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SPECIAL SECTION: AMERICAN SHAD AND RIVER HERRING

# Striped Bass Consumption of Blueback Herring during Vernal Riverine Migrations: Does Relaxing Harvest Restrictions on a Predator Help Conserve a Prey Species of Concern?

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***Abstract***

**Anadromous blueback herring *Alosa aestivalis* are declining throughout much of their range, and fishery closures in some systems have failed to produce population recovery. A potential contributing factor is increased predation pressure from sympatric striped bass *Morone saxatilis*. We integrated data on the predator–prey interaction between striped bass and blueback herring during vernal migrations into the Connecticut River with data on the in-river striped bass fishery to assess the potential for mitigation of blueback herring mortality via increased striped bass harvest. Striped bass abundance, size structure, diets, and angler catches were assessed within a river segment during spring 2005–2008. We estimate that striped bass consumed 400,000 blueback herring (90% confidence interval = 200,000–800,000) annually in our study area during the spring migration season. The predator–prey interaction between striped bass and blueback herring was predator size dependent. Blueback herring were most commonly found in the stomachs of striped bass between 650 and 999 mm total length. Intermediate size-classes (650–799 mm) made the greatest contribution to population-level consumption. Highly abundant small striped bass (400–549 mm) consumed herring infrequently, yet still made substantial contributions to population-level consumption. Anglers caught 17,000 striped bass in our study area during March–June 2008; only 11% of these fish could be harvested under the current 28-in (710-mm) minimum length limit. Allowing anglers to harvest up to 15,000 sublegal striped bass from a "bonus harvest" slot limit would reduce annual predatory losses of blueback herring by up to 10%. Alternatively, a smaller bonus harvest of legal-sized striped bass could achieve reductions in consumption of up to 7%. The recreational fishery in our study area, however, may not be intense enough to realize such harvest levels.**

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Fishery closures may fail to produce significant recovery of depleted fish populations (Dempson et al. 2004; Hutchings and Reynolds 2004). Factors potentially contributing to recovery failure include maladaptive changes in life history traits (Hutchings 2005; Walsh et al. 2006), release of interspecific competitors (Swain and Sinclair 2000; Link and Garrison 2002), and intensified predation (Bailey and Houde 1989; Walters and Korman 1999). Predation is of particular concern to fisheries managers, as depensation (a decline in the per-capita population growth rate) can occur when predators drive prey to low abundances (Shelton and Healey 1999; Frank and Brickman 2000). Populations subject to depensation often shift into domains of population behavior that are unresponsive to management and can even decline toward extinction (Hilborn and Walters 1992; Spencer 1997; Walters and Kitchell 2001). In such situations, managers have additional options to improve the prospects for population recovery if a directed fishery for key piscivores exists. Regulations that encourage increased predator harvests may reduce the natural mortality of threatened prey species and help effect population recovery (Yodzis 2001). Studies evaluating the efficacy of such management strategies can aid in the development of ecosystem-based approaches to fisheries management, as the failure to adequately incorporate predation is an oft-cited shortcoming of traditional fisheries management models (Vetter 1988; Bax 1998; Moustahfid et al. 2009).

A predator–prey interaction of interest in this context is that between striped bass *Morone saxatilis* and anadromous river herring (alewife *Alosa pseudoharengus* and blueback herring *A. aestivalis*) in Atlantic coastal ecosystems. River herring make vernal spawning migrations or "runs" into many coastal rivers along the Atlantic seaboard (Loesch 1987). These seasonal aggregations provide an important source of forage for many marine, aquatic, and terrestrial predators (MacAvoy et al. 2000; Yako et al. 2000; Dalton et al. 2009; Walters et al. 2009). Recent rangewide declines in run size have prompted concerns over the loss of ecosystem services historically provided by river herring (Limburg and Waldman 2009). Concurrently, once-depressed coastal populations of predatory striped bass have increased to historic levels following the imposition of strict fisheries management measures during the 1980s (ASMFC 2009; Figure 1). Striped bass are prized by recreational and commercial fishers alike, and their recovery is a widely celebrated example of successful fisheries management (Richards and Rago 1999). The ecological consequences, however, of increases in striped bass predation may be considerable. In particular, coastal populations of alosines, which are the preferred prey of striped bass in many systems (Axon and Whitehurst 1985; Walter et al. 2003; Grout 2006), have likely experienced increased natural mortality from striped bass predation (Hartman and Brandt 1995; Uphoff 2003; Heimbuch 2008). Striped bass management therefore has significant implications for river herring population dynamics. In particular, management scenarios producing increased striped bass harvests may ameliorate the natural mortality operating on river herring populations and thus improve their recovery prospects.

We selected the Connecticut River, a large river that empties into Long Island Sound in the northeastern United States, to study the predator–prey interaction between striped bass and river herring and assess the role that striped bass management can play in affecting river herring recovery. The pronounced decline of the blueback herring run in the Connecticut River segment between Hartford, Connecticut (the head of tide), and the Holyoke Dam in Massachusetts (the lowest main-stem dam) is well documented; annual returns have declined four orders of magnitude at the Holyoke Dam over the last 25 years (USFWS 2011; Figure 1). This and other regional declines prompted a river herring fishery closure in Connecticut in 2002, closely followed by closures in the neighboring states of Massachusetts and Rhode Island in 2005 (Davis and Schultz 2009). Despite the fishery closure, the Connecticut River blueback herring run shows no signs of recovery (Figure 1). Striped bass, conversely, have become abundant in the Connecticut River during spring in recent decades (Figure 1). Strong correlative evidence supports the hypothesis that increased predation by striped bass has recently contributed significantly to blueback herring declines in the Connecticut River (Savoy and Crecco 2004). Moreover, persistent striped bass predation may be preventing blueback herring recovery and could have depensatory effects. Given current low prey abundances and the perceived importance of predation, the Connecticut River is a system in which reductions in predator abundance could reasonably be expected to produce a positive effect on a depressed prey population. Additionally, an intensive springtime recreational fishery for striped bass exists along the entire river south of the Holyoke Dam (Jacobs and O'Donnell 2002; Davis et al. 2011). This fishery offers managers a mechanism by which to achieve reductions in predator abundance.

Recognizing the potential to reduce predatory pressure on a species of conservation concern and provide anglers a new harvest opportunity, the Connecticut Department of Energy and Environmental Protection (CDEEP) instituted experimental regulations on the spring recreational fishery for striped bass in the Connecticut River. The Connecticut fishery had previously been managed under blanket coastwide striped bass regulations (28-in [710-mm] minimum length limit, 2 fish daily creel limit). The experimental regulations instituted by CDEEP allowed anglers to harvest two striped bass per day within a 22–28-in (560-710-mm) slot limit from the Connecticut portion of the Connecticut River during May and June. This "bonus harvest" program was created by transferring an unused commercial quota (approximately 24,000 lb [10,886 kg]) to the recreational fishery; the bonus harvest was capped at 4,000 fish so as not to exceed the quota. A voucher system was instituted to maintain the bonus harvest within this annual limit. The bonus harvest was first implemented in 2011, after diet sampling and abundance estimates of striped bass described below revealed the potential for considerable predatory losses of blueback herring.

