American shad and harvest rates for striped bass. Future management decisions on yellow perch will also benefit from this work. Finally, future determination of predatory effects should be designed to reduce the error around variables needed to estimate the numbers of prey eaten (e.g., predator densities, prey sizes eaten, and diet).

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