

Abstract—Starvation is often proposed as the mechanism of size-dependent mortality of overwintering temperate fishes, yet little is known about the energetics of fish at low temperatures. Young-of-the-year (YOY) Hudson River striped bass (*Morone saxatilis*) suffer a winter energy deficit and experience size-selective winter mortality in some years that may influence recruitment. To better understand the role of energetic stress in winter mortality, we determined diet composition and measured consumption rates of wild fish. Gastric evacuation rates were measured in the laboratory at 2°, 5°, 8°, and 11°C. Measured evacuation rates for YOY striped bass were among the lowest reported, with 25% of the initial meal remaining after 150 hours at 2°C. Variation in evacuation rate data increased as temperature decreased. Diets of fish captured in winter were dominated by gammarid amphipods and shrimp species. Gut fullness ranged from 0% to 7%, averaging 0.4% body weight. Evacuation rates, gut fullness values, and river temperatures were combined to estimate daily consumption rates on 29 dates over five winters. Consumption estimates ranged from 0% to 0.29%bw/day and were generally higher in early winter than in late winter and not correlated with river temperatures. Stomach fullness was negatively correlated with the level of lipid energy reserves at the individual level. The patterns may reflect an internal control on appetite, or a depression of prey availability in late winter. These findings indicate that the potential for winter starvation may be influenced by both internal and external constraints on consumption rate.

Diet and consumption rates of overwintering YOY striped bass, *Morone saxatilis*, in the Hudson River*

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Although the feeding and growth of many temperate fish species have been extensively examined during summer months, details of the feeding ecology of most species during winter remain largely unknown. Knowledge of the winter energetics of many fish species is restricted to the observation that growth decreases markedly in autumn and often becomes negligible during winter. There are only scattered reports of the feeding patterns of overwintering temperate fishes (Daiber, 1956; Keast, 1968; Foltz and Norden, 1977; Diana, 1979), and few estimates of consumption rates (but see Diana, 1979; Minton and McLean, 1982). This lack of information on the winter energetics of fishes applies also to laboratory-based physiological measurements, including gastric evacuation rates and metabolic rates. Despite the observation that temperature is the predominant factor regulating digestion, for none of the 22 species listed in a compilation of gastric evacuation data (He and Wurtsbaugh, 1993) had rates been measured at the minimum temperatures likely to be encountered in winter.

Many temperate fish species lose energy throughout the winter, relying upon stored lipid reserves to fuel metabolism (Toneys and Coble, 1980; Schultz and Conover, 1997; Hurst et al., 2000). Reliance on lipid reserves is believed to be necessary because consumption rate is severely limited by the ability of fish to digest food at low temperatures. However low consumption rates of overwintering fish may also be limited by low food availability (Cunjak and Power, 1987; Foy and Paul, 1999).

Winter mortality that selects against smaller fish has been documented in a number of temperate species (Sog-

ard, 1997) and is most commonly attributed to depletion of lipid energy reserves and starvation. Smaller fish have higher starvation mortality rates because they tend to have lower energy reserves and higher weight-specific metabolic rates than larger fish. An implicit assumption in the "starvation hypothesis" is that overwintering fish have little or no capacity to obtain energy by feeding. However, in several experiments, fish allowed to feed *ad libitum* had higher winter survival rates than unfed fish (Post and Evans, 1989; Thompson et al., 1991; Hurst and Conover, 1998). Although wild fish are unlikely to have access to unlimited food, these results suggest that fish benefit from feeding during winter. Furthermore, some overwintering fish increase consumption rates in response to depletion of internal reserves (Metcalf and Thorpe, 1992; Bull et al., 1996; Hurst and Conover, 2001). These findings suggest the need for a more complete understanding of the energetics of overwintering fish, including consumption rates of wild fish and an evaluation of factors that regulate consumption in winter.

The striped bass (*Morone saxatilis*) is a relatively well studied, commercially important species along the east coast of the United States and Canada (Boreman and Austin, 1985). Previous work has shown that recruitment to the Hudson River population may be regulated by the severity of the winter that age-0 fish encounter (Hurst and Conover, 1998). In addition, size-select-

tive winter mortality has been documented among young-of-the-year (YOY) striped bass in both the Hudson River and Miramichi River populations (Hurst and Conover, 1998; Bradford and Chaput¹).