The goal of this study was to assess the reductions in predatory losses of blueback herring that might be achieved through

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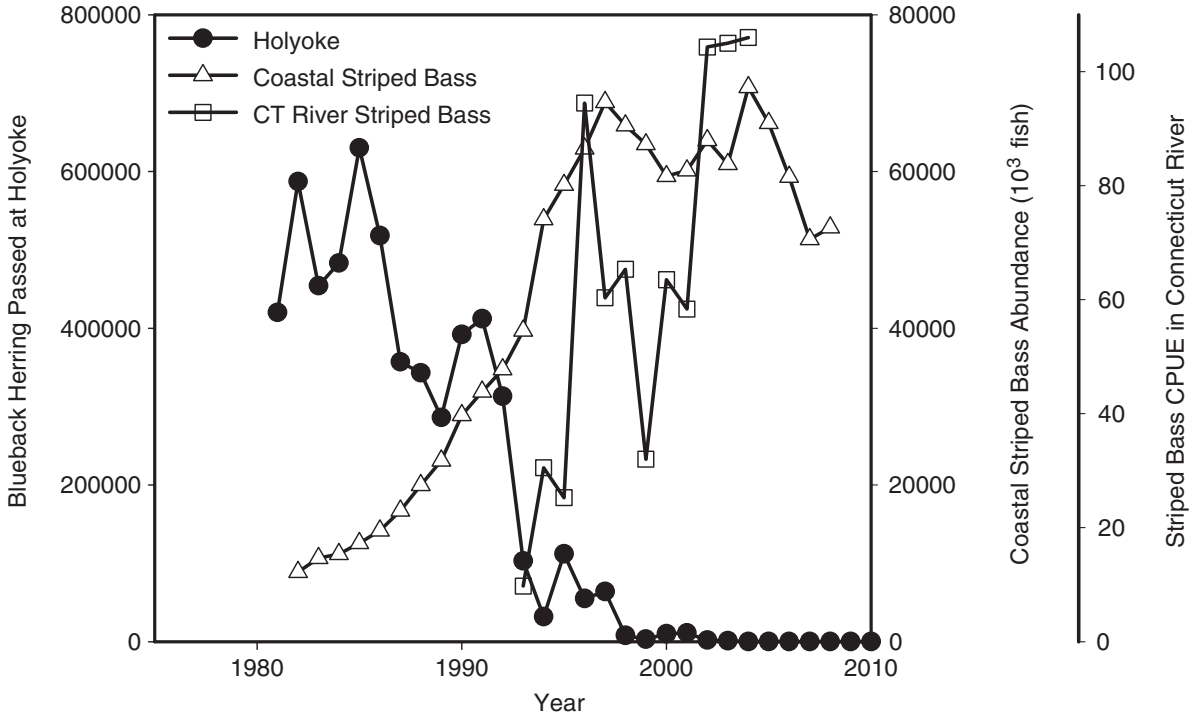



FIGURE 1. Annual passage of blueback herring at the Holyoke fish elevator during 1981–2010 (USFWS 2011), coastal striped bass abundance (ASMFC 2009) during 1982–2008, and striped bass electrofishing catch per unit effort (T. Savoy, unpublished data; 1 unit effort = 1 electrofishing sample night) at Windsor Locks in the Connecticut River during spring 1993–2004.

alternative management of the striped bass fishery in the Connecticut River. To quantify these reductions, we integrated data on trophic interactions with data on the recreational striped bass fishery in the Connecticut River. The specific objectives of this study were to (1) assess striped bass abundance and size structure in the Connecticut River during the vernal migration; (2) quantify the prevalence of blueback herring in the diets of striped bass at various predator sizes; (3) estimate the population-level consumption of blueback herring by striped bass; (4) survey recreational anglers to estimate the numbers and sizes of striped bass caught and harvested; and (5) forecast reductions in population-level consumption under several hypothetical alternative management regulations.

## METHODS

*Sampling for striped bass size structure, food habits, and absolute abundance*.—We collected striped bass by nighttime boat electrofishing (Smith Root Model SR-18 equipped with a 5.0 GPP electrofisher and two SAA-6 electrode arrays) in the Connecticut River segment between Wethersfield, Connecticut (near the head of tide), and the dam at Holyoke (a 64-km stretch hereafter referred to as the "study area"; Figure 2) during spring 2005–2008. We selected this river stretch for several reasons: (1) large, migratory striped bass are known to aggregate there during spring (Savoy and Crecco 2004; Figure 1); (2) striped bass predation on anadromous alosines has previously been documented in the area immediately below the Holyoke Dam (Warner and Kynard 1986); (3) it is small enough to permit weekly comprehensive sampling; and (4) its physical configuration (relatively narrow and shallow) facilitated boat electrofishing. Sampling began as soon as river stage permitted access (typically in early May) and ceased once striped bass catch rates became consistently low and/or river stage became too low for safe navigation in June. During 2005–2007, we sampled the same five sites (Figure 2) weekly, river conditions and equipment permitting. In 2008 sampling concentrated on the Windsor Locks site (see below).

Boat electrofishing is an effective technique for collecting warmwater fishes from the littoral zone of large rivers (Guy et al. 2009). Accordingly, we sampled fixed transects located parallel to the shoreline in nearshore, shallow habitat ($\leq$2 m depth). We classified available macrohabitats within the littoral zone at each site into six categories (main stem, coves, tributaries, tailraces, cove–main stem interface, tributary–main stem interface, and tailrace–main stem interface) and distributed electrofishing transects as evenly as possible across the available macrohabitat types at each site. Transects were sampled by positioning the boat perpendicular to shore and drifting downstream with ambient current, although slow currents (<0.5 m/s) in some areas necessitated upstream shocking (Guy et al. 2009).

In 2005–2007, we assessed the along-river relative abundance (electrofishing catch per hour [CPH]), size structure, and food habits of striped bass. All striped bass collected were

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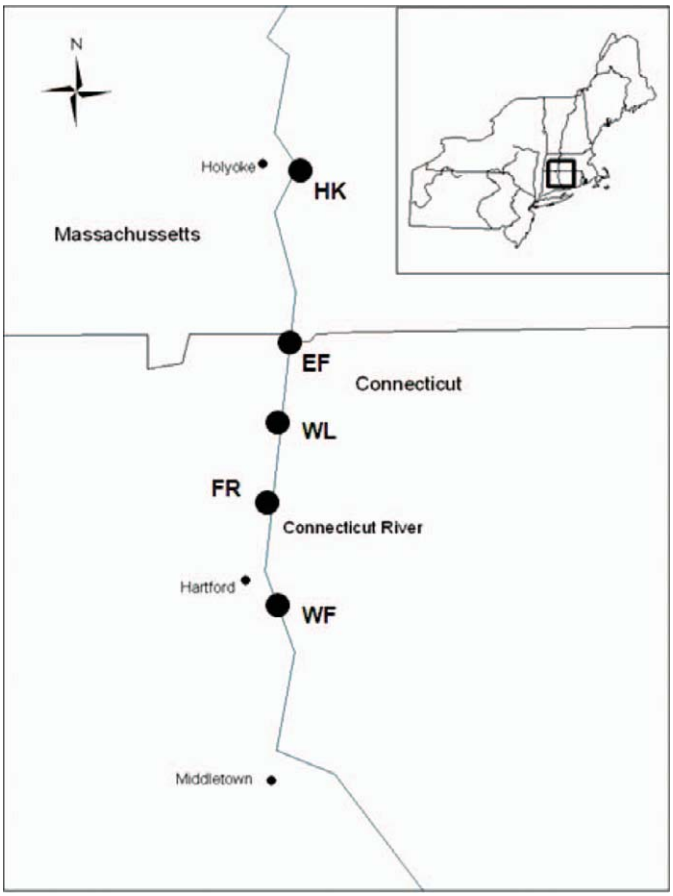



