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J. B. K. Leonard · J. F. Norieka
B. Kynard · S. D. McCormick

Metabolic rates in an anadromous clupeid, the American shad (*Alosa sapidissima*)

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Abstract To assess the energetics of migration in an anadromous fish, adult American shad (*Alosa sapidissima*) were swum in a large respirometer at a range of speeds (1.0–2.3 body lengths (BL) s^{-1}, 13–24 °C). Metabolic rate (M_{O_2}) was logarithmically related to swimming speed (Bl s^{-1}; $r^2 = 0.41$, slope = 0.23 ± 0.037) and tailbeat frequency (beats × min^{-1}; $r^2 = 0.52$, slope = 0.003 ± 0.0003). Temperature had a significant effect on metabolic rate ($r^2 = 0.41$) with a Q_{10} of 2.2. Standard metabolic rate (SMR), determined directly after immobilization with the neuroblocker gallamine triethiodide, ranged from 2.2–6.2 $mmolO_2\ kg^{-1}\ h^{-1}$ and scaled with mass (W) such that $SMR = 4.0\ (\pm 0.03)W^{0.695(\pm 0.15)}$. Comparison of directly determined and extrapolated SMR suggests that swimming respirometry provides a good estimate of SMR in this species, given the differences in basal activity monitored by the two methods. Overall, American shad metabolic rates (M_{O_2} and SMR) were intermediate between salmonids and fast-swimming perciforms, including tunas, and may be a result of evolutionary adaptation to their active pelagic, schooling life history. This study demonstrates variability in metabolic strategy among anadromous fishes that may be important to understanding the relative success of different migratory species under varying environmental conditions.

Key words American shad · *Alosa sapidissima* Metabolism · Respirometry · Clupeidae

J.B.K. Leonard (✉) · J.F. Norieka
B. Kynard · S.D. McCormick
Conte Anadromous Fish Research Center,
Biological Resources Division,
United States Geological Survey,
Turners Falls, MA 01376, USA

J.B.K. Leonard · S.D. McCormick
Department of Biology, University of Massachusetts, Amherst,
MA 01003, USA

Abbreviations *BL* body length · *Hb* hemoglobin · *GTE* gallamine triethiodide · M_{o_2} metabolic rate · *SMR* standard metabolic rate · *TBF* tail beat frequency · *U* swimming speed · U_{crit} critical swimming speed

Introduction

Respirometers have been used to evaluate the energetic costs of swimming for several decades (e.g., Brett 1964; Webb 1971); most early work concentrated on relatively small salmonids (< 30 cm e.g., Brett 1964; Brett and Glass 1973). Until recently, few studies had examined larger fish, particularly non-salmonid species, but interest in large marine species such as tuna (e.g., *Thunnus albacares*, *Euthynnus affinis*, *Katsuwonus pelamis*, Dewar and Graham 1994; *Thunnus alalunga*, Graham and Laurs 1982), pelagic sharks (*Sphyrna tiburo*, Parsons 1990; *Negaprion brevirostris*, *Triakis semifasciata*, *Isurus oxyrinchus*, Graham et al. 1990), large Atlantic salmon and mackerel (*Salmo salar*, *Scomber scombrus*, Lucas et al. 1993) and dolphin fish (*Coryphaena hippurus*, Benetti et al. 1995) is expanding the size range of fish examined. With the exception of salmonids, notably Pacific salmon and some trout species, there has been little work investigating the cost of locomotion in species with a diadromous life history. These species typically undergo long, non-feeding migrations between the adult oceanic foraging habitat and the freshwater spawning habitat. During upriver migration, these fish may encounter steep riverine gradients, high current flows and a variety of man-made obstacles that may impact the locomotory cost of migration. Additionally, many species of diadromous fish are iteroparous and the cost of returning to the adult foraging environment therefore plays a role in determining fitness. To investigate the cost of migration due to locomotion in large diadromous fish, we constructed a swimming respirometer designed to evaluate oxygen consumption relative to swimming performance of adult anadromous fishes native to the eastern United States.

American shad (*Alosa sapidissima*) are currently one of the most abundant anadromous fishes found in the eastern rivers of North America and their numbers are increasing in western rivers where they have been introduced (Welander 1940; Quinn and Adams 1996). This clupeid is a schooling species that spawns in large rivers in the spring. Young-of-year spend the summer in their natal rivers and migrate to sea in the fall. Fish generally spend 2–3 years at sea and then return to their natal river to spawn. Females are usually older (3–5 years old) than males (2–4 years) at first maturity. The species is variably iteroparous; southern populations are almost entirely semelparous, northern populations are largely iteroparous and mid-Atlantic populations are intermediate (Glebe and Leggett 1981). Spawning American shad enter their natal rivers during the peak of the high flow season. This is also typically a period of rapid increase in river temperature. For example, in 1994 temperatures in the Connecticut River increased from 9 °C to 17 °C during May (Leonard and McCormick 1999). Additionally, in many rivers fish must pass through a variety of fish passage facilities such as fish ladders and fish elevators. These factors can create energetically demanding conditions for migrating adults by varying flow velocities and delaying migration (Hinch et al. 1996).

