

# Activity-related constraints on overwintering young-of-the-year striped bass (*Morone saxatilis*)

Thomas P. Hurst and David O. Conover

**Abstract:** The importance of activity to overwintering fishes has received little attention. Activity imposes two constraints: maximum swimming speed limits habitats that can be occupied for short periods of time, while the metabolic cost of swimming limits the habitats that are suitable for long-term residence. We measured the energetic consequences of activity and maximum swimming speeds of young-of-the-year striped bass (*Morone saxatilis*), a species that overwinters in tidal estuaries. The energetic cost of swimming was determined from energy changes in unfed fish forced to swim at various speeds, while energy changes in fed fish provided a measure of their ability to offset swimming costs through feeding. In high-velocity treatments, mortality was size-dependent and appeared to be related to fatigue rather than to depletion of energy reserves. The energetic cost of swimming increased with swimming velocity, but fish increased food consumption and thereby met their metabolic needs. In a second experiment the thermal dependence of swimming capacity in winter-acclimated striped bass was measured. Swimming speeds increased with temperature, from 2.7 body lengths (BL)/s at 2°C to 4.8 BL/s at 8 and 11°C, but were considerably below observed flow velocities in the Hudson River, suggesting a need for behavioral or physical refuge from tidal currents. These results indicate the flexibility of energy budgets of overwintering fishes, allowing energetic stress to be minimized by reducing activity or elevating food-consumption rates when sufficient prey are available.

**Résumé :** Chez les poissons, l'importance de l'activité en hiver a rarement été étudiée. L'activité impose deux contraintes : les vitesses maximales de nage restreignent le choix des habitats qui peuvent être occupés pendant de courtes périodes, alors que le coût métabolique de la nage rend les habitats moins bien adaptés aux séjours de longue durée. Nous avons mesuré les conséquences énergétiques de l'activité et les vitesses de nage maximales chez des Bars rayés (*Morone saxatilis*) de l'année, une espèce qui passe l'hiver dans les estuaires sous l'influence des marées. Le coût énergétique de la nage a été déterminé à partir des changements énergétiques observés chez des poissons à jeun forcés de nager à des vitesses variées, alors que les changements observés chez des poissons nourris ont servi à mesurer leur capacité de compenser les coûts reliés à la nage en s'alimentant. La mortalité chez les poissons forcés de nager à haute vitesse dépend de la taille de ces poissons et semble due à la fatigue plutôt qu'à une diminution des réserves énergétiques. Le coût énergétique de la nage augmente en fonction de la vitesse, mais comme les poissons augmentent leur consommation de nourriture, leurs besoins métaboliques sont comblés. Dans une seconde expérience, nous avons mesuré la dépendance thermique de la capacité de nage chez des Bars rayés acclimatés aux conditions hivernales. La vitesse de nage augmente en fonction de la température, de 2,7 longueurs du corps/s à 2°C à 4,8 longueurs/s à 8 et à 11°C, mais ces valeurs sont bien en-deçà de la vitesse du courant observée dans les eaux de l'Hudson, ce qui souligne la nécessité de refuges comportementaux ou physiques pour échapper aux effets des courants de marée. Ces résultats démontrent la flexibilité des bilans énergétiques chez les poissons pendant l'hiver, propriété qui permet de minimiser le stress énergétique par minimisation de l'activité ou par augmentation des taux de consommation lorsqu'il y a suffisamment de proies.

[Traduit par la Rédaction]

## Introduction

The importance of energy reserves in determining survival of overwintering fishes has been documented in a number of populations (Oliver et al. 1979; Thompson et al. 1991; Schultz and Conover 1999). This reliance on stored energy is generally believed to be necessary because of physiological con-

straints on food consumption at low temperatures and the reduced production of prey in winter (Lemons and Crawshaw 1985; Cunjak et al. 1987; Sullivan 1986; Foy and Paul 1999). Depletion of these energy reserves is believed to be responsible for size-dependent winter mortality (Sogard 1997). Most laboratory studies examining patterns of winter mortality have been conducted in static water tanks, greatly reducing the energetic demands on fish. Elevated energetic costs associated with residence in high-velocity habitats may increase the risk of winter starvation, implying a need for refuges from flow velocities below measured maximum swimming speeds (Cunjak 1996).

Resting (or standard) metabolic rates have been measured in many fishes, but the actual costs of activity for wild fish are still poorly understood (Boisclair and Leggett 1989). Specifically, the additional metabolic costs associated with

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holding position against ambient currents in the environment has not been examined in detail (but see Facey and Grossman 1990). Metcalfe and Thorpe (1992) have shown that overwintering juvenile Atlantic salmon (*Salmo salar*) responded to depletion of energy levels by elevating food-consumption rates, which suggests the need to examine potential compensatory responses by other fishes. Ultimately, the role of energetic constraints on fishes overwintering in flowing water will depend on the metabolic costs of activity and the ability to consume energy to meet metabolic demands.