FIGURE 2. Map of the Connecticut River in northern Connecticut and southern Massachusetts. The five sites electrofished in 2005–2008 are as follows: WF (Wethersfield), FR (the lower Farmington River), WL (Windsor Locks), EF (Enfield), and HK (Holyoke). The 2008 creel survey covered the river segment between Middletown and Enfield.

counted, measured (total length [TL]; mm), and subjected to gastric lavage. We released all striped bass at the capture location after an onboard workup. Diet samples were placed on ice immediately after collection and frozen within 12 h. After thawing, diet items were sorted to the lowest possible taxon. Stomachs yielding only fragmentary remains (scales or small numbers of bones) were not scored as containing prey because we assumed that these remains derived from prey consumed more than 24 h before sampling.

In 2008, we estimated the absolute abundance of striped bass via mark–recapture. Fish were captured and tagged by nighttime boat electrofishing and subsequently recaptured by nighttime boat electrofishing and by anglers. We focused our tagging efforts exclusively on the Windsor Locks site (Figure 2) to maximize the number of fish tagged (electrofishing CPH was consistently highest at this location in 2005–2007; see Davis et al. 2009). We limited the mark–recapture effort to the month of May because the recommended study period length for closed population models is less than 1 month (see review by Pine et al. 2003). We tagged all striped bass 300 mm TL or longer with a t-bar internal anchor tag. Tags featured a phone number for capture reports. We used two different tag colors to designate standard and high-reward tags (worth \$15 and \$50, respectively) to estimate standard tag reporting rates (Pollock et al. 2001). Cooperating anglers phoned in the capture date, location, and disposition (harvested or released) of recaptured striped bass. The absolute abundance of striped bass 300 mm or longer ($\hat{N}$) was estimated using the Schnabel method (Hayes et al. 2007):

$$\hat{N} = \frac{\sum_{d=2}^{t} c_d M_d}{1 + R_e + R_{a,h} + R_{a,s}\lambda^{-1}}; \quad (1)$$

$t$ = number of sampling days; $c_d$ = total fish captured on sampling day $d$ (by both anglers and electrofishing); $M_d$ = the number of tagged fish at large for sample day $d$; $R_e$ = total recaptures obtained by electrofishing; $R_{a,h}$ = total angler returns of high-reward tags; $R_{a,s}$ = total angler returns of standard reward tags; $\lambda$ = the standard reward tag reporting rate.

The parameter $\lambda$ was estimated as in Pollock et al. (2001), that is,

$$\lambda = \frac{R_{a,s} T_h}{R_{a,h} T_s}, \quad (2)$$

where $T_h$ is the total high-reward tags released and $T_s$ is the total standard-reward tags released. Every day in May was treated as a sampling day. The total catch ($c_d$) of striped bass 300 mm or longer on each day was estimated as the sum of electrofishing catch (if electrofishing was conducted) and estimated angler catch. Electrofishing catch was known; catch by recreational anglers was estimated from creel survey data (see the section on assessing the recreational fishery below). For sample days without creel surveys, catch was estimated as the mean catch for that day type stratum (weekend versus weekday) during May. Because we conducted tagging and creel surveys only in the Connecticut portion of the study area, we similarly restricted angler recaptures used in estimating abundance ($\hat{N}$) to those obtained between Wethersfield and the Massachusetts border (42 km); to expand the abundance estimate to the entire study area, we standardized $\hat{N}$ to river kilometer and then multiplied by the length of the study area (64 km).

*Estimating population-level consumption of blueback herring*.—We modeled striped bass population-level consumption as a function of our tag-based 2008 population estimate and size structure and diet estimated from the 2005–2007 electrofishing samples. The population of striped bass 300 mm or longer was divided into 50-mm size-classes, lumping together all fish 1,000 mm or longer. The number of striped bass in each 50-mm size-class ($\hat{n}_i$) was estimated as

$$\hat{n}_i = \hat{N}\left(\sum_j p_{i,j} w_j\right), \quad (3)$$

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where $\widehat{N}$ is the estimated absolute abundance of striped bass from equation (1) expanded to the entire study area; $p_{i,j}$ is the proportion of striped bass in size-class $i$ at site $j$ (across all 2006–2007 electrofishing samples at site $j$; 2005 samples were excluded because mechanical issues with the electrofishing boat in that year reduced capture efficiency for larger fish and thus biased the estimates of size structure); and $w_j$ is a weighting factor for site $j$ calculated as

$$w_j = \frac{\bar{E}_j}{\sum_j \bar{E}_j}, \tag{4}$$

where $\bar{E}_j$ is the mean electrofishing CPH of striped bass 300 mm or longer at site $j$ (across all 2006–2007 electrofishing samples at site $j$). Weighting factors were used to correct for potential biases introduced by unequal numbers of sampling nights across sites during 2006–2007. The population-level consumption ($\widehat{C}$) of blueback herring by striped bass 300 mm or longer over the vernal migration period was then estimated as

$$\widehat{C} = V \sum_i \left( \widehat{n}_i \sum_j q_{i,j,1} w_{i,j} \right) + \left( 2 \left( \widehat{n}_i \sum_j q_{i,j,2} w_{i,j} \right) \right), \tag{5}$$

where $V$ is the number of days in the migration season; $q_{i,j,1}$, $q_{i,j,2}$ are the proportions of diet samples from striped bass in size-class $i$ at site $j$ that contained one or two blueback herring, respectively (across all diet samples collected in 2005–2007); and $w_{i,j}$ is the weighting factor for size-class $i$ at site $j$. We restricted diet outcomes to one or two herring (i.e., we assumed that striped bass consumed a maximum of two herring per day) as less than 5% of striped bass stomachs with herring contained more than two.

We quantified the uncertainty in our population-level consumption estimates via a Monte Carlo randomization (Hilborn and Mangel 1997). For each of 10,000 model runs, simulated data on absolute abundance, size structure, and diet composition were created using appropriate probability distributions. Striped bass abundance ($\widehat{N}$ in equation 1) was randomized by sampling the total number of recaptures (the sum of $R_e$, $R_{a,s}$, and $R_{a,h}$; see equation 1) from a Poisson distribution with mean $\lambda$ equal to the total number of recaptures (we used a Poisson distribution because we obtained less than 25 recaptures; see Hayes et al. 2007). Size structure was randomized by sampling the number of striped bass measured during 2006–2007 electrofishing samples from a multinomial distribution parameterized with observed proportions at length ($\sum p_{i,j} w_j$ from equation 3). The randomly sampled size distribution data set yielded a randomized vector of proportions at length that was substituted for the observed proportions at length in equation (3). Diet composition for each striped bass size-class was randomized by sampling the number of striped bass in the size-class that was lavaged in 2005–2007 from a multinomial distribution parameterized with the observed proportions of striped bass in size-class $i$ that consumed 0, 1, and 2 herring ($\sum q_{i,j,n} w_{i,j}$ from equation 5). The randomized matrix of proportions of striped bass consuming 0, 1, and 2 herring was substituted for the observed diet proportions in equation (5). The number of days in the vernal migration season ($V$ in equation 5) was randomized by sampling integers between 30 and 50 from a uniform distribution (based on observed season lengths during 2005–2008; see Davis et al. 2009). Randomized data sets were created in SAS (SAS Institute 2003) using the IML Procedure (multinomial) and the Rand function (Poisson). We summarized the results of the Monte Carlo simulation as median consumption rates with 5% and 95% confidence limits (i.e., with a 90% confidence interval [CI]).

