

# SWIMMING ENERGETICS OF STRIPED BASS (*MORONE SAXATILIS*) AND BLUEFISH (*POMATOMUS SALTATRIX*): HYDRODYNAMIC CORRELATES OF LOCOMOTION AND GILL VENTILATION

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## SUMMARY

1. Swimming patterns of striped bass and bluefish were monitored using a miniature accelerometer to record instantaneous acceleration and instantaneous deceleration during tail-thrusts over a wide range of swimming speeds. In addition, ventilatory excurrent flow patterns were visualized in swimming striped bass by injecting milk via a buccal catheter.

2. Both species accomplish steady swimming with both symmetric and asymmetric thrusts; other transient swimming patterns were observed as well.

3. Over the transition range from active branchial to ram gill ventilation, no measurable change in forward acceleration amplitude occurred with adoption of ram gill flow in both species; this can only occur if drag does not change over the ventilatory transition.

4. From metabolic measurements and from implications about swimming drag deduced from acceleration amplitude, the cost of active ventilation just prior to adoption of ram gill ventilation was estimated to be 8.1% and 8.4% of total metabolism for striped bass and bluefish respectively.

5. Ventilatory effluent flow patterns during cyclic ventilation in swimming striped bass induce substantial turbulence and probably boundary layer separation. Flow patterns during ram ventilation result in streamlined flow over most of the length of the fish.

6. The results show that transfer from active to branchial to ram gill ventilation provides important hydrodynamic advantages to these fishes at cruising velocities.

## INTRODUCTION

Analysis of the biomechanics and hydrodynamics of fish locomotion is both fascinating and problematic. Many issues crucial to understanding swimming remain unanswered due to complex interactions between fish as flexing hydrofoils and the medium in which they move. One of the most fundamental problems is the resistance incurred by an actively swimming fish. While the body shape of many fishes is

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streamlined, calculation of theoretical drag for an equivalent rigid body by standard hydrodynamic equations reveals large discrepancies with measured values; this is probably due to the movements of swimming fish which change the flow around the body sufficiently to make the rigid body analogy untenable (Lighthill, 1971; Webb, 1975*a*). Experimental studies of swimming drag should consider the dynamic nature of fish locomotion; in recent years some have approached the problems in these terms by rather ingenious methods (Webb, 1971*a, b*; DuBois, Cavagna & Fox, 1975, 1976).

Allied to this basic problem is assessment of the various postulated drag reduction mechanisms used by fishes (reviewed by Bone, 1975). One possible mechanism involves the ventilatory excurrent flow whereby the effluent is added to the boundary layer of a swimming fish to delay or prevent transition from laminar to turbulent conditions (Breder, 1926; Walters, 1962; Gray, 1968). On the basis of a reduction in energy expenditure that occurs simultaneously with the shift from active branchial to ram gill ventilation in swimming striped bass and bluefish, a favourable change in body drag characteristics has been hypothesized (Freadman, 1979).

In this study, a miniature accelerometer was used to monitor instantaneous acceleration and instantaneous deceleration during steady swimming of striped bass and bluefish. From metabolic measurements and from implications about swimming drag deduced from acceleration amplitude, the proportionate cost of cyclic ventilation during locomotion in these fishes was estimated.

#### MATERIALS AND METHODS

Collection and maintenance of striped bass (*Morone saxatilis* Walbaum) and bluefish (*Pomatomus saltatrix* L.) as well as a description of the respirometer used in this study were included in a previous paper (Freadman, 1979).

##### *Ventilatory activity monitoring and accelerometer placement*

Animals were anaesthetized (tricaine methanesulphonate,  $0.1 \text{ g l}^{-1}$ ) and placed on an operating table designed to produce a flow of seawater (with half the initial anaesthetic concentration) over the gills. An electrode pair (0.07 mm diameter, stainless steel, epoxy-coated wire, Johnson Matthey, Ltd) with tips bared and hooked was inserted into the *adductor mandibularis* (left side) to monitor ventilatory activity while the fish was swimming. This electrode pair was skin sutured at the entry point and just anterior to the first dorsal fin.

A single-axis, miniature accelerometer (EGBL-125, Entran Devices, Inc.) was inserted to a depth of 0.75 cm through a midline incision between the first and second dorsal fins and the incision closed with two skin ties, anchoring the unit in place. The sensitive axis of the accelerometer was oriented in the anterior-posterior axis of the fish by a 0.5 cm guide pin cemented to the unit. The device weighed 0.5 g and was 3.56 mm across and 6.86 mm long. The accelerometer is an oil damped, Wheatstone Bridge made of semiconductor strain gauges bonded to a cantilever beam loaded with a mass at its end. With acceleration, the mass moves and bends the beam causing a bridge unbalance, which is proportional to acceleration.