The reduced locomotor ability of ectotherms at low temperatures (Guderley and Blier 1988; Bennett 1990) suggests that swimming ability, or the availability of flow refuges, may also limit habitat suitability in flowing-water systems (streams, rivers, and estuaries). It is often assumed that displacement from habitats with flows above maximum swimming speeds results in mortality (Bodensteiner and Lewis 1992; Quinn and Peterson 1996). The flow characteristics of microhabitats of overwintering stream fishes have been thoroughly documented for several species, particularly salmonids (reviewed in Cunjak 1996). These habitat preferences are generally based on in-situ observations of fish locations compared with available surrounding habitat. Unfortunately, direct observation of fish overwintering in less accessible systems such as estuaries is impossible. In such species, an alternative approach is to determine maximum swimming capacities and match these with flow patterns in the environment (Matthews 1985).

The striped bass (*Morone saxatilis*) is an anadromous species residing along the east coast of North America from Nova Scotia to Florida. During the first winter of life, striped bass in northern populations have been shown to experience size-selective winter mortality (Bradford and Chaput 1997; Hurst and Conover 1998). Although young-of-the-year (YOY) striped bass in the Hudson River continue to feed at low levels throughout winter (Hurst and Conover<sup>2</sup>), fish suffer from a winter energy deficit (Hurst et al. 2000) that may make them vulnerable to winter starvation. Initial laboratory experiments suggested that starvation was not the primary source of mortality, but fish were not forced to swim in this experiment and displayed minimal activity levels (Hurst et al. 2000). Current velocities in the estuarine wintering grounds of YOY striped bass can exceed 1 m/s (Oey et al. 1985), indicating the need to evaluate the constraints imposed by activity on winter energy budgeting and survival.

We conducted laboratory experiments to describe relationships between activity levels and energy budgets to infer the habitat requirements of YOY striped bass in the Hudson River. In the first experiment the energetic consequences and mortality risk associated with various activity levels in overwintering fish were determined. Rates of energy loss in unfed fish provided a measure of the costs of activity, while rates of energy loss in fed fish indicated how much of this cost could be offset through feeding. In a second set of experiments we measured the maximum swimming speeds of YOY striped bass at winter temperatures to determine the need for flow refuges.

## Methods

### Energy-change experiment

Two groups of YOY striped bass (14 fish per group) were swum simultaneously at each of four current velocities at ambient winter temperatures for 1 month. One group at each velocity was not fed during the experiment, while the other group was fed to satiation daily. Energy change was estimated for each fish in the experiment by comparing the energy level measured at the end of the experiment with an estimate of the initial energy level based on a sample sacrificed at the start of the experiment. Using this approach we were able to determine the costs of activity and the ability of fish to offset costs through feeding.

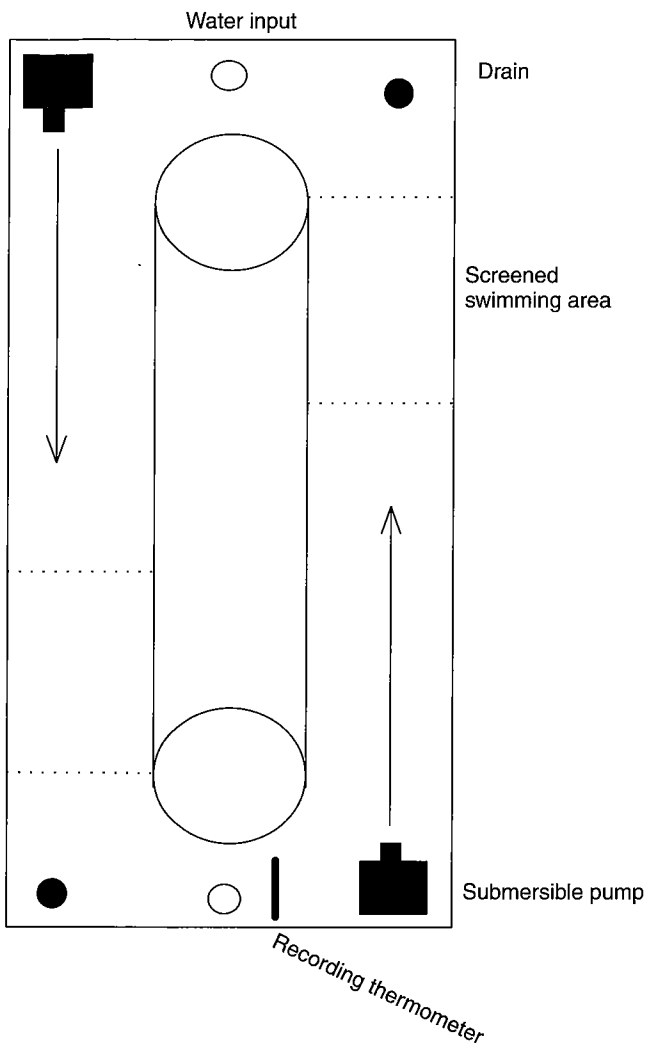
YOY striped bass were collected from the Hudson River estuary in the vicinity of Croton Point, New York, in early November 1996, prior to their down-estuary migration (Dovel 1992). The fish were transported in river water (~10 ppt) to the Flax Pond Marine Laboratory of the State University of New York and transferred to tanks with water of similar salinity. Salinity in the tanks was raised to that found in the overwintering area (approximately 25 ppt) over 3 days. Fish were given a prophylactic treatment of 15 ppm oxytetracycline for 7 days to reduce the risk of infection. During the acclimation period, fish were maintained in flow-through tanks and fed frozen adult brine shrimp (*Artemia* sp.) daily until the initiation of experiments. Fish used in all experiments were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care. Only fish appearing healthy and behaving normally were used in the experiment.