Despite the high abundance of American shad and their apparent importance in riverine ecosystems, little is understood about their biology and physiology. Few studies have been conducted on clupeids since they are difficult to handle successfully and are noted for their susceptibility to scale loss and handling stress (Barry and Kynard 1986). Some work has been attempted, however. Routine metabolic rates have been reported for Baltic herring (*Clupea harengus harengus*, Chekunova 1979), Atlantic herring (*Clupea harengus*, Johnstone et al. 1993), Atlantic menhaden (*Brevoortia tyrannus*, Durbin et al. 1981) and juvenile American shad (Ross and Backman 1992; Ross et al. 1992). None of these studies worked with fish swimming at a series of controlled speeds. They do suggest a fairly high metabolic rate for the clupeids, but it is difficult to extrapolate from the juvenile to the adult stage or between species.

This study is the first to evaluate the energetic cost of swimming in adult, migratory American shad. We compare the active metabolic rate of American shad to other species and discuss how species differences in metabolic strategy may impact migratory success. Additionally, we examine what role standard metabolic rate (SMR) may play in the energy balance of these and other fish.

Materials and methods

Handling and maintenance

American shad were taken from two hydroelectric facilities on the Connecticut River: Cabot Station fishladder in Turners Falls, Mass. (198 km upriver from the river mouth) and Holyoke Dam fish lift in Holyoke, Mass. (139 km upriver). Fish were confined in the trap located at the top of each passage facility for less than 10 min and then netted into a fish transport truck supplied with recirculating, oxygenated Connecticut River water. The fish were transferred immediately to the Conte Anadromous Fish Research Center (CAFRC) in Turners Falls, Mass. and placed in a 4.6-m diameter tank (1 m water depth). This tank was equipped with flow-through river water and a submersible pump that generated a current velocity of 30–45 cm s^{-1}. Fish were acclimated to these conditions for 1–10 days prior to testing. Temperature in the holding tank was the same as the river and photoperiod was natural daylength. No attempt was made to feed the fish during this period because shad do not generally feed during their upriver migration (Chittenden 1976). All experiments occurred during the normal period of upstream migration of American shad, specifically May 19–July 6 1995, May 21–June 24 1996 and May 29–July 1 1997 (adult shad are not resident in freshwater at other times of the year).

Swimming respirometer design

A modified Brett-type swimming respirometer (e.g. Brett 1964) with the test chamber above the opposing loop was constructed at CAFRC. The respirometer (volume of 259 l) consists of a test chamber, elbows with turning vanes, a metered straight section, and cooling and oxygen injecting systems (Fig. 1). The test chamber is a transparent acrylic tube 1.25 cm thick, 30.5 cm inner diameter, and 1.2 m in length. The section is flanged on either end for attachment to the rest of the respirometer and fitted with acrylic taps for air release valves and velocity meter access ports. An acrylic open-topped box affixed to the tube allows introduction of the fish to the chamber. An acrylic lid, fitted with pressure gauges and air/water release valves, is secured with quick clamps. The top flange is gasketed to prevent air/water leaks and the inner portion of the lid lies flush with the inside of the test chamber. An acrylic insert was used to reduce the lateral aspect (20.3 cm width) of the chamber and prevent small shad from turning around during testing. The test chamber attaches to steel reducing elbows on either end. On the upstream side of the chamber, the elbow is fitted with a series of flow straightening screens, while on the downstream side there is a single retaining screen. The upstream straightening screens consist of two stainless steel woven screens (~1.5 cm apertures) and two polypropylene perforated plates (~0.5 cm diameter perforations). All three steel elbows in the respirometer are fitted with flow straightening vanes (three per elbow) that minimize flow separation in the elbows and maintain a uniform velocity. Each vane consists of a curved steel plate welded into the elbow parallel to the flow stream. Each set of vanes divides the elbow into thirds. Velocity profiles in the respirometer were evaluated with a two-dimensional pitot tube monitored by a computer data acquisition system. Velocity traverses were taken at two longitudinal locations. Velocity profiles were essentially uniform. Most velocities were ±10% from the average velocity in the test section, although a wall effect was detected within several centimeters of the wall surface. This wall effect was not, however, utilized by the fish: all test animals swam in the center of the test section. Additionally, there was a negligible effect of solid blocking since shad have a low cross-sectional area due to their lateral compression (based on the eqs. of Webb 1975).

Flow in the respirometer is provided by a variable speed, 60 horsepower, end suction pump, placed in one corner of the loop, which is controlled by a variable frequency drive unit. This pump also provides flow for two bypass loops (Fig. 1) that facilitate temperature control before and during runs and reoxygenation between runs. Oxygen is introduced into the system via two parallel membrane oxygen injectors (Bard Cardiopulmonary, Tewksbury, Mass.) while temperature is controlled using a stainless steel heat exchanger.