The accelerometer leads (four conductor cable, less than 1.5 mm in diameter) are

Leads to the EMG electrodes were skin sutured just posterior to the second dorsal fin and lap-wound to prevent entanglement with the fish's tail during an experiment.

Animals were transferred to the respirometer for recovery from surgery and were given a 12–14 h acclimation period at 5–10 cm s<sup>-1</sup>. During the second hour of respirometer acclimation, they were subjected to extensive training for steady swimming.

After the acclimation period, flow velocity was increased in steps (usually 4–10 cm s<sup>-1</sup>) and ventilatory activity and instantaneous acceleration and instantaneous deceleration occurring with tail beats during steady swimming were monitored on a two-channel polygraph (Model 79, Grass Instrument Co.) at each velocity.

### *Visualization of branchial excurrent flow*

Swimming velocities below and above those speeds necessary to induce transfer from active branchial to ram gill ventilation were selected to visualize patterns of excurrent flow at the opercular margins of striped bass using skim milk injected into the mouth via an implanted catheter. The buccal catheter (PE 60, Clay Adams) was implanted using procedures described previously (Freadman, 1979). At each velocity, skim milk was slowly injected via the catheter during filming from above the fish with a tripod-mounted Fujica movie camera (Model Single 8, Z8000) at 36 frames s<sup>-1</sup>. This arrangement allowed clear observation of excurrent flow patterns in relation to the 'action' of the opercular doors at swimming speeds bracketing transition velocities for ram ventilation.

## RESULTS

### *Swimming patterns*

During the course of this study, many different patterns of swimming were recorded by use of the accelerometer. All the patterns shown in Fig. 1 were used by both striped bass and bluefish. The 'burst and glide' pattern was observed at the beginning of a swimming bout as imposed swimming velocities were increased. The animals also used this pattern at higher velocities as they would alternate between hard thrusts with gliding and steady swimming. Large single accelerations were recorded at high velocities as fishes contacted the rear grid of the swimming tube with their tails; this behaviour often alternated with steady swimming as well. During steady swimming, the animals relied on three different thrust patterns. Symmetric thrusts were used primarily at slow swimming speeds up to 1 bl s<sup>-1</sup> (body length). Slightly asymmetric thrust patterns were observed at velocities up to about 1.5–2.0 bl s<sup>-1</sup> and very asymmetric thrusts were often used for swimming at higher velocities. It has been suggested that asymmetry in tail motion may aid steering during steady swimming at high velocities (DuBois *et al.* 1975) when the tail-beat frequency reaches 5–6 beats s<sup>-1</sup>.

### *Acceleration amplitude and swimming drag*

Records of forward acceleration of striped bass and bluefish at imposed swimming velocities are shown in Figs 2 and 3. The symmetric, slightly asymmetric and very asymmetric thrust patterns were observed at characteristic velocities in the 8 fish of each species tested.