All fish were measured (to 1 mm total length (TL)) and weighed (to 0.01 g) and assigned to one of nine groups on 21 February 1997. Fish used in the experiment ranged in size from 65 mm TL (2.21 g) to 147 mm TL (28.74 g), with the distribution skewed toward smaller fish. To ensure similar size distributions among all treatments we used a stratified allocation system (three groups) in assigning fish to groups. There were no significant size differences among the nine groups ( $p = 0.98$ ). Eight of the nine groups were randomly assigned to experimental flow/feeding treatments and the final group were sacrificed with an overdose of anaesthetic (MS 222) for estimating initial energy levels. In each of the four flow treatments (0, 90, 180, and 280 mm/s) there were two feeding treatments: one group of fish was fed ad libitum once per day and food was withheld from the other group throughout the experiment. Given the large variability in body size among YOY striped bass, we set experimental velocities to ensure that at the higher velocities, energy of the largest fish would be measurably depleted, although we expected that the smallest fish might not be able to maintain swimming against those velocities.

Four tanks with identical designs (Fig. 1) were used for the flow treatments. Flows were maintained in each tank with submersible pumps equipped with flow spreaders. Water velocities were measured with an electronic flywheel flowmeter (Kent Type 265 miniflow). Fish in tanks with flow were acclimated for 24 h at flow velocities of ~90 mm/s (<1.3 body lengths (BL)/s), after which flow was increased to the treatment velocity over a period of approximately 8 h. The tank with a prescribed flow of 0 mm/s had continuous water exchange, which generated an irregular flow (always less than 5 mm/s). Fish were always found swimming in the upstream half of the tank, where flows were relatively uniform (never deviating from the prescribed flow by more than 10%). The entire system contained approximately 1600 L of water that was circulated among the four tanks, constantly being replaced with ambient water from a local embayment. The experiment was carried out in an unheated greenhouse, thereby exposing fish to ambi-

<sup>2</sup>T.P. Hurst and D.O. Conover. Diet and consumption rates of overwintering YOY striped bass, *Morone saxatilis*, in the Hudson River. Submitted for publication.

**Fig. 1.** Diagram of the tank design used in the energy-change experiment.



ent light cycles and temperatures. Temperatures were monitored with digital recording thermometers and were consistent across tanks ( $p = 0.929$ ), generally between 3.5 and 6.5°C (hourly extremes were 2–10°C). Once per day the flow was shut off for up to 1 h during which fish in the feeding treatments were offered food in small measured increments until satiation. Tanks were cleaned prior to resuming flow to ensure that fish in nonfeeding treatments had no access to food. Fish were considered dead and removed from the experiment when they could no longer maintain swimming against the flow (although they were often still alive). Tanks were checked for these “mortalities” at least twice per day, and these fish were removed, measured (to 1 mm TL and 0.01 g body mass), and frozen for energetic analysis. After 29 days of exposure to flow, all surviving fish were sacrificed, measured (to 1 mm TL and 0.01 g mass), and frozen for energetic analysis.

Energetic analyses were conducted on all fish used in the experiment and on the sacrificed initial sample. Soxhlet extraction with petroleum ether as the solvent was used to determine the mass of storage lipids. The remaining tissue was ashed to determine the remaining organic content. The amount of energy in each fish was then expressed according to the formula

$$\text{energy (kcal)} = (\text{lipid mass (g)} \times 9.45 \text{ kcal/g}) \\ + (\text{dry lean tissue mass (g)} \times 4.80 \text{ kcal/g})$$

Details of the energy-analysis procedures can be found in Hurst et al. (2000) and Schultz and Conover (1997).

### Analysis

Patterns of survival were compared among the flow and feeding treatments by means of survival analysis (Cox's  $F$  test; Miller 1981). This approach analyzes survival of fish over the entire time series of the experiment instead of just the percentage surviving at the end of the experiment, but can only test one factor at a time. The feeding effect was therefore tested independently of the flow effect, and their interaction was inferred from the results of main-effect tests.