Young-of-the-year striped bass in the Hudson River experience a winter energy deficit that varies in severity among years (Hurst et al., 2000). This interannual variability may be related to feeding conditions in the environment. Although studies of the summer feeding habits of YOY striped bass are available from most east coast estuaries (Markle and Grant, 1970; Boynton et al., 1981; Gardinier and Hoff, 1982; Rulifson and McKenna, 1987), information for overwintering fish is extremely limited (Hartman and Brandt, 1995a). A bioenergetics model has been developed for juvenile striped bass (Hartman and Brandt, 1995b), describing metabolic rates and maximum consumption rates of fish across a wide range of temperatures. This type of deterministic bioenergetic modeling does not take into account the observed variability in energy storage and depletion cycles (Hurst et al., 2000) or compensatory feeding responses observed in response to depletion of reserves (Metcalf and Thorpe, 1992). A better understanding of the energetics of overwintering juvenile striped bass, including *in situ* estimates of consumption rates, is required to fully evaluate the potential for winter starvation in this species.

In our study, we present results of experiments measuring gastric evacuation rates at winter temperatures necessary to determine consumption rates of wild fish. We also describe the diet of overwintering YOY striped bass and estimate consumption rates of overwintering fish on 29 dates over five winters. Finally, we analyze feeding patterns at both the individual and population level to determine the factors regulating consumption rates of overwintering fish and discuss these results as they relate to the potential for winter starvation.

Methods

Gastric evacuation experiments

Wild fish were captured from the Hudson River estuary and transported in river water to the Flax Pond Marine Laboratory of the State University of New York at Stony Brook in Old Field, New York. Fish were treated with 0.60 ppm copper sulphate for 5 minutes and 15 ppm oxytetracycline for 5 days to reduce risk of mortality from infection. Fish were acclimated to laboratory conditions for at least 3 weeks prior to use and only fish appearing healthy and behaving normally were used in the experiment. Temperatures during the acclimation period were maintained between 1° and 5°C, and salinities were maintained at 15 ppt. Fish were fed frozen adult brine shrimp

(*Artemia* sp.) and sand shrimp (*Crangon septemspinosa*) daily during the acclimation period. Prior to experimentation, groups of fish were acclimated to the test temperature ($\pm 0.5^\circ\text{C}$) for at least one week. Fish rarely fed voluntarily at low temperatures and were not offered food for between 3 and 5 days prior to use in the experiment.

Evacuation rates were measured at 2°, 5°, 8° and 11°C. Temperatures in the experimental tanks were maintained by recirculating fluid chillers; they never differed from the prescribed temperature by more than 0.5° and were generally within 0.2°C. Fish used in the experiment ranged in size from 88 to 150 mm TL (5.6 to 31.4 g wet weight), the natural size range of YOY striped bass in winter. To reduce stress during the feeding process, fish were weighed (to 0.01 g wet weight) and acclimated to 65-L test tanks for 12 hours prior to feeding. Individual fish were captured with a dip-net from the test tank, force-fed the meal, and returned to the test tank within 1 minute. Fish were fed by opening the mouth and forcing the meal through the esophagus with a pair of blunt forceps. A meal comprised a single whole or partial *C. septemspinosa* weighing approximately 2% of the fish's body weight. A ration level of 2% body weight was chosen because it falls in the upper range of, but is well below the maximum, gut fullness levels observed among wild fish. Each fish remained in the test tank until the time of sampling, when it was netted and sacrificed with an overdose of MS-222 anesthetic and measured (to 1.0 mm TL). The remaining stomach contents were dissected from the fish, dried of excess water, weighed (to 0.001 g), and dried to a constant weight at 60°C. In no cases did fish regurgitate the meal following feeding or during the netting and sacrifice procedure.

The evacuation rate of at least 3 fish was measured at each of 10 or more time points at each temperature (min. 33 fish at 11°C; max. 43 fish at 2°C). The maximum interval between feeding and sacrifice encompassed the majority of the evacuation time at each temperature and ranged from 72 hours at 11°C to 168 hours at 2°C. The minimum interval used was 0.25 hours at all temperatures. Fish were exposed to a 10:14 light:dark cycle to mimic the natural winter photoperiod. Feeding time was standardized to the light:dark cycle, and fish were exposed to light for the first 8–10 hours of digestion.

Evacuation of the meal was described with an exponential model allowing a time-lag prior to the beginning of evacuation because of its utility in estimating rations among wild fish (Elliott and Persson, 1978; Bromley, 1994). The model was fitted by using biphasic nonlinear regression of untransformed data on the percentage of initial meal remaining over time with the equation

$$\% \text{ remaining} = \begin{cases} 100 & \text{if } t < (c_0 + c_1 T) \\ 100e^{-(b_0 e^{b_1 T})[t - (c_0 + c_1 T)]} & \text{if } t \geq (c_0 + c_1 T), \end{cases}$$

where T = temperature;

t = time in hours since ingestion;

b_0 and b_1 = the coefficients of the exponential relationship between evacuation rate and temperature; and

¹ Bradford, R. G., and G. Chaput. 1997. Status of striped bass (*Morone saxatilis*) in the Gulf of St. Lawrence in 1996 and revised estimates of spawner abundance for 1994 and 1995. Dep. Fish. and Oceans, Can. Stock Assess Secretariat Res. Doc. 97/16, 31 p. Dep. Fisheries and Oceans, Science Branch, Gulf Region, P.O. Box 5030, Moncton, New Brunswick E1C 9B6, Canada.