*Assessing the recreational fishery*.—A "bus stop" design creel survey (Jones and Robson 1991; Pollock et al. 1994) conducted by the CDEEP in 2008 estimated recreational catches of striped bass in the Connecticut River between Middletown, Connecticut, and the Massachusetts border (Davis et al. 2011). The creel survey segment was divided into two independent survey zones (zone 3: Middletown to Hartford, Connecticut; zone 4: Hartford to the Massachusetts border). The survey within each zone was stratified by 2-month seasons (season 1: March–April; season 2: May–June; season 3: July–August; and season 4: September–October) and secondarily by day type (weekend versus weekday) within each season. Creel agents surveyed each zone on two weekdays, randomly selected, and both weekend days during each calendar week. Surveys started either in the morning (0600 or 0700 hours) or afternoon (1300 or 1400 hours) and lasted for 6 h; an equal number of morning and afternoon surveys were conducted within each day type stratum during each month. No nighttime surveys were conducted.

During each bus stop survey, clerks counted all shore anglers and boat trailers (as a proxy for boat anglers) at a series of access points. Other regularly conducted supplementary surveys estimated the proportion of trailers that were attributable to anglers and the proportion of shore angler effort occurring at sites within a zone that were not surveyed by the bus stop survey (Davis et al. 2011). Clerks also interviewed individual anglers for data on trip length and the numbers and sizes of all fish caught. All harvested fish in an interviewee's possession were measured by the clerk (TL, cm). Interviewees were then asked to estimate the TL of any released fish in inches.

The time interval count estimator and the ratio-of-means estimator (Pollock et al. 1994; Davis et al. 2011) were used to estimate total angler effort (angler-hours) and mean angler catch rate (CPH) of various fish species, respectively, for each bus stop survey day. Both quantities were estimated separately for each angling mode (boat versus shore); the total catch for each mode on each bus stop survey day was then estimated

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as the product of angler effort and mean CPH. Total harvest for each mode was estimated in an analogous manner using estimates of harvest per hour instead of CPH. The total catch or harvest ($\hat{Y}$) of each species for each mode for an entire 2-month season was estimated by the equation (Pollock et al. 1994; Davis et al. 2011)

$$\hat{Y} = D \sum_{w} \left( \frac{n_w}{D} \right) \bar{y}_w \tag{6}$$

where $D$ is the number of days in the season; $n_w$ is the number of days in day type stratum $w$; and $\bar{y}_w$ is the sample mean catch or harvest for day type stratum $w$. The variance of the total catch or harvest estimate [$Var(\hat{Y})$] for the season was estimated as (Pollock et al. 1994; Davis et al. 2011)

$$Var(\hat{Y}) = D^2 \sum_{w} \left( \frac{n_w}{D} \right)^2 \frac{S_w^2}{d_w} \left( \frac{n_w - d_w}{d_w} \right), \tag{7}$$

where $S_w^2$ is the sample variance of catch or harvest for day type stratum $w$ and $d_w$ is the number of days sampled in day type stratum $w$. The standard error of the total catch or harvest estimate was estimated as the square root of the variance (Pollock et al. 1994; Davis et al. 2011).

We approximated the total angler catch and harvest of striped bass in the Connecticut portion of our study area during the 2008 spring migration season by summing the catch and harvest estimates for seasons 1–2 (March–June) for both fishing modes from zones 3–4. The standard errors of the overall catch and harvest estimates were estimated as the square root of the sum of $Var(\hat{Y})$ across zones, seasons, and modes. Zone 3 only partially overlapped our study area (Figure 2); we therefore estimated the percentage of angler effort occurring north of Wethersfield in zone 3 during seasons 1–2 (64%) and adjusted the totals and variances of striped bass catch and harvest in zone 3 accordingly.

*Forecasting reductions in consumption under alternative management regimes*.—We modeled the potential reductions in blueback herring consumption under alternative management regimes for the striped bass fishery in the Connecticut portion of our study area. Each management scenario was modeled as a "bonus" harvest program (i.e., one that allowed harvesting beyond that allowed under the existing 28-in minimum length limit and two-fish daily bag limit). Scenarios were modeled on the bonus harvest program instituted by CDEEP. Five bonus harvest slot limit scenarios targeting sublegal size classes were modeled: 22–27 in (560–690 mm), 20–27 in (510–690 mm), 16–27 in (406–690 mm), 16–23 in (406–584 mm), and 16–21 in (406–533 mm). The annual harvest under each slot limit was varied from 5,000 to 20,000 fish in increments of 5,000 (i.e., 10,000 model runs at each harvest level).

To model the reductions in blueback herring consumption under each bonus harvest scenario, the randomized blueback herring consumption model was run 10,000 times with an additional input that described striped bass removals. For each model run, the number of striped bass harvested from each 50-mm size-class vulnerable to the slot limit was randomly sampled from a multinomial distribution parameterized with estimated proportions of the annual harvest that would be taken from each vulnerable size-class. The proportions of annual harvest taken from each vulnerable size-class ($\hat{r}_i$) were estimated as

$$\hat{r}_i = \frac{\hat{Y}_i}{\sum_i \hat{Y}_i}, \tag{8}$$

where $\hat{Y}_i$ is the estimated angler catch of striped bass from size-class $i$ in the Connecticut portion of the study area during March–June 2008. The estimated harvests within each vulnerable size-class were subtracted from the abundance of striped bass in the class ($\hat{n}_i$ from equation 3) prior to each model run.

We also modeled alternative management scenarios with an unchanged 28-in minimum length limit but increased harvest, such as might be achieved by increasing the existing bag limit. Model runs were conducted in which the total harvest of striped bass 710 mm TL (28 in) or longer from the Connecticut portion of the study area during March–June 2008 was increased by a factor of 2–4. These model runs were conducted in an analogous manner to those for the bonus harvest slot scenarios; the number of striped bass harvested from each vulnerable size-class was modeled as a multinomial variable, and the estimated harvest was subtracted prior to each model run.