The respirometer oxygen, temperature and flow meter systems are linked to a computerized data acquisition system. Temperature is monitored with a thermistor and temperature meter. Oxygen is

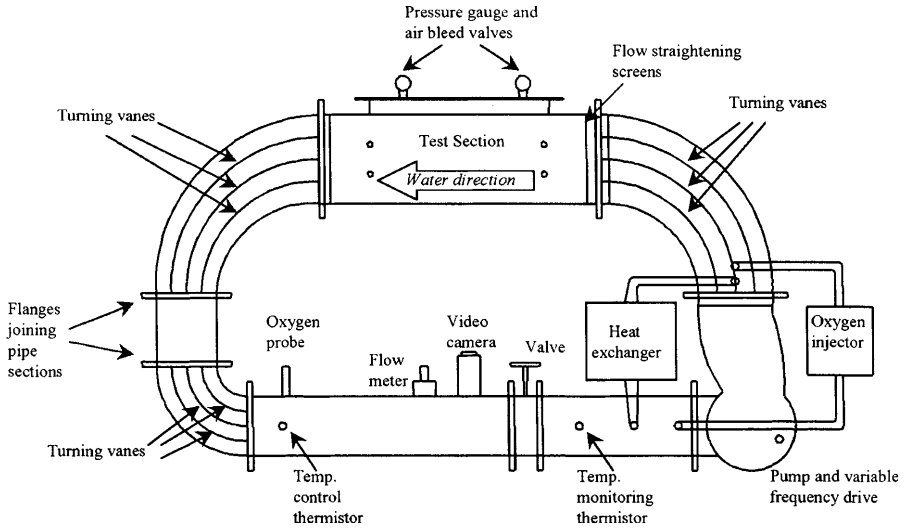

Fig. 1 Schematic diagram of Conte Anadromous Fish Research Center respirometer including 120 cm × 30.5 cm test section and lid equipped with pressure gauges and air bleed valves, flow straightening screens, steel elbows with turning vanes, 60 horse power pump with variable frequency drive, camera with VCR, oxygen probe with meter, thermistors for temperature monitoring and control, flow meter, heat exchanger, and oxygen injector. *Open arrow* indicates direction of water flow. External insulation is not shown. Steel elbows are shown in cutaway view to reveal turning vanes

monitored with a YSI (Yellow Springs, Ohio) model 5730 probe and model 58 oxygen meter. Flow rate is measured with a Data Industrial (Pocasset, Mass.) 900T propeller type flow meter that was calibrated with a venturi meter. Tailbeat frequency (TBF) is monitored using a video camera mounted under the test section. The camera records images on a time-lapse tape recorder; VCR time and computer time are synchronized to the nearest second at the beginning of each test sequence.

Swimming respirometer protocol

Before each experiment, the respirometer was filled with river water and run at a slow speed with air valves open to remove bubbles. The respirometer was then sealed and the temperature brought to within 1.0 °C of the ambient water temperature in the holding tank. Change in dissolved oxygen was monitored before and after experimental runs to evaluate any oxygen consumption by microscopic organisms. This served as a control and was in all cases negligible compared to the oxygen used by the fish.

After the respirometer had been prepared, the system was unsealed and the fish transferred into the test chamber using a dip net. The top was replaced and the fish allowed to acclimate to the test chamber for 1 h while swimming at a slow speed [approximately 0.5–1.0 body fork lengths s^{-1} (BL s^{-1})]. If, by the end of the acclimation period, the fish did not appear calm and display straight swimming behavior, then the fish was removed and a new fish selected for testing. Test fish then followed one of two possible protocols. Protocol I was designed to determine the behavior and stability of metabolic rate in fish swum at constant speed for an extended period of time. In experiments using this protocol, the fish continued swimming at the initial velocity as long as possible. When using this protocol, oxygen consumption data was also recorded during the initial acclimation period. Four fish were swum in the respirometer using protocol I for a maximum of 170–330 min at constant speed. In all cases, oxygen consumption was initially elevated, but decreased steadily and reached a statistically stable ($P = 0.47$) level of oxygen consumption after 2 h. In protocol II, the relationship between speed and oxygen consumption was characterized and only data acquired 2 h after the introduction of the fish into the test chamber was used. The first test velocity used in protocol II was that to which the fish had been acclimated. Water velocity was subsequently increased by approximately 0.25 BL s^{-1} for each interval. Fish swam for 30 min at each test velocity. During each of these 30 min intervals, the first 15 min was used as an acclimation period to the new velocity and oxygen was increased in the chamber as necessary, therefore no data were recorded. In no case was dissolved oxygen in the experimental chamber allowed to fall below 75% of saturation (water saturated air P_{O_2}) or rise above 100% saturation. The second 15 min period was used as the test interval and dissolved oxygen concentration, water velocity and temperature were recorded every minute. Tailbeat was monitored and recorded continuously throughout the test period. This sequence was repeated until the fish could no longer hold position in the test chamber. The test was ended when the fish could not maintain position for 30 s in the test chamber or when the fish rested continuously on or against the downstream screen in the test chamber. M_{O_2} was determined over 5 min intervals and means for 15 min periods were calculated. TBF was determined from five to seven 1-min intervals for each swimming speed and an average calculated for each speed for each individual.

