

Assessing the Contribution of Anadromous Herring to Largemouth Bass Growth

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Abstract.—Juvenile anadromous river herring (alewife *Alosa pseudoharengus* and blueback herring *A. aestivalis*) spend the first 3 to 7 months of life in headwater lakes of coastal systems. Systems that support herring often produce trophy largemouth bass *Micropterus salmoides*. Even though biologists, managers, and anglers have speculated about the value of anadromous herring as a key prey for resident predators, the contribution that herring make to the diets of these predators has not been assessed. Herein, we quantified largemouth bass diets in two coastal lakes, Santuit and Coonamessett ponds, that contained anadromous herring, and we used bioenergetics modeling to evaluate the importance of herring prey to largemouth bass growth. During May through November 1994, largemouth bass diets consisted of various fish species, crayfish, and other invertebrates. Although not the most important prey overall, herring were the most important fish prey consumed in both lakes based on number of individuals consumed. In both lakes, herring were primarily eaten by largemouth bass that were fewer than 300 mm in total length after mid-August. Coonamessett Pond largemouth bass ate more herring and other fish prey and achieved better growth than did those in Santuit Pond. Bioenergetics modeling simulations revealed that water temperature does not explain the presence of trophy largemouth bass in southeastern Massachusetts. Because largemouth bass grow better on a diet that includes herring, we conclude that juvenile herring are an energetically valuable and a potentially key prey for largemouth bass. However, factors other than energetics mediate the use of herring by these resident predators. Further investigations into spatial dynamics, size structure, and foraging behavior are necessary to understand the mechanisms that drive interactions between largemouth bass and anadromous herring.

Predator–prey interactions are dynamic and are strongly influenced by such factors as prey size, prey availability, and structural complexity. Specifically, prey availability may drive the success of a fish population. Fish consume a wide variety of prey but will grow best when key or preferred prey are consumed over other prey (Prout et al. 1990; Yako et al. 1996). Furthermore, survival of young fish is often regulated by the availability of certain key prey (Mills et al. 1989; Post and McQueen 1994). Hence, differences in growth rates within and across fish populations may be observed when key prey are readily available and included in predator diets. In coastal systems in which anadromy is prevalent, anadromous fish may not only act as nutrient vectors (Durbin et al. 1979), thus stimulating primary production in spawning areas, but can also provide a seasonal flux of prey and may promote higher growth and

survival for freshwater predators (Polis et al. 1997).

In coastal Massachusetts, anadromous alewife *Alosa pseudoharengus* and blueback herring *A. aestivalis*, collectively termed river herring, ascend freshwater streams each spring in order to spawn. After spawning, 39–57% of adult herring die (Cooper 1961; Havey 1961; Kissil 1974); the rest may return to the ocean immediately or may remain in freshwater systems for several months. Juvenile herring remain in headwater lakes from 3 to 7 months, after which they migrate to the ocean (Yako 1998). Biologists, managers, and anglers have speculated about the beneficial value of juvenile river herring as a key prey for resident freshwater fishes, especially largemouth bass *Micropterus salmoides*. Interestingly, sizes and presumably growth rates of largemouth bass differ among lakes in Massachusetts, with several coastal systems that contain anadromous herring yielding ‘trophy’ largemouth bass (>3,536 g; Massachusetts Division of Fisheries and Wildlife 1996). Nevertheless, the seasonal contribution of juvenile

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herring to diets of largemouth bass in these coastal lakes has not been quantified.

Bioenergetics models (e.g., Hewett and Johnson 1992) provide a simple method of modeling predator-prey interactions and have become an easily accessible tool for both fisheries biologists and managers. Bioenergetics models are based on a mass-balance energy equation in which consumption equals the sum of metabolic losses (respiration and specific dynamic action), waste losses (egestion and excretion), and the change in biomass. Recently, bioenergetics models have been used to quantify predatory demand (LaBar 1993; Luecke et al. 1994; Hartman and Brandt 1995a; Rudstam et al. 1995; Kitchell et al. 1997), to determine the effect of changing energy density and mean size of prey on daily ration (Rand et al. 1994), to explore seasonal and ontogenetic consumption patterns (Rudstam et al. 1994), and to estimate nutrient cycling by fish (Kraft 1993; Schindler et al. 1993).

In order to quantify the role that juvenile anadromous herring play in the diets of largemouth bass in small coastal lakes, we first assessed largemouth bass growth and diets in two lakes on Cape Cod, Massachusetts. Next we measured the physical characteristics of the lakes that may affect largemouth bass growth. Finally, we used the Hewett and Johnson (1992) bioenergetics model to examine three questions relative to largemouth bass-river herring interactions, including (1) the role of water temperature in regional patterns of largemouth bass growth, (2) the relative importance of individual prey taxa, and (3) the implications of diet variation within and across systems.