We were interested in the feasibility of various levels of annual harvest under each of the modeled regulation scenarios. Specifically, we wished to address the question: Given the available data on angler catch and harvest of striped bass during spring 2008, how likely is it that anglers in the Connecticut portion of the study area could catch and harvest enough striped bass to meet the annual harvest goal under various alternative regulation scenarios? To address this question, we calculated an index of "harvest increase" (*HI*) that compared the size of annual harvests from the vulnerable size-classes for each modeled bonus harvest scenario with angler catches from those size-classes in spring 2008. The index was computed as follows:

$$HI = \frac{1}{m} \sum_{x} \left( \frac{1}{k} \sum_{i} \frac{H_{i,x}}{\hat{Y}_i} \right), \tag{9}$$

where $m$ is the number of model runs (10,000); $k$ is the number of size-classes vulnerable under the regulation scenario; and $H_{i,x}$ is the number of striped bass harvested from vulnerable size-class $i$ in model run $x$. If $HI = 1$ for a bonus harvest scenario, on average Connecticut anglers would have to harvest as many vulnerable striped bass as they caught during spring 2008 to meet the annual harvest goal; higher *HI* scores indicate lower feasibility of achieving annual harvest goals.

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## RESULTS

### Striped Bass Size Structure, Food Habits, and Absolute Abundance

The population of striped bass in our study area during 2006–2007 was composed primarily of sublegal fish (Figure 3a). Approximately three-quarters of the 606 striped bass 300 TL mm (12 in) or longer that we collected were smaller than 710 mm (28 in). The modal sizes were 350–499 mm (13–19 in); a long tail of declining proportions at length culminated in a slightly higher proportion in the aggregated class of fish 1,000 mm (39 in) or longer.

Consumption of blueback herring was predator size dependent (Figure 4). Blueback herring were eaten by striped bass over most of the size range we captured by electrofishing. Herring were most commonly eaten by striped bass 650–999 mm (25–39 in) long; herring were recovered from 19% of these fish, and most of the striped bass containing more than one herring were in this size range (Figure 4).

We tagged a total of 500 striped bass in Windsor Locks during May 2008. A total of 16 recaptures were recorded in the Connecticut portion of our study area during May (13 by anglers, 3 by electrofishing; an additional 5 tags were returned by anglers during May from areas outside the Connecticut portion of the study area). We increased the total return of standard ($15 reward) tags from six to nine to reflect an estimated 68% angler reporting rate, bringing the May recapture total to 19. The total daily catch of striped bass during May 2008 ranged from 48 to 705 fish (mean = 196, median = 138). The Schnabel model (equation 1) yielded an estimate of 81,598 striped bass 300 mm or longer (95% CI = 53,332–130,557) in the Connecticut portion of the study area, or approximately 1,951 fish/river km. Expanding this estimate by the length of the entire study area, we estimate that 125,536 striped bass 300 mm or longer (95% CI = 82,050–200,857) were present during May 2008.

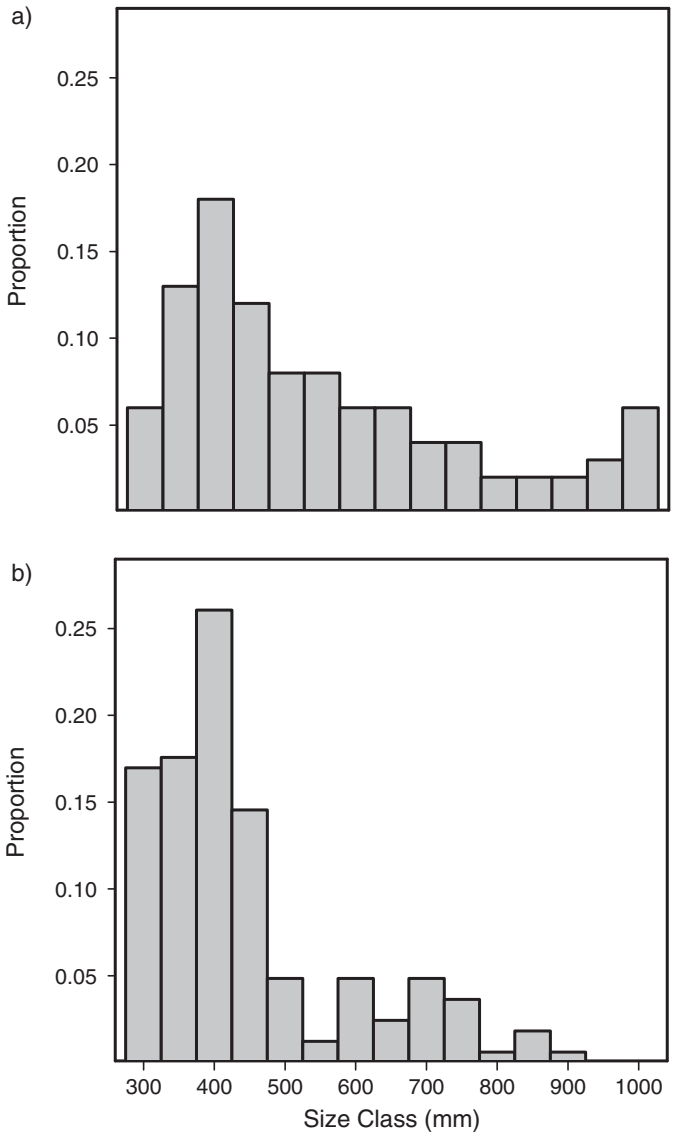



FIGURE 3. Size structure of striped bass 300 mm TL or longer that were captured in the Connecticut River during the spring migration season. Panel **(a)** shows the distribution of fish captured in the study area via electrofishing during May and June 2006–2007 ($n = 606$); panel **(b)** shows that of fish captured by recreational anglers during March–June 2008 in the Connecticut portion of the study area ($n = 165$ catch events recorded by creel survey interviews).

### Population-Level Consumption of Blueback Herring

We estimate (equation 5; $V = 40$ d) that striped bass consumed 370,582 blueback herring. The Monte Carlo model simulation of herring consumption produced an estimate of median striped bass population-level consumption of 395,062 blueback herring (90% CI = 178,153–791,181; Figure 5). Striped bass in the 450-mm (17–19-in), 650-mm (25–27-in), and 750-mm (29–31-in) size-classes consumed the greatest number of herring, accounting for a mean of approximately 40% of population-level consumption across 10,000 model runs (Figure 6). Striped bass between 850 and 999 mm (33–39 in) made a small contribution to population-level consumption (Figure 6) despite their high per-capita rates of blueback herring consumption (Figure 4). Conversely, smaller striped bass that ate herring infrequently (Figure 4) nonetheless made large contributions to population-level consumption (Figure 6) as a result of their high abundances (Figure 3).