SMR apparatus and protocol

SMR was measured in a 67.8-l box respirometer (88 × 33 × 32 cm) equipped with a YSI model 5905 oxygen probe and model 58 meter which transferred data directly to a portable data logger. The data logger also recorded temperature. Activity of the fish was monitored by a camera and heart rate was determined from electrocardiogram (EKG) measurements. Once sealed, the box was placed in a 1-m diameter fiberglass tank with flowing river water to provide temperature control. After netting, the test subject was anesthetized with buffered tricaine methansulfonate (MS-222, 50 mg l^{-1}, pH 7.0), length, weight, and sex were recorded and the fish was injected intramuscularly with gallamine triethiodide (GTE; 2–3 mg kg^{-1} fish), a potent neuroblocker. GTE takes effect rapidly in shad, so the injected fish was removed from the MS-222-containing tank, immediately transferred to the box respirometer and the buccal cavity irrigated using a small pump. The fish was then placed on an acrylic V-board within the box and EKG electrodes were implanted. A catheter was placed in the caudal musculature to allow periodic injection of GTE (1 mg kg^{-1} $dose^{-1}$). GTE was only administered if motion was detected via the video monitor. Throughout these initial procedures fresh river water flowed through the box. The lid was then sealed and a black plastic cover was placed over the apparatus. The animal's oxygen consumption was monitored until it reached a stable minimum using one of two methods. In the first method, the system was kept sealed and oxygen was monitored until it was depleted to approximately 50–60% saturation. In the second method, the system was sealed for 30 min and oxygen monitored. Each test period was followed by a recovery period where river water was passed through the system. This served to increase the dissolved oxygen back to initial levels and oxygen was never depleted by more than 20% during the experiments. Both methods relied on closed respirometry techniques and there were no observable differences in the results obtained using these two methods.

Analysis

M_{O_2} and SMR data were analyzed using multiple and single linear regression. Q_{10} for a given speed was also calculated from the regressions for warm and cold groups using the following eq:

$$Q_{10} = \frac{(M_{O_2w} - M_{O_2c}) \times 10/(T_w - T_c) + M_{O_2c}}{M_{O_2c}}$$

Where T is mean temperature of the warm (w; 19–24 °C) and cold (c; 13–18 °C) groups and M_{O_2} is the rate of oxygen consumption for the warm and cold groups.

Results

Swimming respirometer

We used protocol II to test a total of 18 adult shad in the respirometer: 12 males and 6 females. Gender did not affect metabolic rate ($P > 0.05$). Summary data on fish and conditions during tests are described in Table 1. American shad would not swim to a recognizable critical swimming speed (U_{crit}) as described in Brett (1964) for salmonids. Frequently, fish would begin to lean on the wall of the respirometer or rest their tail against the back screen in the test section at higher speeds. When this occurred, fish were removed from the test section. Therefore, U_{crit} could not be calculated conclusively and data for M_{O_2} and TBF (beats × min^{-1}) are from only steadily swimming fish. TBF was linearly related to swimming speed (U) and showed no dependency upon temperature when evaluated using best subsets regression techniques (Fig. 2a; TBF = 32.9(±6.6) + 89.0 (±3.8) U(BL s^{-1}) (r^2 = 0.87)).

Multiple regression analysis of all the metabolic data suggests that temperature significantly affects metabolic rate (r^2_T = 0.41, $P < 0.001$). For this reason, fish were divided into two groups: warm (tested at temperatures 19–24 °C, mean 21.3 ± 0.5 °C) and cold (13–18 °C, mean 15.6 ± 0.7 °C). Linear regressions were calculated for the log-transformed M_{O_2} for warm and cold temperature in relation to standardized U (BL s^{-1}) and TBF (Table 2; Fig. 2b). All temperature regressions are significant and are significantly different from each other (within U or TBF). Although the regressions of M_{O_2} on U and M_{O_2} on TBF were all significant, the regression coefficients were higher for the last relationship (r^2 = 0.52; Fig. 2a, b). Q_{10} was calculated to be 2.2 using the M_{O_2} vs. TBF regression eqs. for the two temperature groups.

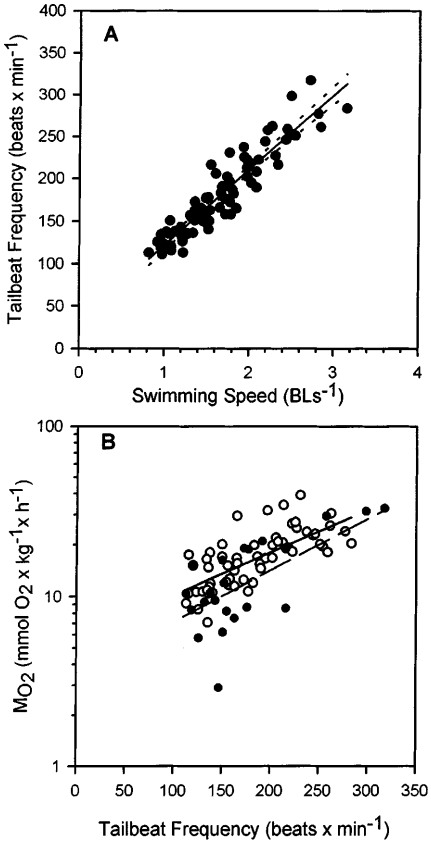

Fig. 2A Relationship between swimming speed (*U*) and mean tailbeat frequency (*TBF*) for adult American shad swum in respirometer (n = 18; 3–8 points per individual). The significant ($P < 0.05$) linear regression is also shown (TBF = 32.9(±6.6) + 89.0(±3.8)U; r^2 = 0.87). 95% confidence intervals are shown as *dashed lines*. **B** Relationship between M_{O_2} (mmol O_2 kg^{-1} h^{-1}) and TBF (beats × min^{-1}) for adult American shad and for warm (○; 18–21 °C) and cold (●; 13–18 °C) groups swum in respirometer. n = 18, 3–8 points per individual. Significant regressions ($P < 0.05$) for warm (-.-.) and cold (- - -) groups are as described in Table 2