Methods

Study sites.—Santuit and Coonamessett ponds were geographically close (within 14.5 km), physically similar lakes (Table 1) serving, respectively, as headwaters for the Santuit and Coonamessett rivers, which flow directly into the Atlantic Ocean. Both systems contained anadromous river herring, although the densities (Table 1) and sizes of juvenile herring differed (Yako 1998). The fish communities of both lakes contained largemouth bass, chain pickerel *Esox niger*, yellow perch *Perca flavescens*, pumpkinseed *Lepomis gibbosus*, bluegill *L. macrochirus*, banded killifish *Fundulus diaphanus*, golden shiner *Notemigonus crysoleucas*, white sucker *Catostomus commersoni*, brown bullhead *Ameiurus nebulosus*, American eel *Anguilla rostrata*, and anadromous alewives and blueback herring, whereas Coonamessett Pond also con-

TABLE 1.—Comparison of study sites, Santuit and Coonamessett ponds, both of which are located in Barnstable County on Cape Cod, Massachusetts.

Measurement	Santuit Pond	Coonamessett Pond
Location	Mashpee	Falmouth
Trophic status ^a	Mesotrophic	Mesotrophic
Surface area (ha)	67.7	63.9
Shoreline (km)	5.1	4.7
Mean depth (m)	1.2	5.8
Maximum depth (m)	3.0	10.4
Mean Secchi depth (m)	1.8	2.5
Emergent vegetation (% of shoreline)	35	25
Submerged vegetation (% of pond)	85	30
Largemouth bass population estimate ^b	692	211
(95% confidence interval)	(507–1,091)	(149–361)
Herring catch/min ^c	22.9	2.2

^a Massachusetts Division of Fisheries and Wildlife, pond survey information.

^b Yako 1998. Results of a mark-recapture population estimate conducted during April 1994.

^c Yako, unpublished data. Catch rate was based on 5-min electrofishing transects performed weekly. Data presented are from surveys performed in October 1994.

tained smallmouth bass *Micropterus dolomieu* and white perch *Morone americana*. The Santuit and Coonamessett pond/river systems were examples of systems in which river herring and largemouth bass coexist; however, Santuit Pond served as the primary system for this study.

Field data.—In order to evaluate the effect of anadromous river herring in the diets of largemouth bass, we first measured largemouth bass growth and quantified diets in both Santuit and Coonamessett ponds. In addition, system-specific data required for the bioenergetics model (e.g., proportion of each prey item in the diet, energy densities, and water temperatures) were collected. We initially sampled largemouth bass using shoreline electrofishing after sunset during April through May 1994 in Santuit and Coonamessett ponds. All fish that were greater than or equal to 290 mm in total length (TL) were individually tagged with a Floy external anchor tag or were marked with a fin clip; fish were then measured (± 1 mm TL), weighed (± 1 g), and released. In order to estimate growth for Santuit Pond, largemouth bass were sampled again in mid-November 1994 (approximately the end of the growing season). All largemouth bass were measured (± 1 mm TL) and weighed (± 1 g), and scales were taken.

Because few tagged fish were recaptured at the end of the growing season, we estimated growth using scale analysis. In order to estimate length at

the beginning of the 1994 growing season, annuli were measured with a digitizer, and length-at-age information was calculated using Fisheries Analysis Tools software (Missouri Department of Conservation 1989). A length–weight relationship calculated from largemouth bass collected in April 1994 was used to calculate weight from length measurements for the beginning of the 1994 growing season: $\ln(\text{weight}) = -14.1464 + 3.5116 \ln(\text{length})$ ($R^2 = 0.9230$; $P = 0.0001$; $df = 266$; $n = 370$). Growth was calculated as the difference in weight between the beginning and end of the growing season. Too few fish were collected from Coonamessett Pond at the end of the 1994 growing season to adequately calculate growth for all size-classes. Therefore, growth rates were estimated from largemouth bass sampled during surveys in Santuit and Coonamessett ponds on 17–18 April 1995. Analysis of scales from these surveys allowed us to obtain length-at-age measurements for the previous, 1994 growing season.

In order to quantify diets, largemouth bass were sampled via shoreline electrofishing after sunset twice monthly in each lake from May through November 1994. Three to 25 largemouth bass were collected, measured, weighed, stomach pumped using pulsed gastric lavage (Foster 1977; Light et al. 1983), and released on 13 dates in Santuit Pond and on 10 dates in Coonamessett Pond. Stomach contents were placed on ice, and diet items were later identified in the laboratory. Largemouth bass of less than 250 mm TL were not sampled thoroughly until August. Because most diet items were intact and easily identifiable, we individually identified prey to the lowest possible taxon. In order to identify items that were partially digested, we used diagnostic features, including wing and head shape for insects (Merritt and Cummins 1984) and cleithra for fish (Hansel et al. 1988; Schulze 1996). We separated prey items into the following five main categories: (1) herring (alewives and blueback herring), (2) other fish, (3) crayfish, (4) other invertebrates (mostly aquatic insects), and (5) amphibians. Some items could not be positively identified and were designated as “unknown” within each category. If intact, lengths (mm) of fish and crayfish were measured as TL and carapace length, respectively. All prey items were then grouped into their respective categories, and wet weights (g) were measured for each category. Finally, samples were dried to a constant weight at 60°C. We described each diet category as a percentage of the total dry weight of prey consumed and the total number of prey consumed on composites of

groups. In addition, we examined whether predation on juvenile river herring was related to largemouth bass body size.