Table 1

Summary of collections and diets of overwintering YOY striped bass collected in the Hudson River Estuary, 1993–97. %F = mean frequency of occurrence, %W = mean percentage of wet weight; *n* = number of fish sampled per date.

		Winter									
		1993		1994		1995		1996		1997	
No. of dates sampled		4		8		7		6		4	
Temperature (°C)		2.0–5.1		4.2–10.4		1.0–9.4		3.3–6.2		5.0–6.1	
<i>n</i>		20–34		15–53		8–37		16–29		18–52	
Percentage empty stomachs		71.0		52.5		72.3		57.6		73.4	
Mean gut fullness ±SE		0.44 ±0.103		0.51 ±0.056		0.34 ±0.066		0.18 ±0.037		0.26 ±0.060	
Prey type	Scientific name	%F	%W	%F	%W	%F	%W	%F	%W	%F	%W
Amphipods	<i>Gammarus</i> sp.	66.7	59.1	92.1	90.2	58.2	39.5	86.3	52.4	34.3	15.7
Sand shrimp	<i>Crangon septimspinosa</i>	37.0	27.1	4.2	4.2	7.1	8.1	0	0	3.1	5.3
Grass shrimp	<i>Palaemonetes pugio</i> , <i>Palaemonetes vulgaris</i>	38.9	6.4	0	0	4.3	4.1	0	0	3.1	7.5
Mysid shrimp		0	0	0	0	0	0	3.0	7.1	18.8	4.3
Unidentifiable shrimp	<i>C. septimspinosa</i> , <i>P. pugio</i> , <i>P. vulgaris</i>	0	0	0.7	0.4	27.5	22.8	16.4	32.5	21.4	26.4
Crabs		33.3	5.7	0	0	0	0	0	0	0	0
Polychaetes		0	0	0	0	17.9	23.3	0	0	0	0
Oligochaetes		0	0	0	0	0	0	0	0	23.9	38.8
Fish	<i>Anchoa mitchilli</i> , <i>Menidia menidia</i> , <i>Ammodytes americanus</i>	1.9	1.7	5.4	5.3	2.9	2.2	7.1	8.0	3.1	1.9
UIR ¹		40.7	24.4	11.9	8.5	28.2	6.0	31.8	29.2	42.2	25.1

¹ UIR = unidentified invertebrate remains. These were not included in the calculation of %W of other prey items.

c_0 and c_1 = the intercept and slope of the linear relationship between temperature and the lag prior to the beginning of evacuation.

If no lag is present in the data, the parameters c_0 and c_1 approach 0. The effect of body size on evacuation was assessed by examining the relationship between fish length and deviation from the best fitting evacuation model.

Diet of YOY striped bass

Overwintering YOY striped bass were collected with a 9-m bottom trawl (38-mm stretch mesh codend) from the lower Hudson River estuary, the only known wintering aggregation for the Hudson River population (Dovel, 1992). Sampling occurred throughout the overwintering period of five consecutive years. Fish were captured during daylight hours between river mile 0 and 9 in conjunction with the New York Power Authority's hatchery evaluation and tagging program. Sampling in each year began in mid-December and ended in late March or early April. Bottom water temperatures were measured during sampling. The number of fish analyzed for diet per date ranged from 8 to 53 depending on catch rates (Table 1). Captured fish were individually wrapped and immediately frozen for

preservation. In the laboratory, fish were thawed, measured (mm TL), weighed (g wet weight), and stomach contents were removed. Prey were identified to the lowest possible taxon and weighed. All prey in each category in each stomach were weighed as a group because the abundance and small size of the dominant prey item made individual measurements unfeasible (gammarid amphipods; often >50/stomach and <0.005 g each). Diets of YOY striped bass were described by the contribution of items expressed on the basis of both weight ($\%W_i = \text{weight of prey}_i / \text{weight of all identifiable prey}$) and frequency ($\%F_i = 100 \times \text{no. of stomachs with prey}_i / \text{no. of stomachs with prey}$). Unidentifiable items were measured separately and are expressed as a percentage of the total weight of all stomach contents.

Estimation of consumption rates

Daily consumption rate estimates were generated by combining gut fullness values ($S = \text{total weight of stomach contents} / \text{fish weight}$) of overwintering YOY striped bass with laboratory-determined gastric evacuation rates with the method of Eggers (1979):

$$C = 24R_e \times \bar{S},$$

where \bar{S} = average gut fullness of field-caught fish; and R_e = exponential evacuation rate at measured field temperatures determined from laboratory experiments described above.