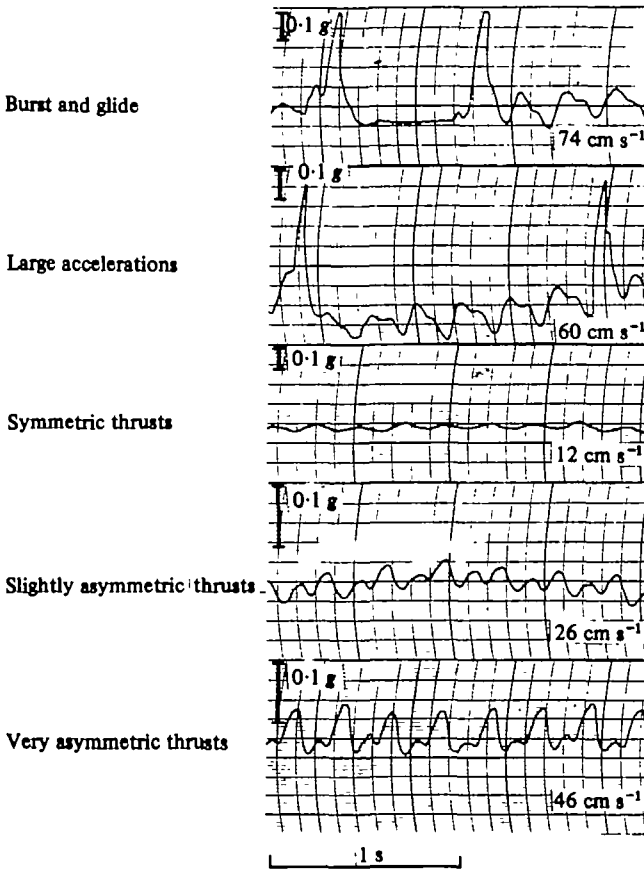


Fig. 1. Swimming patterns recorded from striped bass and bluefish during the course of the study. The top two patterns were recorded from bluefish and the bottom three patterns were recorded from striped bass. All the patterns shown were used by both species but the bottom three were most often characteristic of steady swimming.

The accelerometer records represent the interplay between thrust, drag and mass of the fish. If thrust goes to a minimum at a certain point of the tail cycle, as when the tail reverses direction, then the deceleration observed from an accelerometer record at the moment of tail reversal should be due to drag at that moment. As swimming speed increases, so should deceleration at tail reversal. The minimum thrust/maximum deceleration associated with tail reversal (DuBois & Ogilvy, 1979), and the drag associated with that maximum deceleration probably represents a very large proportion of the total drag. Since the time integral of acceleration equals the time integral of deceleration under steady swimming conditions, the total acceleration/deceleration amplitude will be proportional to drag.

If the drag of a swimming fish varies by a factor of 3-4 times during a body cycle, then the drag during tail reversal is not the same as that during other portions of the tail cycle. Since there is little available information about drag variations during a body cycle, the accelerometer records obtained from striped bass and bluefish i

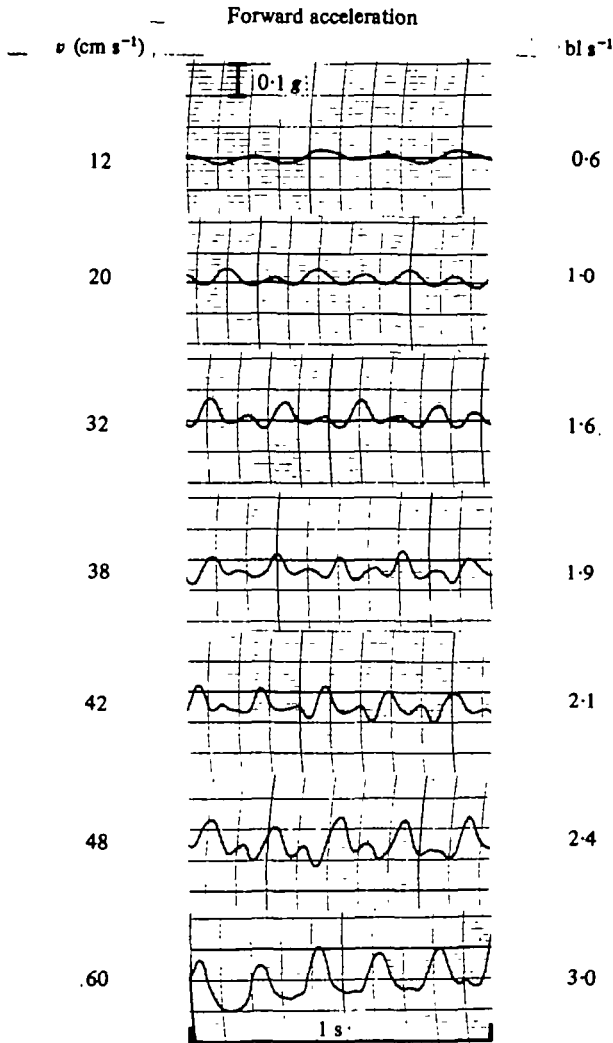


Fig. 2. Record of instantaneous acceleration and instantaneous deceleration of a striped bass (20 cm, T.L.) during steady swimming over a wide range of velocities. The sensitive axis of a miniature accelerometer was oriented in the anterior-posterior axis of the animal.

this study will be treated in a qualitative manner. Swimming drag can increase only if there is an increase in forward acceleration amplitude; in this way, qualitative interpretations about drag are possible.