When possible, energy densities of individual prey items were obtained from published values (Cummins and Wuycheck 1971; Kelso 1973; Rice et al. 1983; Rand et al. 1994). Because we could not obtain published values for all prey items and because published values were not specific to our study lakes, we estimated energy densities for fish species (bullhead, chain pickerel, and yellow perch) using methods described in Hartman and Brandt (1995b) when we were sure that the species-specific regressions were calculated specifically for juvenile fish. In order to calculate energy density, juvenile fish were collected from both Santuit and Coonamessett ponds using a beach seine during July through September 1994. Wet weights were measured, and dry weight was assessed for 2–10 fish per species. Dry weight–wet weight percentages were calculated and used with species-specific formulas (Hartman and Brandt 1995b).

Bioenergetics.—We used a species-specific bioenergetics model for largemouth bass to estimate consumption based on growth (Rice et al. 1983; Hewett and Johnson 1992) and to address three questions relative to the role of juvenile river herring in largemouth bass diets. We first used the model to calculate a P-value (proportion of maximum consumption) for each 50-mm size-class based on growth, diet proportions, and water temperatures observed in Santuit Pond. Because river herring were only consumed in the latter half of the season (see Results), we split the diets of largemouth bass into two diet periods based on our field data. The first model simulation diet period (9 May–15 August) included no herring, whereas the second diet period (16 August–10 November) contained herring prey. Model simulations concentrated on four size-classes of largemouth bass from Santuit Pond, 250–299, 300–349, 350–399, and 450–499 mm, which represented 67.8% of the total largemouth bass population in Santuit Pond (Yako 1998). Sample sizes were not large enough to include largemouth bass from the 150–249- and 400–449-mm size-classes in model simulations. Water temperature was recorded hourly in both Santuit and Coonamessett ponds during March through November 1994 using recording thermographs set at a depth of 1 m, the approximate depth at which largemouth bass were captured. For model simulations, weekly mean temperatures were used. Unless otherwise noted, we used all standard parameters (i.e., diet proportions, energy densities,

TABLE 2.—Standard parameters obtained from Santuit Pond largemouth bass in 1994 and used for bioenergetics model simulations. Diet proportions were based on actual diets collected during 1994; diet period 1 = 9 May–15 August and diet period 2 = 16 August–10 November. Energy densities are in kJ/g wet weight and represent mean values for each prey category; weights are in grams. Calculated *P* values, the proportion of maximum consumption, were calculated using the bioenergetics model and based on largemouth bass observed growth. Sample sizes were not large enough to include the <250-mm or 400–449-mm size-classes in model simulations.

Parameter	Size-class			
	250–299 mm	300–349 mm	350–399 mm	450–499 mm
Diet proportions: (period 1/period 2)				
Herring	0/0.75	0/0.21	0/0.05	0/0
Other fish	0.42/0.03	0.19/0.32	0.12/0.17	0.67/0.45
Crayfish	0.36/0.16	0.60/0.43	0.87/0.77	0.33/0.55
Other invertebrates	0.22/0.06	0.21/0.03	0.01/0.01	0/0
Amphibians	0/0	0/0.01	0/0	0/0
Energy density: (period 1/period 2)				
Herring	5.6/5.6	5.6/5.6	5.6/5.6	5.6/5.6
Other fish	4.4/4.1	4.3/4.0	4.1/4.5	3.3/4.6
Crayfish	3.2/3.2	3.2/3.2	3.2/3.2	3.2/3.2
Other invertebrates	4.6/3.9	4.6/4.1	4.4/5.4	2.8/2.3
Amphibians	1.7/1.7	1.7/1.7	1.7/1.7	1.7/1.7
Largemouth bass energy density	4.2	4.2	4.2	4.2
Start/end weight	163/277	317/438	583/745	1,218/1,452
Calculated <i>P</i> value	0.3928	0.4107	0.4447	0.4185

seasonal weight gain, *P*-values, and water temperatures) obtained from Santuit Pond for each model simulation (Table 2).

Question 1: water temperature.—We compared largemouth bass seasonal growth across systems as a function of variable temperature regimes. If temperatures are warmer in one part of Massachusetts than in another, temperature alone could explain the differences in largemouth bass growth across systems. Hence, we tested the effect of temperature on largemouth bass growth by incorporating into the model temperature data from lakes throughout Massachusetts, including Santuit and Coonamessett ponds in the southeast region, Onota Lake (Massachusetts Department of Environmental Protection, unpublished data) in the northwest region, and Mansfield Lake (Massachusetts Department of Environmental Protection, unpublished data) in the southwest region. Because weekly temperatures were not available for Onota and Mansfield lakes, we used mean monthly water-temperature regimes for these simulations along with the other standard parameters from Santuit Pond (Table 2).

Question 2: individual prey groups.—We next used the bioenergetics model to assess the impact of individual prey taxa on growth. Bioenergetics simulations were run using standard parameters from Santuit Pond (Table 2) and the following four single prey diets and corresponding energy densities, representing general values for each cate-

gory (Yako 1998): herring (5.6 kJ/g wet weight), other fish (4.1 kJ/g wet weight), crayfish (3.2 kJ/g wet weight), and other invertebrates (3.2 kJ/g wet weight). Amphibians were not used in any simulations because they represented such a small part (<1%) of the actual diets of largemouth bass observed in the field.