This simplified version of the Elliott and Persson (1978) model is appropriate when sampling is not conducted in discrete time intervals. We used gut-fullness measures from fish collected throughout the day, as described above. Although fish were sampled only during daylight hours, the sampling interval (24 hours) is substantially shorter than the evacuation time (>72 hours), even at the warmest temperatures observed; hence any diel feeding patterns will have little effect on our consumption estimates.

Standard deviations of consumption estimates were generated from a Taylor expansion of the consumption model

$$\sigma_C^2 = \left(\frac{d\bar{C}}{d\bar{S}}\right)^2 \sigma_S^2 + \left(\frac{d\bar{C}}{dR_e}\right)^2 \sigma_{R_e}^2 + 2\left(\frac{d\bar{C}}{dR_e}\right)\left(\frac{d\bar{C}}{d\bar{S}}\right) \text{cov}(R_e, \bar{S})$$

The variance in the evacuation rate parameter (R_e) was estimated through a bootstrap procedure by fitting the evacuation model to 1000 sets of 152 observations sampled with replacement from the evacuation rate data. Since R_e is a function of temperature, the variance in R_e at a given temperature was determined by inserting the temperature into the 1000 model fits. The variance in \bar{S} was estimated for each date as $\text{var}(S_i)/n$.

The standard deviation of the consumption estimate depends upon the covariance between evacuation rate (R_e), measured in laboratory experiments, and gut fullness (S), observed in wild fish. Because we have no way of measuring the covariance between these parameters, we evaluated the importance of this term by calculating the variance under three assumptions: 1) \bar{S} and R_e are not correlated, 2) they covary perfectly, and 3) they display perfect negative covariance.

Analysis of feeding patterns

We investigated feeding patterns of YOY striped bass by examining the relationship between several factors (body size, time of year, water temperature, and energy storage) and gut fullness, at the individual and population level. Gut fullness was chosen over consumption rate for three reasons. First, gut fullnesses were measured directly, whereas consumption rates were estimated from a model by using gut fullnesses. Second, consumption estimates are directly dependent on temperature, an independent variable in these analyses. Finally, we were interested in determining the conditions that stimulate feeding, which we believe are more immediately reflected in the gut fullness measures.

Feeding patterns at the individual level were investigated by examining the relationships between gut fullness and the independent variables of body size, lipid level, water temperature, and time of year. Gut fullness values of individual fish were dominated by zeros (empty stomachs) and could not be transformed appropriately, preventing the use of parametric statistics. Because empty stomachs

may reflect either a lack of prey availability or reduced appetite, we concentrated analyses at the individual level on the slope of the 95% quantile of gut fullness regressed against the independent variables (Scharf et al., 1998). This technique has been used to examine scatter-plots, when boundaries of a relationship between two factors are of interest, rather than the mean. In our case we were interested in the factors that stimulate feeding as opposed to developing a predictive relationship between independent variables and gut fullness. The 95% quantile line describes the relationship between maximum observed gut fullness and the independent variables. Mean gut fullness of all fish captured on a given date was used to investigate feeding patterns at the population level and was compared to average lipid level of fish captured on that date, time of year, and water temperature, by using Kendall's coefficient of rank correlation (Sokal and Rohlf, 1981).

Lipid levels were determined for a subsample of fish from the diet analysis. This involved determination of the percentage of dry body weight comprising non polar lipids (those used primarily for energy storage). Details of the compositional analysis procedure can be found in Hurst et al. (2000) and Schultz and Conover (1997). Compositional analysis was performed on 15 to 40 fish from each sampling date (except 13 December 1995). The relationship between lipid level and gut fullness at the individual level was examined by using all fish for which both pieces of information were available ($n=587$), whereas analyses at the population level used the average lipid level observed on a given date ($n=28$).