Directly determined SMR

Twenty-three fish (15 males, 8 females) were used in determining SMR directly using the box respirometer. Fish were 42.4 ± 1.0 cm fork length (range 35.0–49.5 cm) and 1.05 ± 0.10 kg mass (range 0.47–1.77 kg). Heart rates ranged from 84–132 beats min^{-1} with a mean of 99 ± 20 beats min^{-1}. Figure 3a shows a typical SMR experiment where the oxygen consumption is ini-

Table 1 Summary data for adult American shad used in swimming respirometer including fork length (*FL*), weight (*W*), average temperature (*T*) and range of swimming speeds (*U*) for fish used in determination of tailbeat frequency (TBF) vs. swimming speed and metabolic rate vs. swimming speed relationship. Values are mean ±1 SEM. (*BL* body length)

Group	*n*	FL (cm)	W (kg)	Temp (°C)	Average U	
					min (BL s^{-1})	max (BL s^{-1})
Cold	6	42.8 ± 2.4	1.15 ± 0.23	15.6 ± 0.67	1.01 ± 0.05	1.77 ± 0.19
Warm	12	40.1 ± 1.2	0.83 ± 0.10	21.3 ± 0.45	1.14 ± 0.07	2.27 ± 0.12

Table 2 Summary of multiple regressions for log M_{O_2} (mmol O_2 kg^{-1} h^{-1}) on temperature (T) and **A** standardized swimming speed (U in BL s^{-1}) or **B** tailbeat frequency (TBF in beats × min^{-1}) for adult American shad. All factors included are significant at $P < 0.005$ and regressions for temperature groups are significantly different from each other. Variables are ±1 SEM. Estimated mean standard metabolic rates (SMR, mmol O_2 kg^{-1} h^{-1}) are shown. Cold group includes fish swum in the respirometer within the 13–18 °C range. Warm group includes fish swum between 18–23 °C

Group	Regression	r^2	estimated SMR
A			
Cold	$\log M_{O2} = 0.30(\pm0.10)U + 0.645(\pm0.05)$	0.31	4.4
Warm	$\log M_{O2} = 0.21(\pm0.04)U + 0.875(\pm0.01)$	0.37	7.5
B			
Cold	$\log M_{O2} = 0.003(\pm0.001)TBF + 0.552(\pm0.04)$	0.43	3.6
Warm	$\log M_{O2} = 0.003(\pm0.0003)TBF + 0.759(\pm0.03)$	0.52	5.7

tially high (~13.3 mmol O_2 h^{-1} kg^{-1}) and then drops to 4.2 mmol O_2 h^{-1} kg^{-1} after approximately 50 min. Based on this decrease which occurred in all individuals, SMR was computed by taking the average oxygen consumption for data generated after 1 h. There was no significant difference ($P = 0.90$) between SMR determined by the two experimental methods. Temperature was not a significant factor in the relationship between SMR and weight ($P = 0.54$). The mean temperature for all runs was 17.5 ± 0.60 °C (range 13–21.5 °C). There was no significant difference between the sexes ($P = 0.93$). SMR ranged from 2.2–6.2 (mean 4.3 ± 0.2) mmol O_2 kg^{-1} h^{-1}; the log-SMR was linearly related to log fish mass (W) by $SMR = 4.0\ (\pm0.03)\ W^{0.695(\pm0.15)}$.

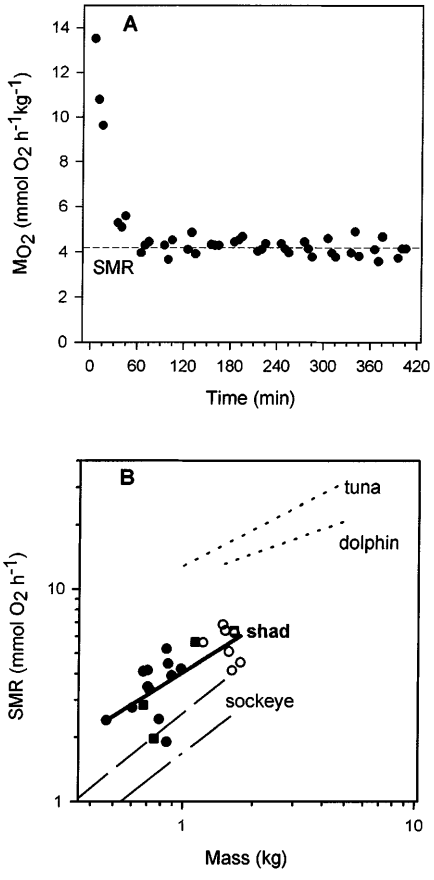

Fig. 3A Data for a typical adult American shad (male, 37.2 cm fork length, 0.6735 kg weight) following injection with gallamine triethiodide (GTE). Calculated standard metabolic rate (SMR; 4.2 mmol O_2 h^{-1} kg^{-1}) is the *dashed line*. **B** Relationship between directly measured SMR (log-SMR) and weight (logW) for adult American shad from this study (shad; ● males method 1, ○ females method 1, ■ males method 2, □ females method 2; 14–20 °C) compared to published values for other species. Sockeye salmon (sockeye, *Oncorhynchus nerka*; 20 °C [—] and 15 °C [- - - -]; Brett and Glass 1973), skipjack tuna (tuna, *Katsuwonus pelamis*; Brill 1979; 23–25 °C), and dolphin fish (dolphin, *Coryphaena hippurus*; Benetti et al. 1995; 25 °C). Regressions are for directly measured SMR except for sockeye where it was extrapolated from swimming respirometry