Question 3: diet variation.—Using actual diet data from both Santuit and Coonamessett ponds, we assessed how diet variation affects largemouth bass growth within and across systems. In order to test the effect of the inclusion of herring in largemouth bass diets, we used standard parameters from Santuit Pond (Table 2) and compared growth of largemouth bass that consumed (1) both early and late season diets from Santuit, as previously described (Table 2), (2) early season Santuit Pond diets only (diets that contained no herring prey), and (3) actual diets and energy densities of prey observed in Coonamessett Pond largemouth bass, diets in which many herring were consumed (Table 3). Because we did not have diets from largemouth bass in the 450–499-mm size-class for Coonamessett Pond, this size-class was not considered in this analysis.

Results

Field Data

We estimated seasonal growth for 57 largemouth bass collected from Santuit Pond in November

TABLE 3.—Diet proportions and energy densities (kJ/g wet weight), representing mean values for each prey category, for prey consumed by Coonamessett Pond largemouth bass during 1994. Diet period 1 = 9 May–15 August, and diet period 2 = 16 August–10 November. Sample sizes were not large enough to split diets between the two periods for the 450–499-mm size-class or to include the <250-mm or 400–499-mm size-classes in model simulations.

Parameter	Size-class		
	250–299 mm	300–349 mm	350–399 mm
Diet proportions: (period 1/period 2)			
Herring	0/0.91	0/0	0/0.04
Other fish	1/0.08	0.98/0.99	0.43/0.17
Crayfish	0/0	0/0	0.56/0.77
Other invertebrates	0/0.01	0.02/0.01	0.01/0.02
Amphibians	0/0	0/0	0/0
Energy density: (period 1/period 2)			
Herring	5.6/5.6	5.6/5.6	5.6/5.6
Other fish	4.8/4.1	4.7/4.7	4.6/4.7
Crayfish	3.2/3.2	3.2/3.2	3.2/3.2
Other invertebrates	5.4/5.4	5.4/5.4	5.4/3.7
Amphibians	1.7/1.7	1.7/1.7	1.7/1.7

1994. Weight gain varied from 80.9 g for largemouth bass that were 150–199 mm TL to 234.2 g for those 450–499-mm largemouth bass (Table 2; Yako 1998). In our lake-to-lake comparison based on fish collected in April 1995, Coonamessett Pond largemouth bass were significantly larger at all ages than were Santuit Pond largemouth bass (Figure 1; analysis of covariance: $F = 176.0$, $df = 5,109$, $P = 0.0001$).

During May through November 1994 in Santuit Pond, we sampled 189 largemouth bass stomachs, 67% of which contained food. In Coonamessett Pond, we sampled stomachs of 88 largemouth bass, 59% of which contained food. Largemouth bass diets in both lakes included juvenile herring, other fish species, crayfish, other aquatic and ter-

restrial invertebrates, and amphibians (Figure 2; Yako 1998). In Santuit Pond, other fish made up the highest percentage of weight of prey consumed in May (99.5%), June (61.7%), and August (59.0%), whereas crayfish made up the highest percentage of weight of prey consumed in July (74.8%), September (61.8%), and November (70.9%) (Figure 2A). In Santuit Pond, juvenile herring were not found in the stomachs of any largemouth bass until mid-August, were only an occasional diet item in September, and dominated diets in October (79.0%). Similarly, in Coonamessett Pond, other fish and crayfish dominated largemouth bass diets during May through August (Figure 2B). Herring first appeared in the diets of Coonamessett Pond largemouth bass in mid-September and dominated

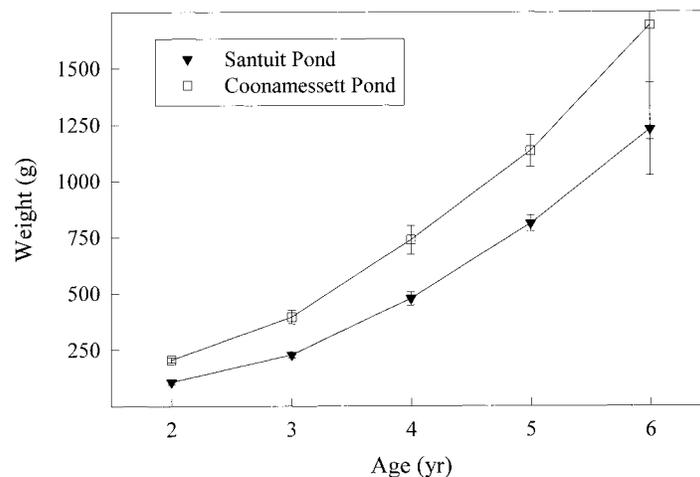


FIGURE 1.—Mean weight at each age for largemouth bass collected from Santuit and Coonamessett ponds, Massachusetts, during April 1995. Data are mean \pm SE.