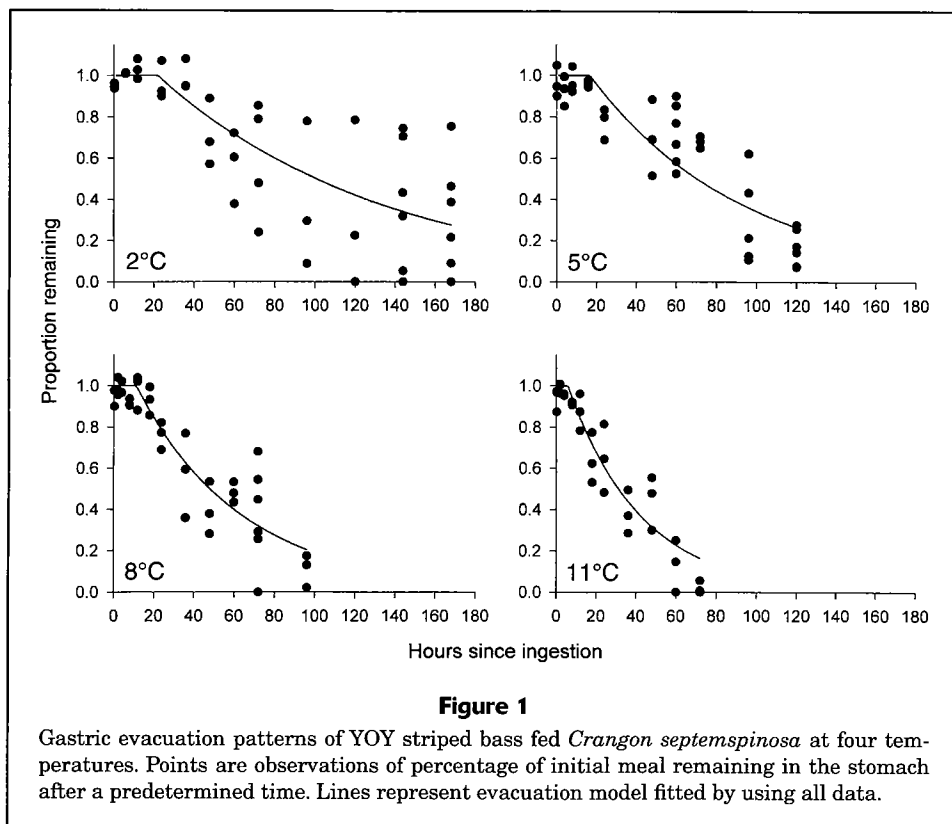
Results

Gastric evacuation rate

Evacuation rates of overwintering YOY striped bass declined greatly with temperature. At mid-winter temperatures, evacuation rates were among the lowest reported for any fish species. Time to 50% evacuation ranged from 31 hours at 11°C to 101 hours at 2°C (Fig. 1). The best fit parameters in the evacuation model were $b_0 = -0.00685$, $b_1 = 0.126$, $c_0 = 25.757$, and $c_1 = -1.8033$.

We observed a lag between feeding and a measurable loss of material from the stomach. The length of the observed lag decreased as temperature increased from 18.2 hours at 2°C to 6.1 hours at 11°C. The exponential models used here to describe digestion fitted the experimental data as well as, or significantly better than, other common models (linear and square root; Bromley 1994).

The amount of variability among individuals in evacuation rate increased as temperature decreased, leading to a poorer fit of the evacuation models at the lower temperatures (Fig. 1). Deviations from the model increased significantly as temperature decreased ($P=0.018$; ANOVA of absolute value of sample deviations from evacuation model). Body size had no effect on evacuation rate among juvenile striped bass. We found no correlation between residual values from the evacuation model and fish length ($r = -0.03$ $P=0.685$).



Diet composition

Benthic invertebrates were the dominant prey of YOY striped bass overwintering in the lower Hudson River estuary, making up 95.0% of the diet by weight; the remaining 5.0% were various fish prey (Table 1). Most striped bass captured during winter had empty stomachs (64.8%), and on two dates, all fish sampled had empty stomachs (30 March 1994 and 6 December 1994). Unidentifiable stomach contents ranged from 6.0% weight (%W) in 1995 to 29.2%W in 1996. The most common item in the diet was gammarid amphipods (those identified to genus were *Gammarus* sp., but most were not identified) making up 51.3%W and occurring in 81% of stomachs with food (%F). Several species of shrimp were also common dietary items, including sand shrimp (*C. septemspinosa*) and grass shrimps (*Palaeomonetes* spp.). Other invertebrates that were important items on several dates included mysid shrimp, polychaetes, and oligochaetes. Fish were rarely found in the stomachs of YOY striped bass (3.8%F) but included bay anchovy (*Anchoa mitchilli*), Atlantic silversides (*Menidia menidia*), and American sand lance (*Ammodytes americanus*).

The importance of individual prey taxa varied among years and among dates within each year, although low sample sizes of fish with prey prevent drawing strong conclusions from these data. In 1994, striped bass fed almost exclusively on gammarid amphipods (90.2%W and 92.1%F), but these prey were less important in other years. Shrimp were important in 1993 (33.5%W, mostly *C. septemspinosa*) and 1995–97 (34.9 to 43.6%W all species).

Polychaetes were observed in striped bass diets only in 1995 (23.3%W and 17.9%F). Oligochaetes were found commonly in 1997, averaging 18.5%F and 23.9%W of the diet but did not occur in other years.