Discussion

Evaluation of SMR and active metabolic rate in fish allows us to understand some of the limitations placed by their physiology on an animal's scope for activity. This is particularly important in a species like the American shad that is affected by man-made and environmental stressors during its critical upstream migration. Migration may serve as a challenge to the maximal physiological range of activity and the success of the upstream journey may be linked to energy management within this scope (Hinch et al. 1996).

Standard metabolic rate

The direct measurement of SMR using GTE in this study has provided us with a mechanism to check the accuracy of swimming respirometry as a method of metabolic rate determination in American shad. Johnstone et al. (1993) suggested that testing fish individually, particularly schooling species, in any tunnel respirometer may lead to stress and artificially elevated M_{O_2} levels. The direct SMR method allowed us to remove the effects of swimming from oxygen consumption and monitor the reduction of oxygen consumption as stress of the fish. Brill (1987) found this methodology satisfactory with no significant difference between SMR measured using direct, anaesthetizing respirometry and extrapolated SMR values from swimming respirometry in both aholehole (*Kuhlia sandivicensis*) and rainbow trout (*Oncorhynchus mykiss*). SMR values based on di-

rect measurements in American shad are approximately 13% lower than those calculated from the regression equations based on our swimming respirometer; however, they do fall within the 95% confidence intervals of this regression. A slight overestimation may be expected using swimming respirometry since the extrapolated values include the energetic costs of opercular movement and maintenance of positional orientation which are eliminated in the direct SMR method. This was also noted by Brill (1987), but was found to be statistically non-significant. There may also be a slight metabolic depression, however, from GTE administration (Brill 1987; Taylor 1996). Therefore, it is likely that the true SMR is intermediate between the measurements obtained using the two methods. The comparative data from the two methods for American shad suggest, however, that swimming respirometry derived data provides an acceptable, although slightly elevated, estimate of SMR, even in species that are susceptible to stress from handling and isolation.

SMR has been repeatedly shown to be related to mass in a double-logarithmic relationship (Beamish 1964; Brill 1987; Dewar and Graham 1994). Figure 3b shows the data from the directly determined SMR from this study and compares it to values from the literature. American shad demonstrate intermediate SMRs between "typical" teleosts (e.g. salmonids) and some fast swimming perciform fishes. The mass exponent of the relationship between SMR and fish size is approximately 0.695 in American shad; a value similar to most teleosts which range from 0.65–1.0 (Beamish 1964), although tunas (0.496–0.573; Brill 1987) and dolphin fish (0.384; Benetti et al. 1995) are outside this range. Various authors (Brill 1987; Dewar and Graham 1994; Benetti et al. 1995) have suggested that this variation may arise because, in scombrids, the mass exponent scales with total respiratory (gill) area rather than internal organ weight as has been proposed for other teleosts (e.g. Oikawa and Itazawa 1984 a, b; Oikawa and Itazawa 1985).

Active metabolic rate

TBF is closely related to U in American shad, demonstrating that measures of TBF will be of use in determining instantaneous U in future studies. It is interesting to note that the relationship between TBF and metabolic rate is slightly more explanatory than that between measured U and metabolic rate. Measured U is only an index of performance whereas muscle activity (as indicated by tail movement) is more directly related to energy use during locomotion.

Temperature had a significant effect on metabolic rate of American shad. The data (Table 2) suggest a Q_{10} of 2.2 at 1 BL s^{-1}, which is similar to the rate usually seen in fish in the 15–20 °C range (Beamish 1964; Jobling 1997; Taylor et al. 1997). In the case of American shad, this calculation is based on animals held close to the preferred temperature of the species (13–16 °C; Leggett and Whitney 1972), relative to shad at 22 °C, a temperature associated with the end of migration and return to colder ocean water (Leggett and Whitney 1972). Individual variation is an important factor in our data for metabolic rate of American shad. We observed different individuals of the same general description (i.e. size, sex, condition) performing at markedly different levels. These differences were not specifically related to temperature changes, but it is possible that some of this variability may be a function of differential motivation during different periods of the run. Alternatively, this variation may stem from simple differences in individual motivation and/or performance capacity. Individual variability has been documented in fish locomotor performance (Gibson and Johnston 1995). Such individual variation may be important to migratory success in American shad. Future investigations should seek to address this factor more fully to determine how individual variability impacts reproductive success at the individual and population levels.