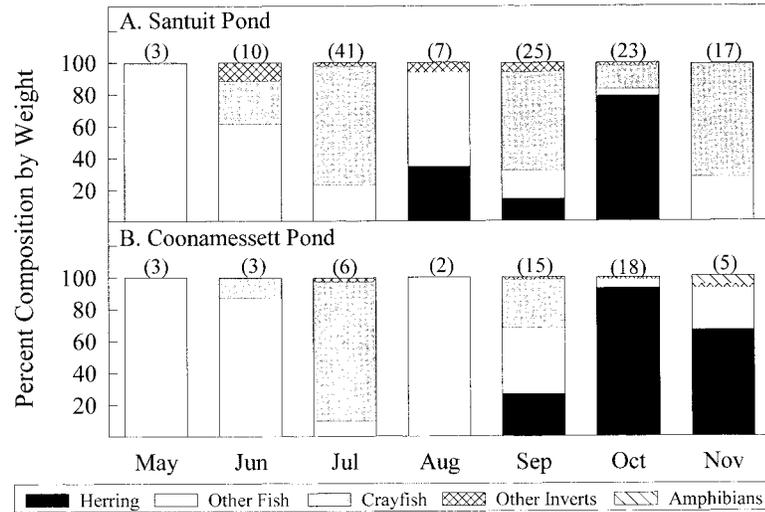


FIGURE 2.—Percent composition by weight (g) for monthly diets of largemouth bass from (A) Santuit Pond and (B) Coonamessett Pond, Massachusetts, collected during May through November 1994. Numbers in parentheses indicate sample size for each month.

diets by weight in both October (93.1%) and November (66.8%).

Diet composition differed with size of largemouth bass. In Santuit Pond, herring constituted 51–64% of the total weight of prey consumed by largemouth bass of 150–299 mm TL (Figure 3A). However, largemouth bass that were greater than 350 mm consumed few to no herring and instead ate primarily crayfish and other fish. Similarly, in

Coonamessett Pond, herring constituted 93–94% of the diet of largemouth bass that were less than 250 mm (Figure 3B). With the exception of largemouth bass that were 400–499 mm TL in Coonamessett Pond, larger largemouth bass in both lakes consumed few herring and concentrated primarily on other fish and on crayfish prey. Of all fish species consumed, herring constituted a higher percentage of the total weight of prey consumed

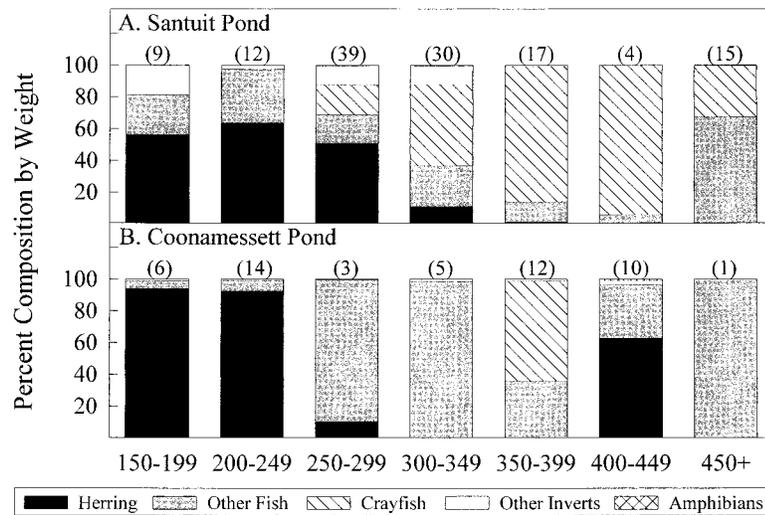


FIGURE 3.—Percent composition by weight for diets of 50-mm size-classes of largemouth bass from (A) Santuit Pond and (B) Coonamessett Pond, Massachusetts, collected during May through November 1994. Numbers in parentheses denote sample size for each size-class.

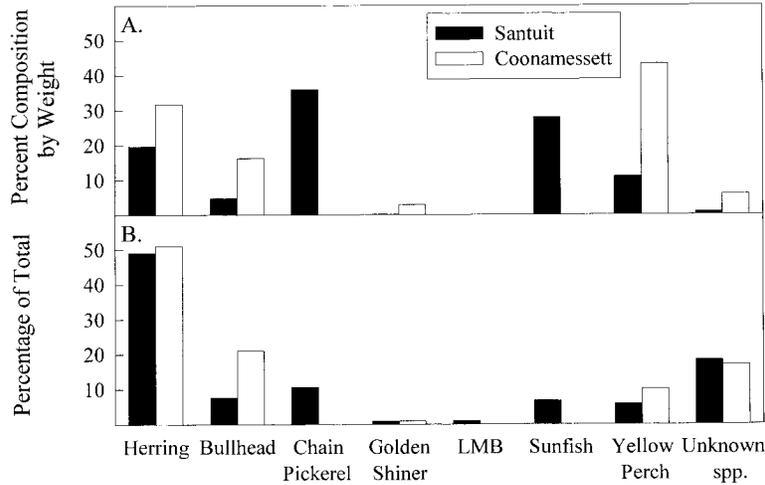


FIGURE 4.—Diet composition including (A) percentage of total weight consumed and (B) total number of individuals consumed for all fish species found in largemouth bass stomachs collected during May through November 1994 in Santuit and Coonamessett ponds, Massachusetts.

of any fish species except chain pickerel and sunfish (i.e., pumpkinseed and bluegill) in Santuit Pond and yellow perch in Coonamessett Pond (Figure 4A). Herring were consumed in the highest number of any fish species in both lakes (Figure 4B).