Consumption rates

Assuming an exponential evacuation pattern, consumption rate estimates for overwintering YOY striped bass ranged from 0 to 0.29% body weight per day (%bw/day, Fig. 2). Standard deviations of estimated consumption averaged 46% of the estimate (range: 20.2–100.9%). The standard deviation of the consumption estimate was relatively insensitive to assumptions of the covariance between \bar{S} and R_e . The ratio of estimates under the least conservative assumption (perfect covariance) to that under the most conservative assumption (perfect negative covariance) was less than 1.08, with one exception (1.17 on 20 December 1993). The standard deviations presented in Figure 2 are the intermediate values, based on the assumption of no covariance.

Feeding patterns

Among individuals, we observed a strong negative relationship between maximum gut fullness and the level of storage lipids. The 95th quantile of gut fullness was 3% for fish with lipid reserves of 2% dry weight and decreased to under 1% for fish with lipid levels in excess of 19% dry weight (Fig. 3). No significant patterns were observed between individual gut fullness levels and water temperature, time

of year, or body size. At the population level, only date was significantly correlated with mean gut fullness (Kendall's rank correlation: $P=0.032$; Fig. 4). Addition of temperature and average lipid level did not provide significant improvements in the fit of the model ($P>0.20$ for both).

Discussion

Evacuation rates

Laboratory-measured evacuation rates of YOY striped bass at representative winter temperatures were among the

lowest reported for any fish species. None of the estimates compiled from multiple studies by He and Wurtsbaugh (1993) included rates as low as the 0.027 we measured at 11°C. The reason for this observation is not that striped bass have exceedingly low digestion rates compared with other fishes, but rather that evacuation rate is strongly related to temperature and is rarely measured at the lower end of temperatures encountered by each species. For example, the lowest temperature at which evacuation rates in white perch (*Morone americana*) have been measured is 12.6°C (Parrish and Margraf 1990), despite the fact that this fish often occupies waters near 0°C. The only evacuation rates we found in the literature comparable to those we measured were those for largemouth bass at 4°C ($R_e=0.006$; Cochran and Adelman, 1982, from data in Markus, 1932) and for brown trout at 1.8°C ($R_e=0.026$; Jensen and Berg, 1993), both measured near the species' thermal minima.

Factors other than temperature have been found to influence evacuation rates such as prey type, method of feeding (voluntary vs. force-feeding), and body size. All of our experiments were conducted with a single prey type (*C. septemspinosa*) at one ration level (2% of body weight). Meal size has been found to affect evacuation rate in laboratory studies (Smith et al., 1989; Andersen, 1998), but this effect is substantially smaller than that of temperature (He and Wurtsbaugh, 1993). Our meal size was slightly higher than the mean, but well within the range observed among individual fish. We found that body size did not affect evacuation rate over the size range of overwintering YOY striped bass (88–150 mm). In several studies comparing evacuation rates of various prey, large bodied shrimp, including *C. septemspinosa*, were found to be evacuated at lower rates than soft bodied prey or smaller shrimp species (Nelson and Ross, 1995; Singh-Renton and Bromley, 1996; Lankford and Targett, 1997), whereas other studies found no differences among prey types (Juanes and Conover, 1994; dos Santos and Jobling, 1995). Although *C. septemspinosa* and other shrimp species are common diet items of YOY striped bass, they were not the dominant item. If other prey items, such as amphipods, are digested and evacuated more rapidly, consumption rates of wild fish will be underestimated when non-shrimp prey dominate the diet.

We allowed a lag in our description of meal evacuation based on laboratory observations. Such a lag has been observed in several other studies, including both those where fish fed voluntarily (Gerald, 1973; Grove et al., 1985) and were force-fed (Vondracek, 1987). The length of the lag observed in juvenile striped bass decreased as temperature increased, as seen in juvenile turbot (*Scophthalmus maximus*; Grove et al., 1985). The lag prior to beginning of evacuation could be an artifact of experimental conditions or a natural delay in the passing of food from the stomach to the intestine following ingestion of shelled prey. Our model estimated the evacuation rate parameter (R_e) after the lag because this parameter represents the rate of passage of food from the stomach. Consumption rates based on gut fullness levels may be overestimated if there is a considerable lag prior to the beginning of digestion. However, the digestive lag we observed was short compared with