Forward acceleration amplitude was measured from records of instantaneous acceleration and instantaneous deceleration occurring during five tail-thrust cycles of steady swimming at a particular velocity. For swimming patterns where the peaks of acceleration were unequal, the trough to peak values were measured for each half-cycle and an average acceleration for the velocity calculated.

Results for two striped bass and two bluefish are shown in Table 1. This table also

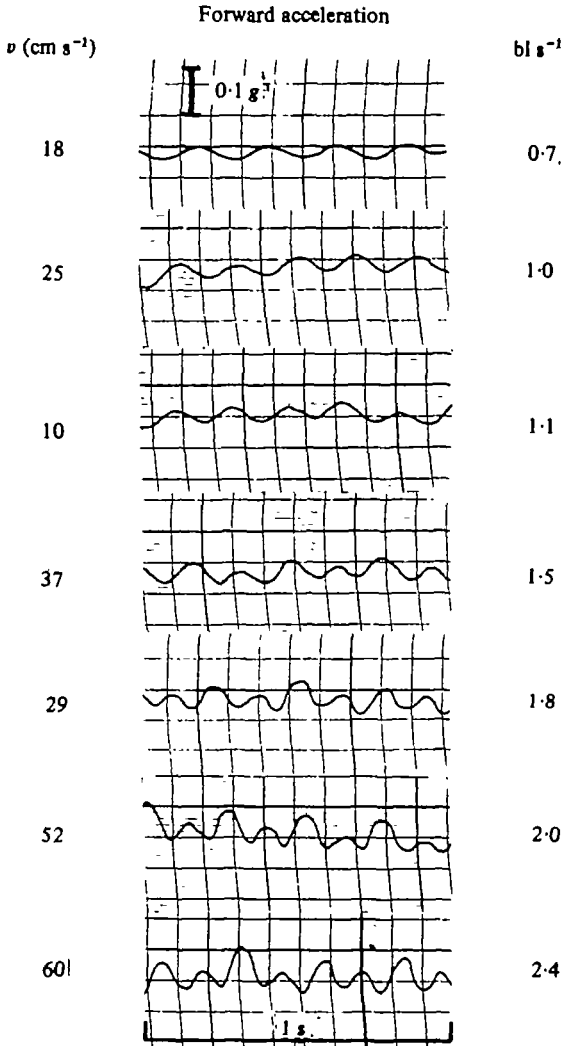


Fig. 3. Record of instantaneous acceleration and instantaneous deceleration of a bluefish (25.4 cm, T.L.) during steady swimming over a wide range of velocities. The sensitive axis of a miniature accelerometer was oriented in the anterior-posterior axis of the animal.

includes other correlates of swimming, including ventilatory mode, forward velocity, tail-beat frequency,  $Re$  (Reynolds Number based on length, Alexander, 1977) and predominant thrust pattern. Just after these fishes adopt the ram mode, the acceleration amplitude is the same as that at the next lowest velocity during which the animals utilize cyclic ventilation. Moreover, at this lowest ram adoption velocity, tail-beat frequency remains the same as well, further suggesting that swimming drag does not increase. These drag relations were not associated with a change in thrust pattern since the animals were using the same slightly asymmetric thrusts for forward locomotion before and after the shift in ventilatory modes. It should also be pointed out that both species adduct and fair the pectoral fins well before the adoption of ram g