For both lakes combined, total body size of prey consumed increased significantly with largemouth bass body size (Figure 5; $R^2 = 0.1425$, $P = 0.0004$). Although many larger and smaller prey were also consumed, largemouth bass from both lakes generally ate prey that were 20–23% of their total body length ($[\text{prey length}/\text{predator length}] \times 100$). Specifically, sizes of chain pickerel and yellow perch consumed fell above the regression line, herring fell near it, and other species, including crayfish, fell below it.

Bioenergetics: Question 1—Water Temperature

Mean monthly water temperatures from Santuit Pond, Coonamessett Pond, Onota Lake, and Mansfield Lake were not significantly different (Figure 6A; analysis of variance: $F = 0.25$; $df = 3,23$; $P = 0.86$). Weight gain for all size-classes of largemouth bass was similar using temperature regimes from Santuit, Coonamessett, and Onota (Figure 6B). However, weight gain (g) for all largemouth bass size-classes was 11–28% lower using the water-temperature regime from Mansfield Lake, likely because water temperatures were 3–5°C cooler than the other three lakes during May through August (Figure 6A). Thus, temperature alone did not explain the growth difference between Coonamessett

Pond, the high-growth system in the field portion of the study, and other systems with and without large largemouth bass.

Questions 2 and 3—Individual Prey Groups and Diet Variation

A diet of only herring allowed the highest growth potential (g) of any prey category considered (Figure 7A). Specifically, a herring diet resulted in 2–3 times better growth than did a diet of the other fish category, a diet that was 7–82 times better than a crayfish diet, and a diet that was 8–137 times better than a diet of the other invertebrates category. For all size-classes, largemouth bass were predicted to grow 35–62 g ‘better,’ a 19–70% increase in weight, with diets actually observed in Santuit Pond compared with growth as a result of early season Santuit diets, which contained no herring (Figure 7B). All size-classes grew even better on diets observed in Coonamessett Pond, which contained more herring and other fish prey (Figure 7B). Thus, overall growth was 83–159 g greater using herring-rich Coonamessett Pond diets than with herring-poor Santuit Pond diets.

Discussion

In both Santuit and Coonamessett ponds, more anadromous herring, a seasonally available prey item, were consumed than any other fish species, but herring were not utilized by largemouth bass as frequently as expected. Specifically, herring were not consumed in either Santuit or Coona-

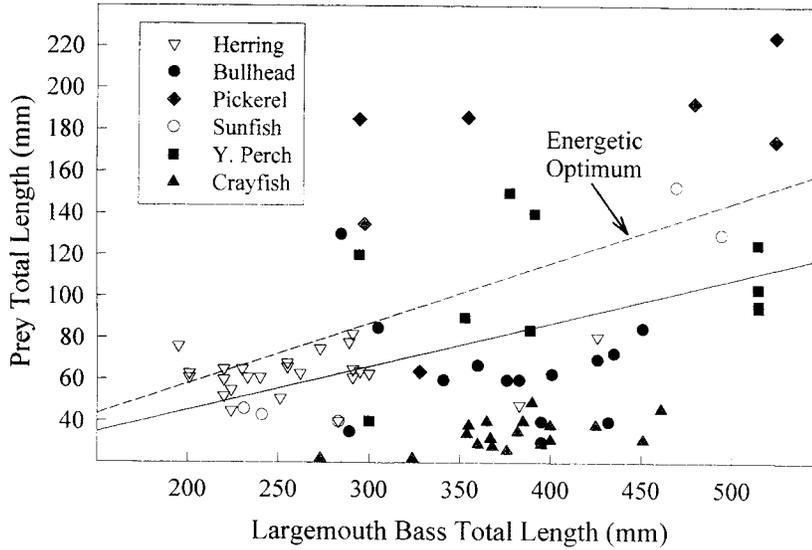


FIGURE 5.—Lengths of fish and crayfish prey consumed by largemouth bass in Santuit and Coonamessett ponds, Massachusetts, during May through November 1994. The dashed line represents the theoretical optimum prey-to-predator size ratio, 29% of largemouth bass total body length, at which handling time to energy content is minimized (Hoyle and Keast 1987). The regression line (solid line) is defined by $y = 7.44 + 0.19x$ ($R^2 = 0.1425$; $P = 0.0004$).

messett Pond until mid-summer, nor were herring readily consumed by the largest largemouth bass. Herring were not consumed in equal numbers between lakes, which may have led to the observed differences in largemouth bass growth. Hence, the

interactions between largemouth bass and juvenile anadromous herring in these two study systems likely are complex.