### Recreational Fishery

Striped bass angling dominated the recreational fishery in the river stretch between Middletown and the Massachusetts border during March–June 2008: 64% of anglers there targeted striped bass. We estimate that anglers caught 17,077 striped bass (SE = 3,701) in the Connecticut portion of our study area during March–June 2008, of which 14,122 were at least 300 mm. The recreational catch was composed overwhelmingly of fish less than 710 mm (28 in; Figure 3b). We estimate that only 11% of the striped bass landed were legal-sized (≥710 mm or 28 in) and that 77% were less than 500 mm (20 in). We estimate that

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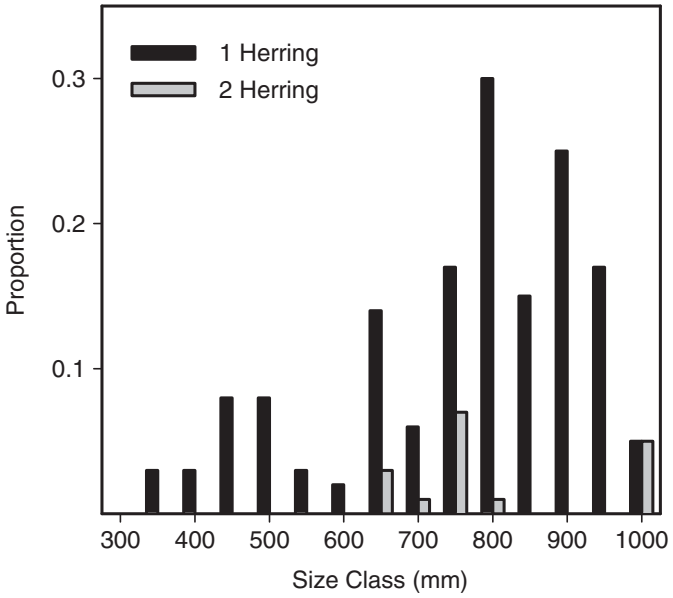



FIGURE 4. Proportion of striped bass diet samples ($n = 642$) collected in the study area during May–June 2005–2007 that contained one or two blueback herring, by 50-mm striped bass size-class.

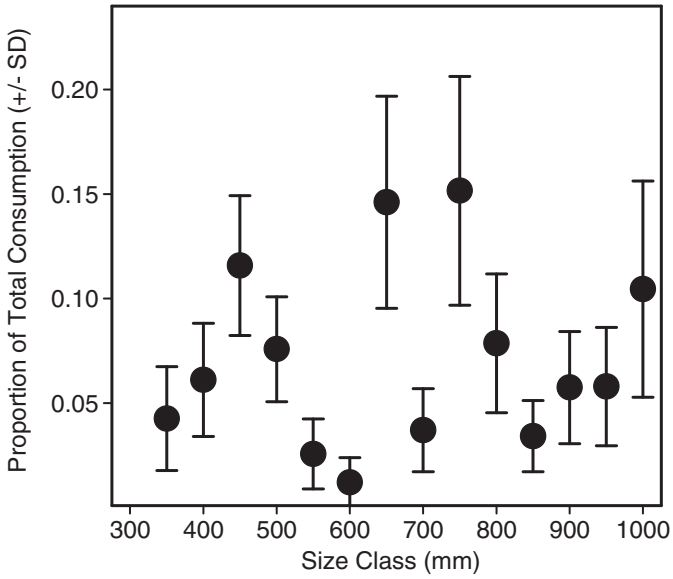



FIGURE 6. Mean proportions of blueback herring consumption attributable to the various 50-mm striped bass size-classes in 10,000 runs of the Monte Carlo consumption model. The error bars indicate SDs.

anglers harvested 70% (1,311) of the legal-sized striped bass caught, but this harvest estimate was imprecise (SE = 764).

### Reductions in Consumption under Alternative Management Regimes

The bonus harvest scenarios that yielded the greatest reduction in herring consumption were the least likely to be fulfilled.

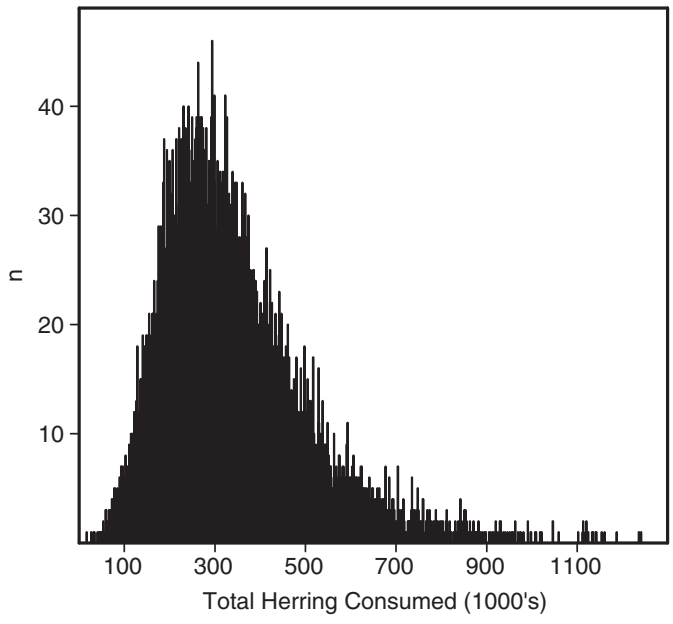



FIGURE 5. Frequency distribution of population-level blueback herring consumption outcomes from 10,000 iterations of the Monte Carlo consumption model.

Bonus slot limits operating on larger fish yielded the greatest reduction in median total consumption of blueback herring (Figure 7). At an annual harvest level of 15,000 striped bass, the 22–27-in and 20–27-in bonus slots yielded 11% reductions in median consumption; slots operating on smaller fish yielded about 8% reductions (Figure 7). Such sizeable annual harvest of larger fish, however, may be difficult to achieve. For instance, we estimate that an annual harvest of 15,000 striped bass from a 22–27-in bonus slot operating in the Connecticut portion of the study area would require anglers to achieve a harvest 12–13 times larger than the estimated catch of slot-sized striped bass there in March–June 2008 (Figure 8). Broader slot limits permitting harvest of smaller striped bass would have a greater probability of achieving total harvest goals (Figure 8). The broadest slot limit (16–27 in) provided the greatest reduction in median consumption among the slots that operated on smaller fish (Figure 7) and had the best (lowest) *HI* scores (Figure 8). Harvest of an additional 1,000–4,000 legal-sized (≥28-in) fish provided reductions in blueback herring consumption comparable to those achieved by bonus slot limits at much higher levels of annual harvest (Figure 7) and appeared relatively feasible (Figure 8).

## DISCUSSION

### Striped Bass Size Structure, Food Habits, and Absolute Abundance

Our study documented a large contingent of striped bass (estimated at >100,000 fish at a mean density approaching 2,000 fish/river km) above the head of tide in the Connecticut River. The appearance of striped bass in this area is coincident with

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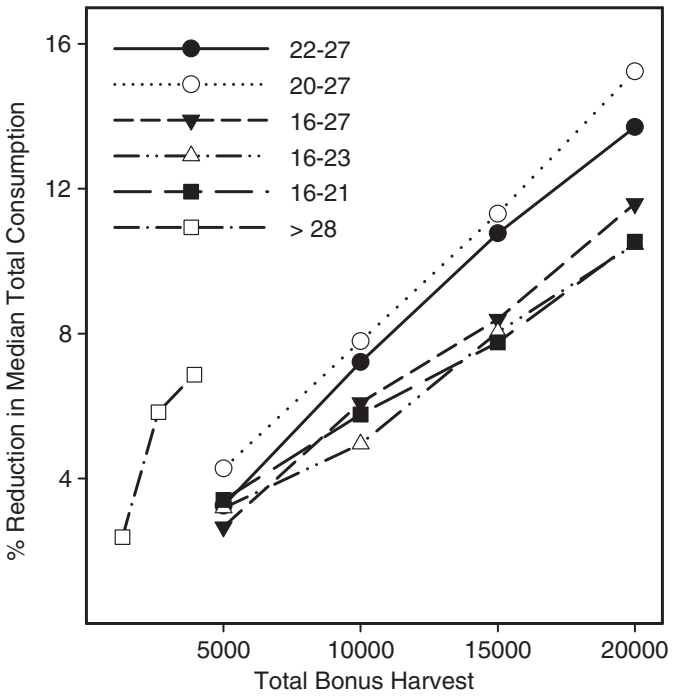



FIGURE 7. Percent reductions in median total consumption of blueback herring under six alternative bonus harvest management scenarios for striped bass at varying levels of total annual harvest.