Daily food-consumption rates in the feeding treatments were expressed relative to fish mass. The mass of fish in each tank was estimated by subtracting the mass of all fish dying in the tank up to that date from the cumulative mass of fish stocked into the tank, i.e., food-consumption rate (% body mass/day) = [amount of food eaten / (cumulative initial mass – cumulative mass of dead fish)]  $\times$  100. Because fish in all tanks tended to eat more on warmer days ( $p < 0.001$ ), consumption rates were analyzed using analysis of covariance (ANCOVA) with daily average temperature as the covariate.

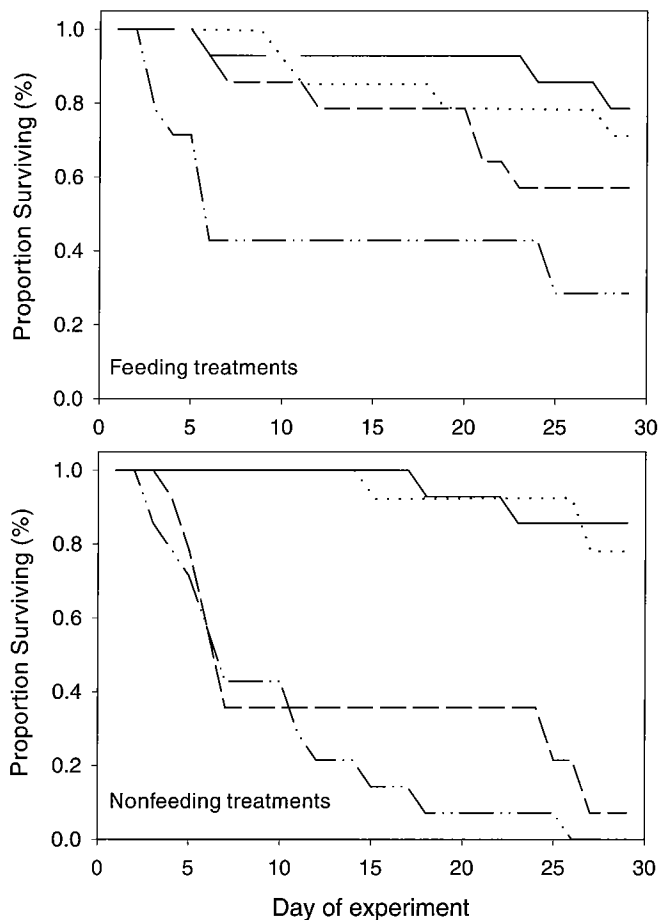
The amount of energy lost or gained by each fish during the experiment (net energy change) was determined as the difference between its energy measured at the end of the experiment and its estimated initial energy content. The initial energy content of each fish was estimated from the wet mass measured at the beginning of the experiment, using the relationship energy (kcal) =  $-0.27033 + 0.8202 \times$  wet mass, which was derived from the wet masses and energy contents of fish in the initial sample that were sacrificed ( $r^2 = 0.993$ ). Because individual fish were not marked, we assumed that the rank order of fish lengths did not change from the beginning to the end of the experiment, i.e., the initial mass of the longest fish at the end of the experiment was taken to be the wet mass of the longest fish measured at the beginning of the experiment. That this is a valid assumption is based on previous experiments (Hurst and Conover 1998) in which changes in length were found to be minimal at temperatures below 10°C.

The difference between initial and final energy contents was divided by the number of days the fish lived during the experiment. This approach allowed us to include the net rates of energy change for fish that died partway through the experiment, which was particularly important in the higher flow treatments, where few fish ultimately survived. We excluded from the analysis any fish that died during the first 5 days of the experiment because in such cases (i) differences between initial and final energy contents were likely due to error in estimating initial energy levels, and (ii) mortality was likely related to some factor other than energy content (i.e., an inability to maintain swimming velocity or tolerate handling stress).

### Maximum swimming speed experiments

We conducted a separate set of experiments to measure the critical swimming speeds ( $U_{crit}$ ) of YOY striped bass at representative winter temperatures. Fish were captured from their Hudson River nursery grounds in the vicinity of Croton Point, New York, in August 1998 and transported to the laboratory in river water. In the laboratory, salinity was raised to ~25 ppt over 7 days. Fish were maintained in large (1.8 m diameter) flow-through tanks in a greenhouse prior to use in experiments and were exposed to ambient seawater temperatures and a natural photoperiod. During the holding time, fish were fed a combination of adult brine shrimp (*Artemia* sp.) and artificial food (Moore-Clark striped bass feed, diet C). Experiments were conducted between March and May of the following year. Current was generated in the holding tanks with submersible pumps and varied from approximately 100 mm/s at the outer edge of the tank to near 0 mm/s near the center.