Migratory American shad appear to have elevated metabolic rates over other clupeid species, although comparison is difficult since most previous studies using clupeids are concerned with routine rates of respiration. Chekunova (1979) reported metabolic rates for "normally swimming" Baltic herring (*Clupea harengus membras*) which varied seasonally and with temperature. Routine respiration rates have also been reported for Atlantic herring (*Clupea harengus*) held in captivity for long periods of time (100 days; Johnstone et al. 1993). He and Wardle (1988) reported data for swimming endurance, but not metabolic rate, at "intermediate" speeds (2–4 BL s^{-1}, 25 cm fish, 13.5 °C) for Atlantic herring. Durbin et al. (1981) did extensive work with the Atlantic menhaden, *Brevoortia tyrannus*, including determination of costs of locomotion during and after feeding. These experiments were performed in a large annular respirometer with numerous fish in each trial and suggested a rapid and large increase in oxygen consumption with increasing speed from an extremely low (1.1 mmol O_2 h^{-1} kg^{-1}) extrapolated SMR. Finally, Ross and coworkers have evaluated the costs of swimming in larval and juvenile Hudson River American shad at "routine" speeds during schooling (Ross and Backman 1992; Ross et al. 1992); The metabolic rates were not as high as we have observed for adult migratory American shad in any of these studies. It is intriguing, and still unclear from our present study, whether American shad have a relatively high metabolic rate throughout their lifetimes or whether the data we have collected are elevated due to the spawning migration. Changes in metabolic rate have been observed in fish in coordination with ontogenetic changes during migration (e.g., elevated M_{O_2} following smoltification in salmonids; McCormick and Saunders 1987; Cowley et al. 1994), however, this has not yet been documented in American shad of any age. It should also be noted, however, that American shad are capable of shifting the patterns of their metabolic enzyme systems during up-

stream migration (Leonard and McCormick 1999). Adult American shad increase their capacity for aerobic metabolism and increase their ability to mobilize stored energy (both lipid and protein) as they proceed upriver (Leonard and McCormick 1999). This suggests an up-regulation of aerobic metabolism that could be reflected by a higher metabolic rate (M_{O_2} and SMR) during migration than is seen during the non-riverine phase of the life cycle.

Migrating American shad also have a high active metabolic rate in comparison to many other teleost fishes (Fig. 4). This metabolic rate is still below the levels of warm-bodied scombrid teleosts, however. Analysis of available data on metabolic rate among fish species indicate that there are two categories of species that are similar to those discussed in Wardle (1977; Fig. 4). The first group comprises those species, including salmonids and menhaden, with relatively low extrapolated SMR and sharply increasing energy use with increasing speed (suggested by the steep slope and low *y*-intercept of these regressions). The other group, which includes the scombrids, is characterized by higher SMRs and relatively shallow-sloped regressions implying a slower increase in energy needed to swim at higher speeds. Ectothermic scombrids that have been tested (Atlantic mackerel) also seem to demonstrate this shallow slope pattern although their metabolic rate is not as high as endothermic scombrids (Fig. 4, Lucas et al. 1993). This suggests a tradeoff between maintenance of low SMR and minimizing energy expenditure at high swimming speed. Graham et al. (1994) also noted this phenomenon and attributed the separation of tunas from other teleosts to the specialized tuna "bauplan". They proposed that tuna body morphology resulted in increased swimming efficiency visualized through a shallow line slope for the M_{O_2} to U relationship. In our study, American shad are intermediate between the two groups in magnitude, but like the Atlantic mackerel, belong to the group demonstrating a shallow-sloped relationship between speed and metabolic rate (Fig. 4). This suggests that there may be physiological similarities between the phylogenetically distant scombrids and alosines.