Table 1

Fish	Ventilation mode	Forward velocity (cm s <sup>-1</sup> )	TBF (hz)	Re	Thrust pattern	Mean acceleration amplitude (cm s <sup>-2</sup> )
No. 3 Striped bass (25.4 cm, T.L.; 212.33 g)	A	20	2.40	4.32 × 10 <sup>4</sup>	S.	26.59
	A	23	2.80	4.97 × 10 <sup>4</sup>	S.	32.59
	A	26	3.00	5.62 × 10 <sup>4</sup>	S.A.	38.63
	A	33	3.00	7.13 × 10 <sup>4</sup>	S.A.	43.62
	R	39	3.30	8.42 × 10 <sup>4</sup>	S.A.	43.62
	R	41	3.40	8.86 × 10 <sup>4</sup>	V.A.	43.89
	R	49	3.60	1.06 × 10 <sup>5</sup>	V.A.	44.12
	R	55	4.30	1.19 × 10 <sup>5</sup>	V.A.	59.68
	R	63	4.90	1.36 × 10 <sup>5</sup>	V.A.	79.76
No. 5 (25.4 cm, T.L.; 216.65 g)	R	71	5.10	1.53 × 10 <sup>5</sup>	V.A.	88.76
	A	19	2.40	4.10 × 10 <sup>4</sup>	S.	29.95
	A	22	2.80	4.75 × 10 <sup>4</sup>	S.	31.16
	A	26	3.20	5.62 × 10 <sup>4</sup>	S.A.	38.22
	R	33	3.20	7.13 × 10 <sup>4</sup>	S.A.	38.22
	R	37	3.30	7.99 × 10 <sup>4</sup>	V.A.	39.22
	R	41	3.60	8.86 × 10 <sup>4</sup>	V.A.	42.63
	R	44	3.75	9.50 × 10 <sup>4</sup>	V.A.	47.53
	R	49	3.80	1.06 × 10 <sup>5</sup>	V.A.	49.99
No. 1 Bluefish (25.4 cm, T.L.; 225.46 g)	R	51	4.00	1.10 × 10 <sup>5</sup>	V.A.	61.26
	R	55	4.50	1.19 × 10 <sup>5</sup>	V.A.	66.62
	R	60	4.90	1.30 × 10 <sup>5</sup>	V.A.	70.57
	R	63	4.95	1.36 × 10 <sup>5</sup>	V.A.	82.80
	R	69	5.00	1.49 × 10 <sup>5</sup>	V.A.	89.75
	A	12	1.55	2.59 × 10 <sup>4</sup>	S.	20.99
	A	20	2.16	4.31 × 10 <sup>4</sup>	S.A.	27.99
	R	27	2.16	5.83 × 10 <sup>4</sup>	S.A.	27.99
	R	30	2.20	6.48 × 10 <sup>4</sup>	S.A.	29.38
No. 5 (22.9 cm, T.L.; 174.59 g)	R	35	2.45	7.56 × 10 <sup>4</sup>	S.A.	32.90
	R	40	3.00	8.64 × 10 <sup>4</sup>	S.A.	37.07
	R	45	3.90	9.72 × 10 <sup>4</sup>	V.A.	40.60
	R	54	4.30	1.17 × 10 <sup>5</sup>	V.A.	46.21
	R	60	4.60	1.30 × 10 <sup>5</sup>	V.A.	53.90
	R	65	5.00	1.40 × 10 <sup>5</sup>	V.A.	59.51
	R	70	5.30	1.51 × 10 <sup>5</sup>	V.A.	63.68
	A	13	1.58	2.53 × 10 <sup>4</sup>	S.	13.98
	A	20	2.20	3.89 × 10 <sup>4</sup>	S.A.	28.01
No. 5 (22.9 cm, T.L.; 174.59 g)	R	28	2.20	5.44 × 10 <sup>4</sup>	S.A.	28.01
	R	35	2.40	6.80 × 10 <sup>4</sup>	S.A.	30.09
	R	40	2.90	7.78 × 10 <sup>4</sup>	V.A.	34.30
	R	47	3.70	9.14 × 10 <sup>4</sup>	V.A.	40.58
	R	55	4.20	1.07 × 10 <sup>5</sup>	V.A.	46.20
	R	63	4.85	1.22 × 10 <sup>5</sup>	V.A.	53.21
	R	70	5.20	1.36 × 10 <sup>5</sup>	V.A.	60.90

Locomotor correlates for two striped bass and two bluefish during steady swimming. Included are ventilation mode (A = active branchial; R = ram gill ventilation), forward velocity, tail-beat frequency, calculated Reynolds number, predominant thrust pattern (S. = symmetric, S.A. = slightly asymmetric, V.A. = very asymmetric) and forward acceleration amplitude estimated from a record of instantaneous acceleration and instantaneous deceleration during a body cycle at various swimming velocities.

ventilation. Therefore, such changes in 'shape' cannot affect drag at ram adoption speeds. In addition, the  $Re$  value at which a fish adopts the ram mode is well below the laminar to turbulent transition range of  $5 \times 10^5$ , so this correlate of locomotion does not in itself predict any gross flow changes which would explain the results.

The acceleration amplitude after the mode shift in ventilation indicates that swimming drag increases at a slow rate over a 10–14 cm s<sup>-1</sup> range in velocity but at higher swimming speeds increases at a rate similar to that observed when the animals used active ventilation.