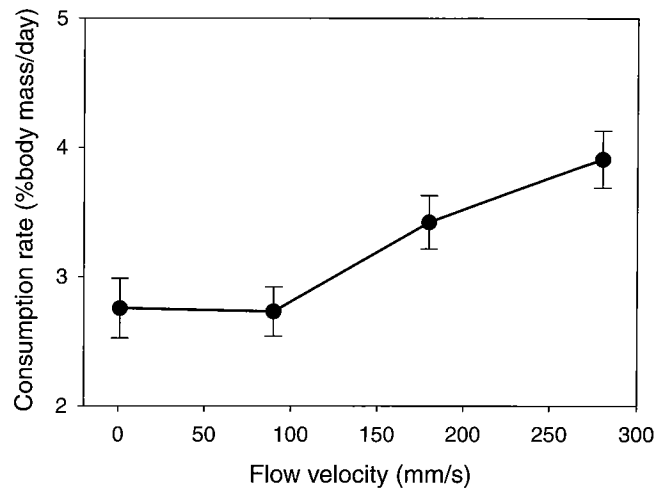
**Fig. 2.** Survival curves for YOY striped bass (*Morone saxatilis*) in feeding and nonfeeding treatments in the energy-change experiment. —, 0 mm/s flow; ·····, 80 mm/s; - - - -, 180 mm/s; - · - · - ·, 280 mm/s.



Fish were transferred to indoor tanks for temperature acclimation prior to use in experiments. Temperatures were changed to the experimental temperature at a rate of not more than 0.5°C/day and maintained there for at least 1 week prior to experiments. Acclimation tanks did not have pumps generating current, so fish were tested within 3 weeks of acclimation to the experimental temperature. Fish were starved for 24 h prior to swimming trials. Swimming trials were conducted at 2, 5, 8, and 11°C and tested fish ranged from 77 to 143 mm TL (3.6–25.3 g mass).

$U_{crit}$  was measured in a Vogel-style flume (Vogel 1981) modeled after Kelsch (1996). The system consisted of a 200-L reservoir, a water-delivery loop of 10 cm diameter flexible PVC piping, and an open-top U-shaped 100 × 10 × 10 cm swimway made of rigid PVC. All surfaces (except that of the water in the swimway) were insulated and water temperature was controlled with a recirculating water chiller. A variable-speed motor with a digital tachometer was mounted at the intersection of the reservoir and the delivery loop and forced water through the swimway. The velocity of water in the flume was regulated by varying the speed of the propeller and measured with an electronic flywheel flowmeter (Kent Type 265 miniflow) calibrated to tachometer readings, and was confirmed periodically. Flows were not directly measured during swimming trials. Rectilinear flows in the swimway were generated with honeycomb collimators (3 mm diameter openings) at the upstream end of the swimway. Fish were forced to swim in a 40 cm long section (swimming chamber) near the downstream end of the swimway. Preliminary trials showed that, when possible, fish remained in a

**Fig. 3.** Food-consumption rates of YOY striped bass during the energy-change experiment. Data points are mean consumption rates ( $\pm 1$  SD of daily consumption rates corrected to 5°C).



shaded portion of the swimming chamber. In trials, a 20 cm long opaque acrylic cover was placed over the upstream section of the swim chamber, minimizing disturbance during observations.

Individual fish were captured from acclimation tanks and transferred to the swim flume at a current speed of 50 mm/s. Once fish oriented to the flow and took up a position under the cover, they were acclimated for an additional 5 min prior to increasing flow velocity. Flow velocity was then increased by 25 mm/s every 5 min until the fish became exhausted. Fish were considered exhausted when they could no longer maintain position in the flume, continuously falling back under the cover and touching the screen at the back of the swim chamber.

When fish were exhausted, they were removed from the swim chamber, sacrificed with an overdose of anaesthetic, measured (TL, to 1 mm), individually wrapped in plastic bags, and frozen for energetic analysis (conducted as described above).

Critical swimming velocities were calculated using the equation  $U_{crit(m)} = V + (v \times T/t)$ , where  $U_{crit(m)}$  is the measured critical swimming speed,  $V$  is the highest speed maintained for a full time interval,  $v$  is the velocity increment (25 mm/s),  $t$  is the time increment (5 min), and  $T$  is the amount of time spent at the fatigue velocity (Brett 1964).  $U_{crit}$  values were corrected for the blocking effects of the fish in the swim chamber with the formula  $U_{crit} = U_{crit(m)}(1 + \epsilon_s)$ ;  $\epsilon_s$  is the fractional error in velocity due to blocking effects and is calculated as  $\epsilon_s = \tau\lambda(A_o/A_t)^{1.5}$ , where  $\tau$  is the drag coefficient (0.8),  $\lambda$  is a shape factor for streamlined objects ( $0.5 \times \text{length}/\text{width}$ ), and  $A_o$  and  $A_t$  are the cross-sectional areas of the fish and the tunnel, respectively (Bell and Terhune 1970; Williams and Brett 1987). Differences in critical swimming velocities were analyzed using ANCOVA with temperature as a main effect and BL and lipid level as covariates.