Juvenile anadromous herring were abundant in both lakes beginning in late April to early May

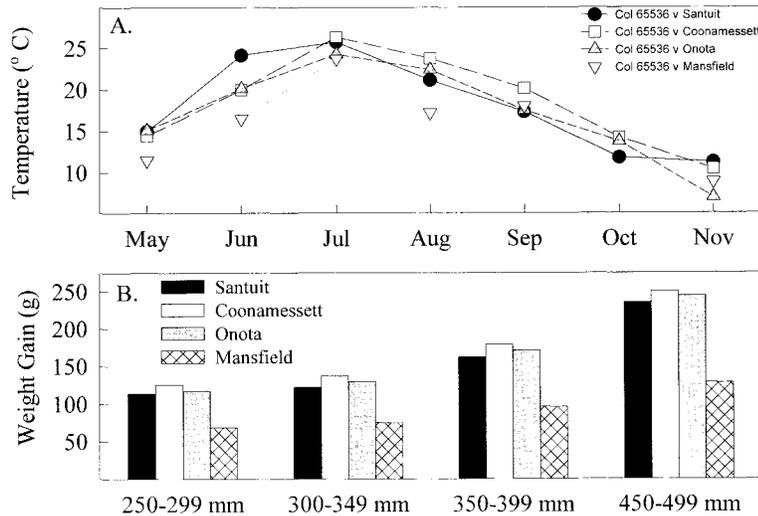


FIGURE 6.—(A) Mean monthly water temperatures from lakes in Massachusetts. Santuit and Coonamessett ponds are both located in the southeastern region of the state, Mansfield Lake is in the southwest region, and Onota Lake is in the northwest region. (B) Weight gain estimates for 50-mm size-classes of Santuit Pond largemouth bass obtained from bioenergetics model simulations using water-temperature regimes from Santuit Pond, Coonamessett Pond, Mansfield Lake, and Onota Lake, Massachusetts. Sample sizes were not large enough to include the <250-mm or 400–449-mm size-classes in model simulations.

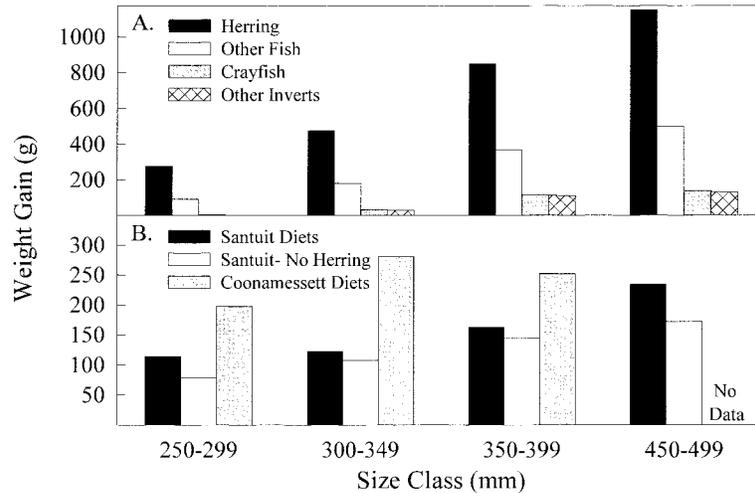


FIGURE 7.—Weight gain for 50-mm size-classes of Santuit Pond largemouth bass resulting from bioenergetics model simulations using (A) single-item diets and (B) actual diets from Santuit Pond (some herring late in season), early season Santuit Pond diets (no herring), and Coonamessett Pond diets (many herring). No data were available for largemouth bass that were 450–499 mm TL from Coonamessett Pond, and sample sizes were not large enough to include the <250-mm or 400–449-mm size-classes in model simulations.

(Kosa 1997), and anadromous herring overlapped spatially with largemouth bass within the littoral zone (L. A. Yako, Massachusetts Cooperative Fish and Wildlife Research Unit, personal observation). However, anadromous herring were not found in the stomachs of any largemouth bass until mid-August in Santuit Pond and until mid-September in Coonamessett Pond, at which time available herring were, on average, 61 mm and 48.5 mm TL, respectively (Yako 1998). Diets of largemouth bass in the spring and early summer consisted primarily of nonherring fish prey and crayfish. Both Storck (1986) and Michaletz (1997) found similar seasonal patterns in systems in which age-0 gizzard shad were not consistently consumed by largemouth bass until July, although they were available in May and June. As is the case with our results, Storck (1986) found that spring and early summer diets of largemouth bass consisted of crayfish, sunfish, and older age-classes of gizzard shad. Both researchers suggest that this dietary switch to age-0 gizzard shad in the summer corresponded with the larger body size of these young gizzard shad. This size-based dietary switch may explain why juvenile herring were not consumed throughout the spring and early summer in our study.