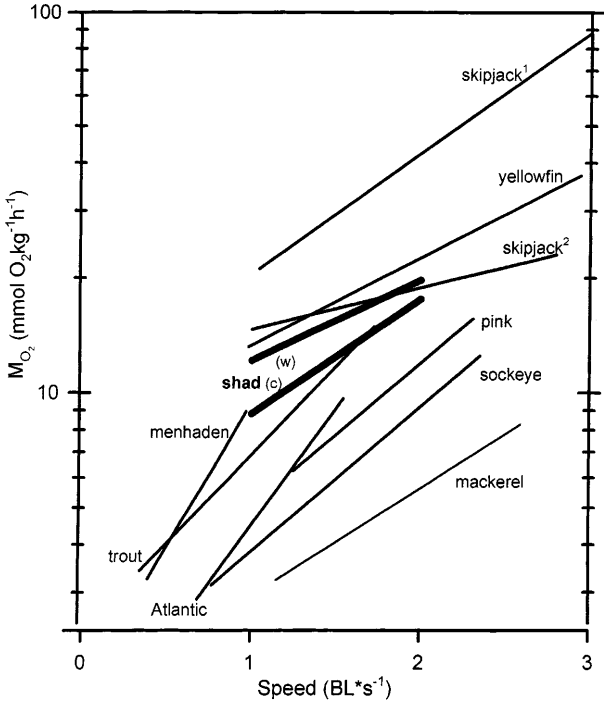

Fig. 4 Linear regressions for log-transformed M_{O_2} (mmol O_2 kg^{-1} h^{-1}) data from adult American shad (shad, 41 cm; (*c*) cold group 13–18 °C, (*w*) warm group 18–23 °C) and previously published data showing the relationship between log-M_{O2} and relative swimming speed (BL s^{-1}). Sockeye salmon (sockeye, *Oncorhynchus nerka*; estimated from Brett and Glass 1973 as modified by Williams, et al. 1986, 20 °C), skipjack tuna (skipjack[1], Dewar and Graham 1994, 25 °C; 48 cm), skipjack tuna (skipjack[2], *Katsuwonus pelamis*; Gooding et al. 1981; 23–24 °C; 48 cm), yellowfin tuna (yellowfin, *Thunnus albacares*; Dewar and Graham 1994; 25 °C; 51 cm), Atlantic menhaden (menhaden, *Brevoortia tyrannus*; Durbin et al. 1981; post-prandial, 20 °C; 29 cm), pink salmon (pink, *Oncorhynchus gorbuscha*, estimated from Williams et al. 1986, 46–49 cm, 15 °C) Atlantic salmon (Atlantic, *Salmo salar*; Lucas et al. 1993; 10 °C; 58 cm), Atlantic mackerel (mackerel, *Scomber scombrus*; Lucas et al. 1993; 10 °C; 34.7 cm) and rainbow trout (trout, *Oncorhynchus mykiss*; Webb 1971; 15 °C; 29 cm)

American shad have a somewhat similar body form to the scombrid species with a narrow caudal peduncle and fairly high aspect ratio tail, although they employ a carangiform swimming mode while tunas are thuniform swimmers (salmonids are sub-carangiform; Webb 1975). Scombrid species and American shad are constantly swimming, pelagic, schooling fishes throughout their entire life history and this similar niche, and its concomitant selective pressures, may have led to parallel evolution of the shallow energy-speed relationship in these groups. This niche characterization might apply to adult salmonids as well, and yet salmonids and American shad utilize different metabolic strategies despite their shared anadromous life history. While salmon have generally been considered highly active, schooling species, they are also known to be stationary during some portions of their life cycles. Parr, in particular, tend to be territorial and spend much of their time near the substrate holding position and defending territories in their natal streams. Adult salmon are also known to maintain position in deep areas in the river in a fairly sedentary manner following upstream migration while they await the spawning season (see Groot and Margolis 1991). This is in stark contrast to American shad that actively school throughout their lives, starting within a few days of hatching (Ross et al. 1992; Limburg 1996). Perhaps the different strategies of energy expenditure in these species have been customized to make energy use as efficient as possible during those life stages when the fish are the most vulnerable: as young juveniles when mortality is high, and as spawning, non-feeding adults when stored energy is at a premium. All stages of the life cycle may therefore be important in determining the evolution of life-long metabolic strategies.

There are a number of specific morphological and physiological characteristics, in addition to endothermy,

present in tuna that have been associated with high metabolic rate and high sustained U (e.g., Wardle 1977) and may be relevant to American shad metabolic rate. These include large gill surface areas (Muir and Hughes 1969), high blood hemoglobin (Hb) levels (Klawe et al. 1963) and large relative amounts of red muscle (Graham et al. 1983). There is no direct information regarding American shad gill area and only limited data for any clupeids. Hughes and Al-Kadhomiy (1988) suggest that during larval and early juvenile stages the gill area of Atlantic herring increases at rates that are similar to rainbow trout (*Oncorhynchus mykiss*). More investigation of clupeid gill morphology and development would be useful. Blood oxygen carrying capacity and Hb content have also been directly related to high aerobic metabolic rates. Hb content in American shad ranges from 10–17 g/dl (J.B.K. Leonard and S.D. McCormick personal observation). Similar Hb levels are found in tuna and other scombroid fishes (Klawe et al. 1963). Red muscle appears highly pigmented in American shad compared to salmonids (J.B.K. Leonard, personal observation) and accounts for approximately 12–15% of total body muscle (J.B.K. Leonard and S.D. McCormick personal observation). In the region of the caudal peduncle, red muscle accounts for as much as 30% of the muscle mass in American shad. This parallels the arrangement of muscle in the ectothermic scombrids *Sardo* and *Scomber* which also have large amounts of red muscle (as much as 30%) concentrated in the caudal region (Greer-Walker and Pull 1975; Graham et al. 1983; McLaughlin and Kramer 1991). In contrast, salmonids have much less red muscle relative to white muscle (J.B.K. Leonard, personal observation). These observations suggest that shad are well supplied with the muscle for the sustained swimming typical of pelagic fishes and the oxygen carrying system to support it.

The swimming metabolic rate is high in migrating adult American shad. This implies that migration upriver is more energetically expensive for this species than for other anadromous fishes such as salmon (Webb 1971; Williams et al. 1986). This cost may well be responsible for the shorter overall migrations seen in this species when compared to salmonids, although anadromous fishes are often not optimally and energetically efficient during their upstream migrations (Bernatchez and Dodson 1987). However, shad may be more efficient migrators through areas of intermediate to high flows (below burst swimming levels) given their greater efficiency at high aerobic swimming speeds.

Recognizing the different metabolic capacities of shad and salmon is important to the sound management of American shad and other anadromous species. Frequently, migratory species management in general, and fish passage design in particular, is based on the salmonid paradigm, regardless of the species of interest. The physiological limitations and energetic demands of swimming vary widely among species. The differing metabolic expenses and patterns incurred by different migratory species should be ascertained and factored into our understanding and management of these species, particularly when evaluating the relative costs of ascending barriers or withstanding delays in migration.

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