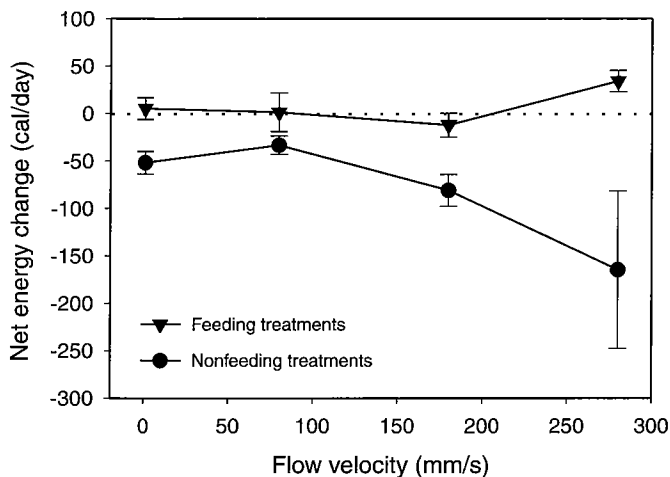
## Results

### Energy-change experiment

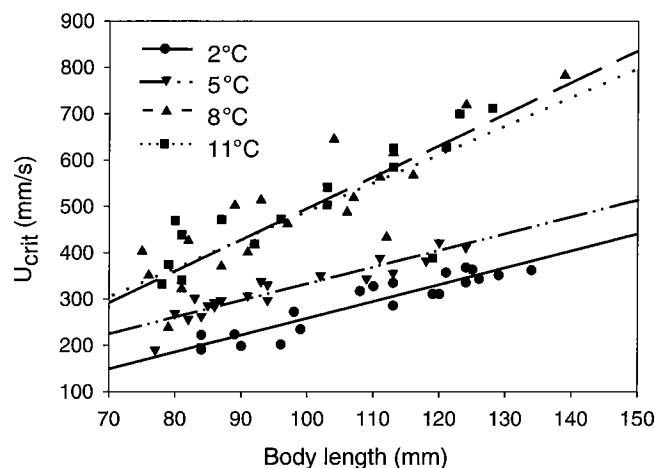
#### Survival rates

Flow velocity had a strong effect on survival of YOY striped bass (Fig. 2). Many fish in the two higher flow treatments died during the first 5 days of the experiment. In both the fed and unfed groups, failures increased with flow velocity. Among unfed fish, survival in the two lower flow treatments was significantly higher than in the high-flow treatments ( $p < 0.001$ ), so there was a strong effect of flow

**Fig. 4.** Changes in energy content of YOY striped bass as a function of flow and feeding treatment. The dotted line represents no net energy change.



**Fig. 5.** Maximum swimming speeds of YOY striped bass tested at four winter temperatures. Lines are linear regressions of  $U_{crit}$  against body length (total length (TL)).



**Table 1.** Total lengths (TL), lipid levels, and correlations between critical swimming speed ( $U_{crit}$ ) and TL for YOY striped bass (*Morone saxatilis*) used in maximum swimming speed experiments.

Temp. (°C)	n	TL <sup>a</sup>	Lipid level (% dry mass) <sup>a</sup>	Relative $U_{crit}$ (BL/s) <sup>a</sup>	Correlation between TL and $U_{crit}$	
					r	p
2	20	110.3±15.9	20.2±6.6	2.7±0.27	0.58	0.007*
5	20	96.0±14.7	25.7±7.1	3.3±0.26	0.21	0.378
8	20	98.7±17.3	19.4±6.2	4.9±0.76	0.40	0.082
11	20	97.1±16.7	19.7±7.2	4.8±0.85	0.24	0.312

<sup>a</sup>Values are given as the mean ± SD.  
\* $p < 0.05$ .

on survival ( $p < 0.001$ ). Among fed groups, the effect of flow ( $p = 0.004$ ) was due to the significantly lower survival rate in the highest flow velocity treatment ( $p = 0.036$ ) than in the three lower flow velocities, which did not differ significantly ( $p > 0.25$  for adjacent treatments). Survival rates were higher in fed than in unfed groups at the two higher flow velocities (180 mm/s;  $p = 0.008$ ; 280 mm/s;  $p = 0.087$ ) but not at the two lower flow velocities ( $p > 0.30$ ).

Survival of fish in the higher flow velocity treatments was strongly size-dependent. When data were pooled across feeding treatments, there was no survival of the smallest fish at both 180 and 280 mm/s, and survival rates increased among the largest fish to 50% at 180 mm/s and 30% at 280 mm/s. At the two lower swimming velocities (0 and 90 mm/s), there were few mortalities and no apparent size-dependent pattern to the mortalities.

**Food-consumption rates**

Fish consumed significantly more food when forced to swim at high velocities than at lower velocities (ANCOVA with temperature as the covariate,  $p = 0.001$ ; Fig. 3). There was an overall effect of temperature on daily consumption rates ( $p < 0.001$ ), but no difference in the slopes of the relationship between temperature and consumption rate among treatments ( $p = 0.383$ ).