#### *Ventilatory excurrent flow patterns*

Skim milk injected into the buccal cavity of resting and swimming striped bass ( $N = 7$ ) and simultaneous filming of the ventilatory effluent flow patterns along the body gave qualitative indications of these flow patterns. While a striped bass was ventilating slowly at rest, the effluent pulsed out only with abduction of the opercular doors. Upon exiting, the effluent formed dense, turbulent clouds at the margins of the doors and posteriorly to about one-half of the length of the fish. At very slow swimming speeds, the effluent flow pattern was much the same as during rest. At higher, sub-ram-supporting speeds, the flow pattern was turbulent at the exit point and posteriorly to about three quarters of the length of the fish. The pulsing pattern was very evident in that no milky flow was observed until the opercula were abducted.

Upon adoption of ram gill ventilation, the effluent flow pattern changed dramatically. Milk injected into the mouth to simulate ventilatory flow exited from the opercular chambers, 'hugged' the body to the caudal peduncle without inducing turbulence and was distributed in the water around the 'sweeping' tail.

The same results were obtained whether the milk was injected in slugs or steadily. The milk did not interfere with ventilatory movements in that animals did not cough with milk injection into the buccal cavity.

#### DISCUSSION

Many fishes swim by oscillation of the body and tail or the tail alone which produces a backward thrust upon the water while the animal is propelled forward. Other fishes use one or another sets of fins for propulsive strokes as in pectoral fin propulsion of the surf perch, *Cymatogaster aggregata* (Webb, 1975*b, c*) and the angelfish, *Pterophyllum eimekei* (Blake, 1979). Regardless of the means of propulsion, thrust is greater than drag during acceleration and the drag exceeds thrust during deceleration. The kinetic energy given to the fish during a thrust carries the animal forward but drag slows the animal down; the next propulsive stroke provides enough energy to overcome the kinetic energy lost to drag previously. For freely swimming fishes, optimal cruising speeds at which these biomechanic-hydrodynamic interactions occur are probably a function of a tail-beat frequency that minimizes inertial losses and at the same time balances forward velocity to levels of sustainable expenditure by the swimming musculature for maximum economy and range.

The miniature accelerometer used to estimate qualitative drag relations is a dynamic method and clearly shows that striped bass and bluefish rely on asymmetric pattern



thrust during steady swimming. The accelerometer was carefully implanted, correct alignment of the unit in fishes was ascertained in water by moving anaesthetized animals in various directions by hand and sometimes the records of forward acceleration changed from symmetric to asymmetric and back again at the same velocity, indicating that the swimming pattern of the fish had changed. These asymmetric patterns have also been recorded from larger bluefish as documented by DuBois *et al.* (1975, 1976).

Weih's (1961) formulated a model predicting the energetic advantages of alternating periods of acceleration with gliding for fishes. The model predicts this swimming pattern would result in energetic savings of 50% in swimming a given distance or increase the range by a factor of nearly three compared to swimming at constant velocity. For striped bass and bluefish, this pattern was usually seen at the beginning of an increment in velocity change or later in a swimming bout at high velocities and was not used for estimation of swimming drag. Since use of the burst and glide pattern was not sustained for long periods with imposed water velocities, it was not practical to make metabolic measurements to test the Weih's model.

The qualitative drag characteristics of active and ram ventilating striped bass and bluefish documented in this study provide interesting information. From accelerometer records over the transition from active branchial to ram gill ventilation, there is no change in acceleration amplitude. This can only occur if there is no change in drag over this transition. It appears that swimming drag does not increase just after the animals switch to ram flow. Over the next 10–14 cm s<sup>-1</sup> range of increasing velocity, drag increases at a slow rate but at higher velocities drag increases at a rate similar to that estimated during active ventilation. At these higher ram-supporting velocities, ventilation volume increases with increasing swimming speed because a higher ram pressure is developed. The result is a parallel increase in gill resistance (Brown & Muir, 1970) and a rise in the cost of locomotion (Freadman, 1979).

Why is there no change in drag over a swimming speed range of 30–44 cm s<sup>-1</sup> after adopting ram ventilation? The answer is indicated by flow visualization. While animals are at rest, active ventilation causes turbulence but does not cause hydrodynamic flow problems. However when swimming at low and intermediate velocities using active ventilation, pulses of ventilatory effluent water directed into the boundary layer create large disturbances which induce flow separation and drag. Upon adoption of ram ventilation in striped bass, the ventilatory current stream stabilizes flow along the body, as shown by the absence of any disturbances. This should reduce frictional drag of swimming fishes. Similar observations have been reported by Aleyev (1977). Therefore, adoption of ram ventilation results in boundary flow stabilization, explaining the reduction in drag in spite of increasing swimming speed. This may be surprising, for while *Re* predicts boundary layer flow conditions, a swimming, oscillating fish may change the flow around the body with secondary flows generated by lateral movements and the gill excurrent stream.