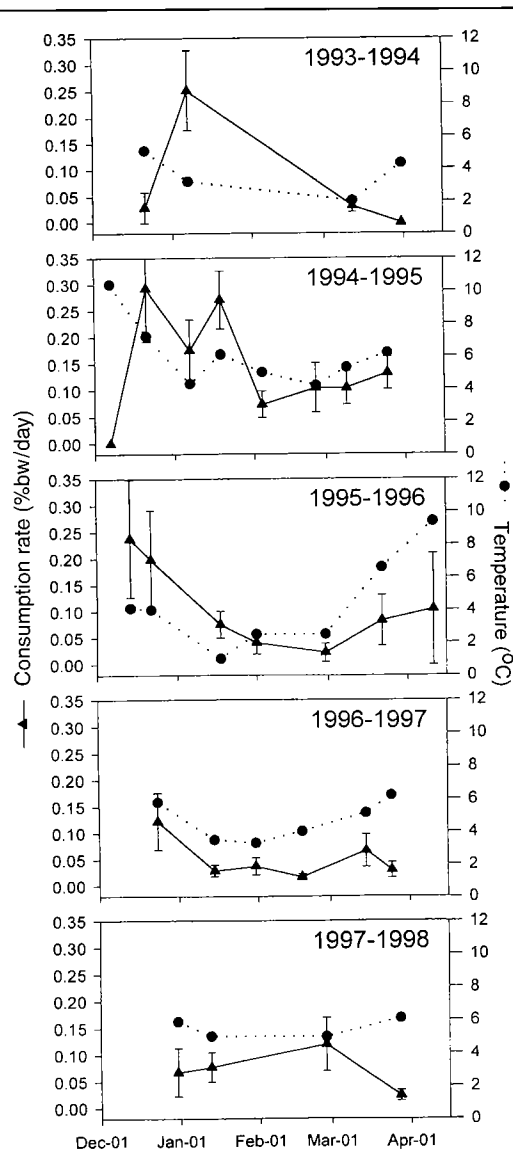


Figure 2

Consumption estimates (%body weight/day [± 1 SD]) for YOY striped bass in the Hudson River estuary through five winters, and bottom water temperatures observed during sampling.

the total evacuation time, averaging only 11% of the time required to reach 75% digestion. Simulations that varied the length of the digestive lag time and the evacuation rate showed that for lag times in the range we observed, consumption rates were overestimated by less than 5%. If the lag observed in the laboratory experiments does not occur in the wild, estimated consumption rates are unbiased.

Diet

Diets of overwintering YOY striped bass in the lower Hudson River estuary were dominated by benthic invertebrates such as gammarid amphipods and several shrimp species. Juvenile striped bass do not appear to undergo a major diet shift from summer to winter but appear to focus more heavily on amphipods in winter. Studies of summer diets of striped bass in the Hudson River from the 1970s and 1990s found a slightly more diverse diet than we observed in winter. Summer diets included copepods, chironomids, and isopods, and more commonly incorporated fish and polychaetes (Gardinier and Hoff, 1982; Hurst, unpubl. data). Data from other estuaries suggest that the diets of overwintering juvenile striped bass may vary regionally. In Chesapeake Bay, Hartman and Brandt (1995a) found that fish prey accounted for 20–25%W of YOY striped bass diets in winter, substantially more than the 2–9%W we observed in the Hudson River. In the Miramichi River estuary, overwintering fish fed primarily on shrimp (mysids and *C. septemspinosa*) and ceased feeding when temperatures fell below 3°C in late November (Robichaud-LeBlanc et al., 1997). The studies from Chesapeake Bay and the Miramichi River estuary did not examine interannual variability in diets.

Overwintering juvenile striped bass appear to be opportunistic feeders, their diets reflective of the epibenthic invertebrate community in the lower Hudson River and similar to published information on the diets of co-occurring species. Although there have been no surveys of the benthic community in the lower Hudson River in winter, data available from summer surveys in the Hudson River estuary and the adjacent Raritan estuary suggest dominance of the epibenthic community by gammarid amphipods, shrimp, and annelids (Ristich et al., 1977; Steimle and Caracciolo-Ward, 1989). The winter fish community in the lower Hudson River is composed primarily of striped bass, white perch, Atlantic tomcod (*Microgadus tomcod*), and winter flounder (*Pseudopleuronectes americanus*). Winter diets of Atlantic tomcod were dominated by gammarid amphipods and copepods and were significantly less diverse in winter than in spring and autumn (Grabe, 1977, 1980). Diets of age-1 and older striped bass overwintering in the lower Hudson River estuary are similar to those of YOY fish, although the incidence