**Energy change**

The rates of energy change in fish during the experiment were strongly affected by both activity level and availability of food (Fig. 4). In general, there was only a weak relationship between body size and energy change during the experiment ( $p < 0.05$  only in the nonfeeding/low-flow treatment), and there were no significant differences in the slopes of the relationship across flow or feeding treatments (all  $p > 0.16$ ). In all but the low-flow treatment, unfed fish had significantly greater energy losses than fed fish (low-flow treatment,  $p = 0.112$ ; all others,  $p < 0.03$ ). Comparisons of adjusted means revealed a significant interaction between feeding and flow velocity ( $p < 0.001$ ). Energy losses in unfed fish increased significantly at higher flow velocities ( $p < 0.001$ ). However, when fish were given an unlimited ration there was no significant difference across flow velocities ( $p = 0.273$ ).

**Maximum swimming speeds**

Temperature had a significant effect on maximum swimming speed ( $U_{crit}$ , mm/s) of YOY striped bass ( $p < 0.001$ ; Fig. 5).  $U_{crit}$  was significantly correlated with BL at all temperatures ( $p < 0.001$ ). We measured swimming speeds ranging from 189 mm/s for a 77 mm TL fish at 5°C to 712 mm/s for a 128 mm TL fish at 11°C. When expressed as a relative velocity (BL/s),  $U_{crit}$  was correlated with BL only at 2°C ( $p = 0.007$ ; all other temperatures,  $p > 0.08$ ; Table 1). Mean

$U_{crit}$  increased from 2.7 ( $\pm 0.27$  SD) BL/s at 2°C to 3.3 ( $\pm 0.25$ ) BL/s at 5°C, and was 4.9 ( $\pm 0.70$ ) and 4.8 ( $\pm 0.80$ ) BL/s at 8 and 11°C, respectively. Lipid levels in fish used in the experiments ranged from 4.7 to 35.6% body mass, but were not correlated with swimming ability ( $p = 0.95$ ).

## Discussion

The energy budgets of overwintering YOY striped bass are more flexible than has been appreciated. Swimming activity at winter temperatures generated significant metabolic costs, but juvenile striped bass displayed considerable ability to increase food consumption when faced with these costs. These experiments suggest that habitat requirements of overwintering juvenile striped bass are not directly constrained by the energetic costs of swimming beyond the constraints imposed by maximum swimming ability, provided that ample prey are available. However, the use of refuges from velocities below maximum swimming speeds would result in metabolic savings and may therefore be important in minimizing energy expenditure during periods when energy reserves are depleted or insufficient prey are available. Maximum swimming speeds were considerably lower than current velocities observed in the Hudson River wintering grounds of striped bass, suggesting a need for physical or behavioral refuges from peak tidal flows.

### Energy-change experiment

Activity level and prey availability were both important factors regulating the survival and energy budgets of overwintering YOY striped bass in the laboratory experiment. Mortality rates increased significantly as fish were forced to swim at higher velocities for extended periods, and were strongly size-dependent at the higher velocities. Most mortalities in the experiment were among fish forced to swim at speeds over 2 BL/s, near the maximum rates measured in the short-term trials, particularly during the first few days of the experiment. The availability of food increased survival at the higher flow velocities, indicating that feeding offset some of the effects of elevated energetic demands on survival. In addition, the rates of net energy change among fed fish were not correlated with relative swimming speed (BL/s,  $p = 0.944$ ), indicating that fish fed sufficiently to maintain energetic condition prior to exhaustion. Although the direct cause of failure of these fish is not known, these results suggest that it was most likely exhaustion as opposed to depletion of energy reserves.

Previous work on Atlantic salmon has shown that overwintering fish respond to energy depletion by temporarily elevating food-consumption rates in order to replenish reserves (Metcalf and Thorpe 1992; Bull et al. 1996). Salmon with initially high energy levels had very low consumption rates compared with fish with depleted energy levels. The interpretation was that fish increased feeding to prevent lipid levels from falling below some threshold level (Metcalf and Thorpe 1992). A model of voluntary reduced feeding activity (termed anorexia by Mrosovsky and Sherry 1980) in Atlantic salmon was developed by Bull et al. (1996) to include the changes in anticipated energy requirements as winter progressed. Anticipated energy needs are greater in early winter than in late winter, hence the energy level that is

“defended” falls as winter progresses. Our observation that YOY striped bass responded similarly to an immediate energy drain may be another facet of the regulation of consumption rates among overwintering fishes.