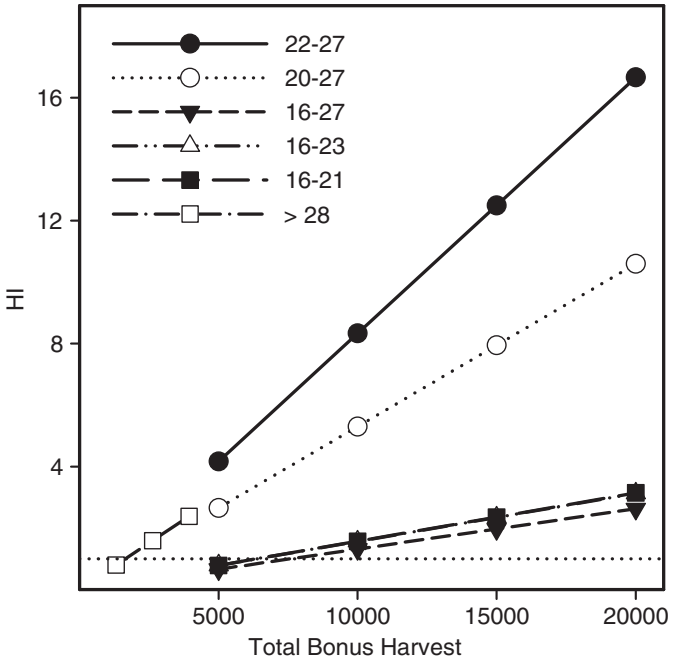



FIGURE 8. Index of harvest increase (*HI*), defined as the mean proportion of angler catch of vulnerable striped bass that would have to be harvested based on 2008 creel survey data, for the six alternative bonus harvest management scenarios at varying levels of total annual harvest. The dotted line near the bottom, for which $HI = 1$, indicates that harvest is equal to the total catch recorded in 2008.

the vernal spawning migration of blueback herring. Electrofishing catch rates of striped bass generally declined to low levels in our study area by mid-June (Davis et al. 2009), and recreational catches of striped bass were negligible in March and July–October (Davis et al. 2011). In addition, anglers returned tags from a wide range of coastal locations during summer and fall (Davis et al. 2009). Taken together, these observations strongly suggest that most of the striped bass migrating to our study area are members of the coastal population that emigrate at the conclusion of spring. We also showed that these migratory predators prey on blueback herring while in the study area. Given that striped bass opportunistically target spawning aggregations of anadromous alosines in other systems (Trent and Hassler 1966; Manooch 1973), striped bass likely migrate to the Connecticut River at least in part to exploit spawning aggregations of blueback herring. Recent observations of increasing numbers of apparently nonspawning striped bass migrating into multiple coastal rivers in the northeastern United States during spring (Grout 2006) support the hypothesis that such vernal feeding forays are a widespread consequence of the recent coastal striped bass recovery. Unfortunately, there are no long-term data on the vernal abundance of striped bass in the Connecticut River to provide our discussion of the current situation with a historical perspective.

Interactions between the Connecticut River blueback herring population and striped bass are not limited to the consumption of adult herring during the vernal migration. Subadult (i.e., $\leq$age 7) striped bass are present in the Connecticut River estuary (south of our study area) for much of the year (Jacobs et al. 2004; Savoy and Crecco 2004) and presumably prey upon young-of-year alosines while there (Hartman and Brandt 1995; Hartman 2003). However, we regard the vernal episode of adult herring consumption as that having the highest potential impact on herring populations. Observed shifts in recent decades among river herring toward fewer old spawners, fewer repeat spawners, and earlier age at maturation suggests that mortality has increased among older age-classes (Davis and Schultz 2009). Moreover, studies of striped bass diets during coastal residence in nearby Massachusetts found a low incidence of alosine prey (Nelson et al. 2003).

There are several potential sources of bias in our estimates of striped bass abundance, size structure, and food habits. We limited our sampling to the littoral zone where the boat electrofisher would be effective (Guy et al. 2009). We therefore did not sample all available habitats at each site and sampled a different proportion of the available habitat at each site. We could not estimate the size selectivity of the boat electrofisher because alternative gears did not yield sufficient catch for comparison. The Schnabel mark–recapture model used to estimate striped bass abundance assumes population "closure" during the study period (Lukacs 2009). We assumed population closure at the height of the migration in May. However, tag returns from outside the study area as well as variation in electrofishing catch rates (CPH within the study area generally varied by a factor

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of 1–4 during May 2006–2007; see Davis et al. 2009) indicate that some movement to and from the study area occurred during this period; our abundance estimates are therefore biased to an unknown degree. Additionally, the underlying assumption of complete mixing of tagged fish into the target population (Seber 1982) may have been violated because we released all tagged fish at the Windsor Locks site. The sampling requirements of more robust models (e.g., Jolly–Seber) could not logistically be met with our available resources within the relatively short temporal window of the vernal migration (Kendall 2009; Schwarz and Arnason 2009). Finally, our approach to expanding the estimate of striped bass abundance in the Connecticut stretch to the entire study area assumed that the mean density of striped bass in Connecticut adequately approximated that in Massachusetts. This assumption was necessary because we did not sample the majority of the Massachusetts stretch (Figure 2). If the density in Massachusetts was significantly higher or lower than that in Connecticut, our expanded abundance estimates would be biased downward or upward, respectively.

### Population-level Consumption of Blueback Herring

We estimate that the contingent of striped bass migrating above the head of tide in the Connecticut River currently consumes approximately 400,000 blueback herring each spring. This predatory loss is sizeable; our estimates of population-level consumption are comparable to the number of blueback herring passing Holyoke Dam during peak years in the late 1980s (Figure 1). Our estimate of consumption may be somewhat conservative because we assumed that striped bass consumed a maximum of two herring daily. We made this assumption because less than 5% of striped bass stomachs sampled with herring prey contained more than two; the additional herring prey within those stomachs were generally at an advanced stage of digestion, suggesting they had been consumed more than 24 h before sampling. Nonetheless, larger striped bass are certainly capable of consuming more than two herring per day if presented the opportunity. Multiple anglers interviewed for the creel survey related anecdotes of finding more than 2 herring in the stomachs of harvested striped bass. Our consumption estimates did not explicitly account for the effects on gastric evacuation rates of water temperature, predator size, or meal size (Elliot and Persson 1978; Elliot 1991; Temming and Andersen 1994). This simplification was necessary because no information is available on the temperature dependence of gastric evacuation rates for large striped bass consuming large piscine prey items.