Interestingly, in both lakes, densities of anadromous herring had greatly declined by mid-summer because of seaward migration, especially in Santuit Pond, where nearly 60% of all herring had migrated

by mid-August and where nearly 96% had migrated by mid-September (Yako 1998). In Coonamessett Pond, herring densities remained high, because migration was restricted as a result of low water levels throughout the summer and early fall (Yako 1998). Unlike resident prey, herring may inadvertently avoid intense predation by largemouth bass through migration, yet predation pressure is not a key factor influencing migration timing (Yako 1998). Consequently, largemouth bass can feed on a high-quality prey without depleting it, whereas herring likely enhance largemouth bass abundance beyond what these study lakes, especially Santuit Pond, can support through nutrient input and an influx of high-quality prey (Polis et al. 1997).

In both study lakes, largemouth bass consumed fish and crayfish prey that were generally 20–23% of their total body length. Largemouth bass commonly consume prey that are 25–50% of their total length (Howick and O'Brien 1983; Miranda and Muncy 1991; Goldstein 1995), and soft-bodied clupeid prey are typically 35–39% of largemouth bass length (Lewis et al. 1974; Horton and Gilliland 1991). In theory, to optimize the energy gained relative to the energy expended, largemouth bass should consume prey that are approximately 29% of their body length (Hoyle and Keast 1987). During 1994, herring never exceeded 103 mm TL in either study lake (Yako 1998). Although anadromous herring were small relative to the body size of the largest largemouth bass, they were

an optimal size for smaller largemouth bass. In fact, smaller largemouth bass consumed herring prey that were of this optimum length. Thus, optimal foraging theory may explain why herring were only eaten by small largemouth bass later in the season. However, it does not explain why larger largemouth bass consumed crayfish and bullheads that were much smaller than the optimum size required for energy gain. This anomaly suggests possible differences in foraging strategies across size-classes of largemouth bass by which larger predators may select benthic prey or may alternatively use habitat differently. Thus, the patterns of size-related predation on herring observed in this study may be partially explained by the small body size of herring early in the season and by possible ontogenetic changes in foraging behavior and habitat use.

Largemouth bass diets differed between Santuit and Coonamessett ponds. Santuit Pond largemouth bass primarily consumed crayfish and other invertebrates, whereas Coonamessett Pond largemouth bass diets were dominated by herring and other fish prey. Overall, largemouth bass in Coonamessett Pond likely grew better than did those in Santuit Pond, because herring and other fish prey had higher energy densities (Table 2) and allowed greater growth potential than did nonfish prey (Junes and Conover 1994; Stahl and Stein 1994). Furthermore, 2-year-old fish in Coonamessett Pond had an initial size advantage that was maintained through life (Figure 1) and that was perhaps gained by utilizing the abundant herring. Despite a consistently higher herring density in Santuit Pond throughout 1994, a higher percentage of the largemouth bass population was between 200–300 mm TL (the size-class that gained the most from herring consumption) in Coonamessett Pond (76.7%; Yako 1998) than in Santuit Pond (58.7%).

Differences in diet composition between Santuit and Coonamessett ponds may have been related to dissimilar physical conditions that affected foraging. Because largemouth bass are visual predators, their foraging ability declines in areas of dense aquatic vegetation (Savino and Stein 1982; Hayse and Wissing 1996), and their reaction distance is reduced when water visibility is poor (Howick and O'Brien 1983; Crawl 1989; Miner and Stein 1996). In the study lakes, submerged vegetation occupied about 85% of Santuit Pond and only about 35% of Coonamessett Pond. In addition, water visibility, measured using a Secchi disk, was, on average, poorer in Santuit Pond (1.8 m, but often as low as 0.5 m; Yako 1998) than in

Coonamessett Pond (2.4 m). Thus, dense vegetation and poor water visibility in Santuit Pond may have decreased the ability of largemouth bass to forage effectively, potentially causing these fish to forage on lower quality prey such as crayfish.

A basic function of bioenergetics models is to predict the growth or consumption resulting from various environmental and biological conditions. Researchers who have evaluated these models in the field have found both a poor fit for esocids (e.g., Wahl and Stein 1991) and a good fit for largemouth bass (Rice and Cochran 1984), sockeye salmon (Beauchamp et al. 1989), and striped bass (Hartman and Brandt 1995c) relative to real field conditions. Our simulations showed that the presence of 'trophy' largemouth bass found in southeastern, coastal Massachusetts was not solely related to water temperature across the state but rather was related to predator diet and, specifically, to the presence of anadromous herring in largemouth bass diets. We also demonstrated that although largemouth bass do not consistently eat herring, these energy-rich prey provide the highest growth potential.

Through diet analysis and bioenergetics model simulations, we have shown that herring can be a key, energetically valuable prey item for largemouth bass. Because of the optimal prey-to-predator size ratio, small largemouth bass profited the most energetically from consuming herring prey. Herring likely were underutilized by resident largemouth bass, because as herring grew larger and potentially became more vulnerable, herring migrated to the ocean. In addition, decreased foraging ability associated with dense vegetation and poor water visibility may have further reduced the vulnerability of herring to largemouth bass, primarily in Santuit Pond. Additional insights into behavior, habitat use, and other factors that define the relationship of largemouth bass, especially those largemouth bass that are less than 200 mm TL, and anadromous herring in a physically complex environment are necessary to fully understand the mechanisms that drive these interactions and that cause variation in lake-to-lake predator-prey dynamics.

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