### Maximum swimming speeds

Maximum swimming speeds of YOY striped bass at winter temperatures were 2.7 BL/s at 2°C, increasing to 4.9 and 4.8 BL/s at 8 and 11°C, respectively (Fig. 5). Freadman (1978) found maximum swimming speeds of 2.9–3.3 BL/s at 15°C for 250 mm TL fish, lower than the speeds we found at 8 and 11°C (4.8–4.9 BL/s). The explanation for the difference is unclear, but may be related to body size, acclimation velocity, or differences in testing regime such as initial and step velocities and step time (Hammer 1995). Maximum swimming velocity generally increases with temperature and then decreases (Hammer 1995), with the peak generally near the upper end of the species’ thermal optimum (Guderley and Blier 1988). We found that the maximum swimming speeds of YOY striped bass were similar at 8 and 11°C, possibly reflecting a maximum between the two temperatures for fish acclimated to winter conditions.

Based on previous work, we expected that the level of lipid reserves might be correlated with maximum swimming speed in overwintering striped bass. Jones and Sidell (1982) found that metabolism in the swimming musculature of striped bass is increasingly fueled by lipids as the temperature decreases. Kolok (1992) found that winter swimming ability of juvenile largemouth bass was correlated with body condition. We found no correlation of  $U_{crit}$  with lipid levels in YOY striped bass at temperatures of 2–11°C ( $p = 0.141$ ). The fish used in the swimming experiments had been maintained in the laboratory for an extended period prior to experimentation and had higher lipid levels than fish used in the energy-change experiment, and higher than those commonly observed in wild fish during winter (Hurst et al. 2000). It is possible that swimming performance might be impacted at lower lipid levels.

YOY striped bass overwinter in the lower Hudson River estuary, where tidal-flow velocities in excess of 1 m/s have been measured (Oey et al. 1985). The maximum swimming speed of YOY striped bass was 4.8 BL/s, corresponding to 312–500 mm/s for the size range of fish tested. While YOY striped bass can be captured in the river channel at all stages of the tide (personal observation), they are clearly not capable of holding position against the ambient current velocities in their wintering grounds. These results suggest that fish are finding refuge from peak flow velocities. Fish may be residing in the benthic boundary layer, where flows diminish rapidly, or undergoing passive tidal excursions by not swimming against the tide, moving up and down the river axis on a tidal cycle. The shoreline of the lower Hudson River has been extensively modified by bulkheading and pier construction (Squires 1992; Wise et al. 1992). Juvenile striped bass are commonly captured in the interpier regions of the estuary in both summer (Able et al. 1998) and winter (personal observation), where velocities are roughly one-third of those in midchannel (P. Woodhead, personal communication). These artificial structures may provide an additional flow refuge for overwintering striped bass.

### Consequences for overwintering

Overwintering striped bass suffer from size-selective winter mortality (Hurst and Conover 1998), which may be related in part to the observed pattern of winter energy depletion (Hurst et al. 2000). The activity requirements of wild fish significantly complicate the energy budgets and habitat needs of fish relative to those of fish maintained in laboratory aquaria. We have shown that while activity necessitates significant metabolic expenditures, striped bass can feed to offset these costs if sufficient prey are available. We observed a similar response among wild fish in winter, in which maximum stomach fullness was negatively related to the level of energy reserves (Hurst and Conover, see footnote 2). The depletion of energy reserves observed in wild fish (Hurst et al. 2000) may indicate that prey availability is limiting during winter in the lower Hudson River estuary.

The observation that overwintering fish were capable of feeding in response to energy depletion, but did not grow, suggests a mortality risk to feeding. For Atlantic salmon overwintering in small streams, foraging may result in displacement or increase vulnerability to mammalian or avian predators (Metcalf and Thorpe 1992; Valdimarsson and Metcalfe 1998). Because very little is known about the behavioral patterns of YOY striped bass overwintering in large estuaries, the potential costs of foraging are unclear. The only known predators of YOY striped bass in winter are older striped bass (Dunning et al. 1997), and it is unclear whether foraging would increase vulnerability. In addition, the risk of displacement may be diminished because of reversing tidal currents. An alternative explanation for the lack of growth in winter may be a physiological constraint on protein synthesis at low temperatures.

Habitat preferences and behaviors of overwintering fishes are believed to represent tactics for conserving energy (Winslade 1974; Cunjak 1996; but see Valdimarsson and Metcalfe 1998). Use of refuges from flow (including tidal excursions) would provide a mechanism for stemming energy losses. For example, Facey and Grossman (1990) found that for overwintering longnose dace (*Rhinichthys cataractae*) and mottled sculpin (*Cottus bairdi*), adherence to the substrate resulted in metabolic rates that were independent of the velocity of the overlying water.

YOY striped bass could not swim at maximum current speeds in their Hudson River wintering grounds, which implies a need for physical or behavioral refuges from flow. However, under laboratory conditions of unlimited prey availability, the energetic costs of activity did not appear to further constrain habitat choice for juvenile striped bass, as they were able to feed at rates sufficient to cover metabolic costs. This compensatory ability may allow striped bass to use a variety of habitats or survive winter in the face of diminished energy reserves.

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