### Recreational Fishery and Reductions in Consumption under Alternative Management

Manipulation of striped bass harvest regulations in the Connecticut River can reduce predation on blueback herring. Reductions in predation mortality of 4–10% can be achieved in our study area if Connecticut anglers harvest 10,000–15,000 currently sublegal striped bass. Similar levels of mortality reduction could be realized with an additional harvest of several thousand currently legal-sized (>28-in) striped bass. The recent survey of the fishery, however, suggests that these levels of additional annual harvest are improbable. Under most modeled scenarios, Connecticut anglers would have to harvest as many or more (in some cases, more than 10 times more) striped bass from vulnerable size-classes as they caught during spring 2008 to meet bonus harvest targets. Nonetheless, many anglers harvest striped bass when presented with the opportunity; anglers harvested 70% of the legal-sized fish caught during spring 2008. Many anglers interviewed during the creel survey communicated a desire to harvest presently sublegal fish because smaller fish are more palatable and contain lower levels of contaminants. A bonus harvest program could therefore increase angling effort by current Connecticut River anglers and may even attract new anglers. Such a change in angler behavior could make annual bonus harvests of the magnitude described here more realistic.

Our model assumed that all harvested striped bass would be removed by anglers before consuming any herring prey and that there would be no compensatory natural mortality of blueback herring (i.e., we assumed that all of the herring "saved" under a bonus harvest scenario would survive for the duration of the migration season). These simplifying assumptions were necessary because the data required to quantify these factors were too coarse (in the case of temporal trends in angler catch) or unavailable (daily probabilities of herring survival).

### Management Implications and Future Directions

Identifying and mitigating the natural mortality of river herring is a primary concern for regional fisheries managers because populations have not recovered following fishery closures. If vernal striped bass predation is the primary factor regulating blueback herring population size and compensatory predation by other predators is minimal, the relatively small reductions in annual mortality described here may yield significant long-term benefits for the Connecticut River blueback herring population. Blueback herring are a short-lived, highly fecund species (Loesch 1987), and thus their populations have high resilience and intrinsic growth rates (Gotelli 2001). Even relatively small reductions in annual mortality can therefore produce appreciable population growth on a decadal scale. Increased in-river harvests of striped bass may cause a sustained decrease in the size of the striped bass vernal migration into the Connecticut River. The likelihood of this hypothesis rests in part on whether the group of striped bass migrating to the Connecticut River is a true "contingent," that is, a distinct, persistent subgroup of the coastal stock defined by a divergent seasonal migration pattern (Clark 1968; Secor 1999). Striped bass have shown fidelity to nonnatal foraging sites (Mather et al. 2009) as well as their natal sites (Mansueti 1961; Nichols and Miller 1967). Although it has not been directly demonstrated, spawning of striped bass in the Connecticut River is possible: we captured ripe-running fish of both sexes during our study, and small, presumably young-of-year fish have been collected in the river during fall (Jacobs et al. 2004). Future studies assessing whether the Connecticut River

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is a spawning site and the degree of interannual site fidelity will elucidate whether the vernal striped bass migration truly represents a contingent susceptible to reductions through increased harvest.

Other considerations suggest that an immediate recovery of blueback herring in the Connecticut River is unlikely. Most alternative management scenarios produced reductions in consumption of less than 10%, and those producing greater reductions appear to be relatively improbable given the current condition of the fishery. Even if herring consumption decreases because of higher striped bass harvest, the herring population may not rapidly recover. The steep declines in blueback herring run size noted during the late 1980s and early 1990s occurred when vernal striped bass abundances were probably well below the reduced abundances modeled here, judging from data on coastal abundance (Figure 1). The management strategies outlined here will also not address other potential stressors on the herring population, such as bycatch in marine fisheries (Cieri et al. 2008), and do not take into account the possibility that increased consumption by other predators will compensate for the reductions in striped bass consumption.

Our findings illustrate the important roles that predator size and selectivity operating at multiple trophic levels (given that anglers are essentially top-level predators in this system) play in determining the trophic implications of fisheries management scenarios. Increased abundance of desirable size-classes is a common management goal that is typically achieved by modulating the magnitude and size selectivity of fishing mortality (Noble and Jones 1999). The resulting changes in the size distribution of managed fish populations have implications for populations at lower trophic levels because predator size plays an important role in determining prey selection and per capita consumption rates (Juanes et al. 1993; Scharf et al. 1997, 1998; Hartman 2000; Johansen et al. 2004; Rudershausen et al. 2005). Management outcomes may not be readily inferred from examination of one or more of these factors at a single trophic level. For instance, our diet data revealed that smaller striped bass (400–549 mm) consumed blueback herring infrequently; however, when population abundance and size structure were considered it was apparent that these smaller fish made relatively large contributions to population-level consumption. Bonus harvest programs focusing on smaller size-classes may therefore yield herring mortality reduction, but only if they promote relatively large annual harvests. Although smaller harvests of larger striped bass may provide comparable reductions in herring mortality, elevated harvests of smaller striped bass may be easier to achieve because of their higher vulnerability and desirability to anglers.

Further analyses employing blueback herring population models that incorporate time-variant estimates of natural mortality arising from striped bass predation will be necessary to fully characterize the benefits of the management programs proposed here. Extending our modeling framework to forecast future blueback herring population states under various striped bass management regimes will require additional information on the relationship between predator–angler foraging behavior and prey–target species abundance. Striped bass typically employ a generalist foraging strategy (Walter et al. 2003) and will therefore opportunistically exploit less desirable but more abundant prey when preferred prey is at low abundance (Chipps and Garvey 2007). Per capita rates of striped bass consumption are therefore likely to be a nonlinear function of blueback herring abundance, typified by a "type 3" functional response (Holling 1959; Beauchamp et al. 2007). Because we measured consumption rates at low levels of prey abundance, these rates may be underestimates of the consumption rates that would result from the recovery of herring populations. Alternatively, it is possible that some size-classes of striped bass specializing on river herring prey will consume a constant proportion of the prey population across a wide range of prey abundances (i.e., a "type 2" functional response). Such a foraging strategy would have depensatory effects on the prey population because striped bass would continue to target and consume blueback herring despite the low abundance of herring in the environment (Yodzis 1994). Similarly, angling effort and catch rates for striped bass in the Connecticut River will probably vary with striped bass abundance and management regime (Eggleston et al. 2003, 2008). If decreases in striped bass abundance result in declining angling quality, anglers may choose to target striped bass in other locations and/or to target other available species in the river. By the same token, a novel opportunity to harvest sublegal striped bass could produce a "numerical response" (Holling 1959), attracting anglers to the river and intensifying angling pressure.

Our study offers a modest-scale case study of how fishery-dependent data, fishery-independent data, and modeling can be integrated to consider management strategies. Regional and rangewide data had suggested a link between the increasing abundance of striped bass and the diminishment of blueback herring. We conducted a multiple-year study in the Connecticut River in order to collect targeted data on the interaction. A creel survey of the Connecticut recreational fishery yielded data on the patterns of angler catch and harvest as well as striped bass abundance. The availability of these data stimulated discussions of new management approaches and permitted parameterization of a relatively simple model designed to assess the efficacy of alternative approaches. Continued local monitoring of the fish species and the recreational fishery will be needed to judge whether managing predation through fishery regulations is effective at restoring a species of concern.

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