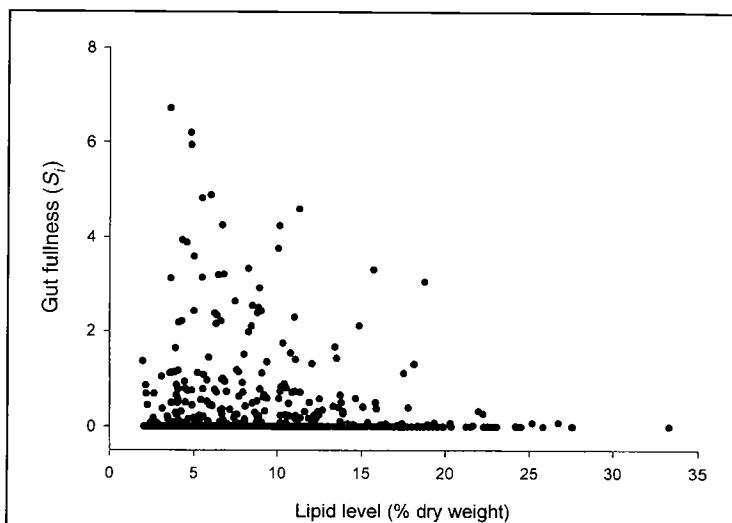


Figure 3

Relationship between gut fullness and lipid level of overwintering YOY striped bass through five winters. Points are gut fullness and lipid levels of individual fish.

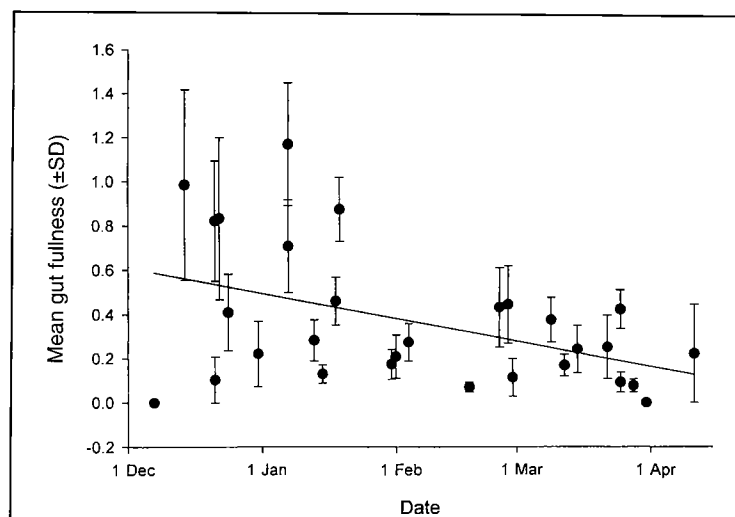


Figure 4

Relationship between mean gut fullness (± 1 SE) observed on a given date and date for collections of YOY striped bass through five winters.

of juvenile fish prey (including YOY striped bass) increased with body size (Dunning et al., 1997).

Consumption rates

Consumption estimates of overwintering YOY striped bass in the Hudson River were consistently below 1%bw/day, with only 34% of captured fish containing prey items. Our field estimates of the consumption rates of overwintering striped bass are significantly lower than pub-

lished estimates of maximum consumption measured in laboratory experiments (Hartman and Brandt, 1995b). Their estimates of maximum consumption (for a 10-g fish) increased from 0.45%bw/day at 1°C to 7.10%bw/day at 10°C. The highest percentages of predicted maximum consumption achieved by YOY striped bass in the Hudson River occurred on 6 January 1994 (25.8%), and on three dates in early winter 1995 (15.5–18.0%). On other dates consumption was generally below 10% of maximum estimated from the Hartman and Brandt (1995b) model.

Bull et al. (1996) developed a model of consumption for overwintering juvenile Atlantic salmon in which appetite was related to anticipated metabolic requirements. To minimize the risks of starvation and predation associated with foraging, they predicted that appetite of overwintering fish should be highest in early winter (when future metabolic needs are greatest) or when internal energy reserves are low. Our results suggest that a similar model might be appropriate for overwintering striped bass. Gut fullness levels of YOY striped bass were related to level of lipid reserves at the individual level (Fig. 3). Although some fish had empty stomachs at all energy levels, the highest observed gut fullnesses were found in fish with low lipid levels. This finding suggests that overwintering striped bass increase feeding activity when energy reserves become depleted. Such feeding patterns have been documented in laboratory experiments with Atlantic salmon (Metcalf and Thorpe, 1992) and striped bass (Hurst and Conover, 2001) but have not previously been observed among fish feeding in the wild.

At the population level, we observed a negative relationship between mean gut fullness and date; gut fullnesses were higher in early winter than late winter (Fig. 4). This pattern was predicted in the Atlantic salmon model (Bull et al., 1996) but could also be due to external factors such as depleted food resources at the end of winter. Benthic prey production is likely reduced by low winter temperatures, and standing stocks may become depleted as winter progresses. Further work is required to determine fully the causes and implications of reduced gut fullnesses observed in later winter. Reduced feeding in late winter may reflect the availability of sufficient energetic reserves and suggests that starvation is unlikely. Conversely, reduced feeding due to depressed prey availability in late winter would indicate a strong potential for winter starvation. The role of starvation in winter mortality will depend greatly on determining if variable feeding patterns among years are due to internally controlled variations in feeding motivation or environmentally imposed constraints on prey availability.

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