An estimate of the cost of active ventilation during swimming in striped bass and bluefish can be made using the metabolic and hydrodynamic data at the ventilatory transition. The metabolic characteristics of the transition from cyclic to ram ventilation of these fishes has been presented in a previous paper (Freadman, 1979). As these

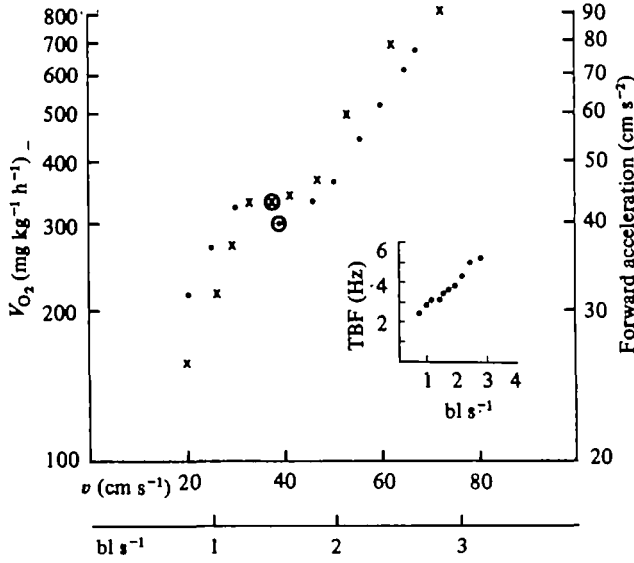


Fig. 4. Composite relationship between oxygen uptake (·), forward acceleration amplitude (x), swimming velocity and tail-beat frequency (inset) of a striped bass (Fish 3, Table 1) at 15 °C over the transition from active branchial to ram gill ventilation. The circles around the data points at 38  $\text{cm s}^{-1}$  represent the velocity at which ram ventilation was adopted.

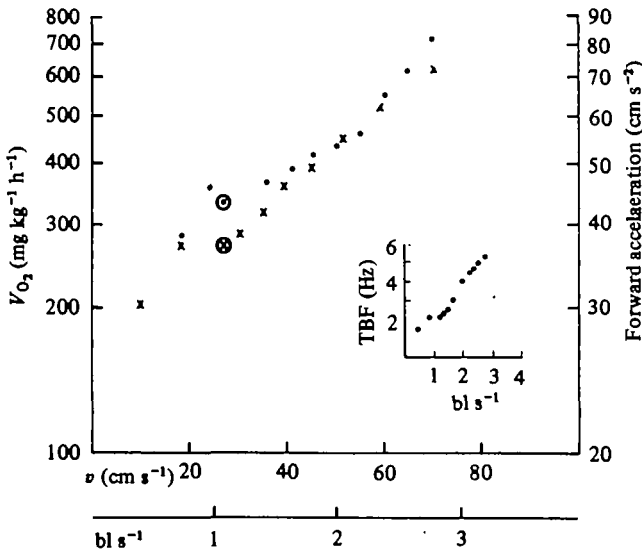


Fig. 5. Composite relationship between oxygen uptake (·), forward acceleration amplitude (x), swimming velocity and tail-beat frequency (inset) of a bluefish (Fish 1, Table 1) at 15 °C over the transition from active branchial to ram gill ventilation. The circled data points at 27  $\text{cm s}^{-1}$  represent the velocity at which the animals adopted ram gill ventilation.

two species switch from ram flow, there is a small but consistent reduction in oxygen uptake. Just after the transition is completed, swimming drag remains the same as that measured at the highest velocity at which the animals used active ventilation, probably due to improved boundary layer characteristics. Figs 4 and 5 represent composite graphs of the relevant data for oxygen uptake, forward acceleration amplitude, swimming velocity and tail-beat frequency over the ventilatory transition range of striped bass and bluefish respectively. Oxygen uptake of animals, fitted with the accelerometer and ventilatory EMG electrodes and subjected to the added drag of the cable, was 9–15% above values for animals without such implants; therefore the rates of oxygen uptake shown in these figures are for animals of the same weight without the devices. These animals adopted ram ventilation at essentially the same velocity as those fitted with the implants. Since the drop in energy expenditure with the shift in ventilatory modes is not associated with a decrease in drag, it should reflect the cost of rhythmic ventilation in swimming striped bass and bluefish just prior to adoption of ram ventilation. This cost averages 8.1% of total oxygen uptake for striped bass ( $N = 10$ , s.e. = 1.2) and 8.4% of total oxygen uptake for bluefish ( $N = 10$ , s.e. = 1.1). These are costs quite reasonable when compared with available estimates (Cameron & Cech, 1970). The cost of active ventilation at rest and slow swimming speeds cannot be estimated from these data. However if swimming does augment the work of ventilation (Hughes, 1960; Roberts, 1975), then the cost of ventilation could reach 15% of total oxygen uptake.

Brown & Muir (1970) have provided an interesting analysis of the cost of ram ventilation for skipjack tuna. This was done by calculation of head pressure losses (buccal, opercular cavities and gill resistance) at a swimming velocity of 66 cm s<sup>-1</sup>. The pressure losses were then related to total swimming drag and translated to metabolic expenditures. The largest component of head pressure losses is the pressure drop incurred in the lamellar channels, which they estimated to be 800 dynes cm<sup>-2</sup> for skipjack tuna. The corresponding trans-gill pressure for ram ventilation in striped bass is 0.5 cm H<sub>2</sub>O or 490 dynes cm<sup>-2</sup> (Freadman, 1979). This suggests that head losses in ram ventilating striped bass may be lower than that for skipjack tuna and that translation of the gill drag into metabolic expenditure may be lower than the cost of 1–3% of total metabolism for ram ventilation indicated by Brown & Muir. For striped bass and bluefish swimming at ram-supporting velocities, the compensatory metabolic cost for the swimming musculature to overcome gill resistance is probably less than would be the cost of active ventilation. Rhythmic pumping for ventilatory flow entails contracting branchial muscles, inertial losses from changing water velocity in the branchial cavity, variation of gill excurrent flow, and alteration in the cross-sectional area of the head due to movements of the mouth and opercular doors. Consideration of these factors suggests the use of cyclic ventilation at intermediate and high swimming velocities is less efficient than adoption of ram gill ventilation. For fishes which continue to rely on active ventilation over their entire sustainable velocity range, the magnitude of the drag incurred by this mode is unknown.

Use of ram assisted ventilation, and the partial energetic advantage shown here, are undoubtedly widely employed among fish. For obligate ram ventilators such as lnas cruising at velocities sufficient for generation of dynamic lift (Magnuson, 1970),

ram ventilation probably improves their drag characteristics as flexing hydrofoils as for striped bass and bluefish. The shark sucker, *Remora remora*, attached to swimming hosts relies on ram ventilation (Muir & Buckley, 1967). Pectoral fin locomotion in *Cymatogaster aggregata* makes a significant contribution to ventilation during swimming, since the power stroke of these fins (adduction) is synchronized with opening of the mouth during active ventilation (Webb, 1975b).

Fast and efficient swimming among fishes presumably is a selective advantage for predator escape and food capture. Some fishes became bottom dwellers and intermittent swimmers relying on cyclic ventilation for respiratory requirements. Other more continuous swimmers generate sufficient anterior pressure between the mouth and opercular door margins to drive ventilatory flow without rhythmic pumping. Thus it is speculated that development of more or less continuous use of the ram mode of gill ventilation evolved with niche and habitat selection as a means to minimize the cost of driving water across the gills.

This work is a portion of a dissertation submitted in partial fulfillment of the requirements for the degree Doctor of Philosophy at the University of Massachusetts, Amherst. I wish to thank Dr J. L. Roberts, my major professor, for advice, encouragement and inspiration throughout the study. Special thanks are extended to Dr J. E. Hanks, Director (NMFS, Milford, Conn.) and the physioecology group at that lab for use of the respirometers and bench space which made this study possible. Dr A. B. DuBois and Mr C. S. Ogilvy (John B. Pierce Foundation and Yale University, New Haven, Conn.) provided stimulating discussions, loaned me miniature accelerometers and reviewed a manuscript for this paper. Dr P. Webb also reviewed a manuscript and offered valuable comments. Animals used in this study were obtained through the courtesy of: C. Wheeler and H. Ruschky (NMFS, Woods Hole, Mass.), D. Westin and B. Rogers (URI, Narragansett, Rhode Island) and B. Young (N.Y.S. Dept of Environ. Conser., Stony Brook, N.Y.).

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