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SWIMMING ENERGETICS OF STRIPED BASS (*MORONE SAXATILIS*) AND BLUEFISH (*POMATOMUS SALTATRIX*): GILL VENTILATION AND SWIMMING METABOLISM

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SUMMARY

1. Striped bass and bluefish use cyclic ventilatory movements to accomplish gas exchange at rest and slow swimming speeds, whereas at intermediate and high velocities, both species routinely shift to ram gill ventilation.

2. Metabolic characteristics of the shift in respiratory behaviour indicate that as an animal adopts the ram mode, energy expenditure departs from an exponential relationship and increases at a shallow rate over the next 15 cm. s^{-1} range in speed. At higher, ram-supporting velocities, oxygen uptake increases once again at an exponential rate.

3. Similar determinations of oxygen uptake at imposed swimming velocities in hatchery-raised rainbow trout reveal an exponential relationship over the entire swimming range. Trout actively ventilate their gills over this velocity range as well.

4. In striped bass, the requisite trans-gill pressure for ram ventilation, as developed between the mouth and opercular door margins, is about 0·5 cm H_2O.

5. Critical swimming velocities for striped bass are 2·9–3·3 bl.s^{-1} while bluefish can maintain station at 4·0–4·6 bl.s^{-1}.

6. The adoption of ram gill ventilation is a velocity-dependent phenomenon over the size-range tested.

7. Transfer of the work load of ventilation from the branchial to the swimming musculature results in substantial metabolic savings well within the cruising ranges of striped bass and bluefish. The savings probably accrue from cessation of rhythmic pumping by the branchial musculature and a change in overall body drag at ram-supporting swimming speeds.

INTRODUCTION

Patterns of gill ventilation in fishes involve mechanisms which result in an unidirectional flow of water over the respiratory surface for gas exchange. Most freshwater, demersal and near-shore fishes rely exclusively on the cyclic operation of the buccal and opercular pumps, the mechanics of which have been extensively studied (Hughes & Shelton, 1958; Hughes, 1960; Saunders, 1961). This active and rhythmic

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mode of ventilation is powered by contractions of antagonistic groups of branchial muscles (Ballintijn & Hughes, 1965; Ballintijn, 1969), but the proportionate cost of gill irrigation at rest and during swimming is not known precisely (White, 1978). Although the ventilation of rainbow trout increases by 30% during moderate exercise (Stevens & Randall, 1967; Webb, 1971), the increase is probably not proportional to swimming effort. Energy expenditure for cyclic ventilation probably does not maintain a constant ratio with total metabolism at different swimming speeds, since other factors related to the act of swimming may reduce the energy requirements of the respiratory pumps. In animals which utilize active ventilation over their entire swimming velocity range, the magnitude of the modulation is uncertain.

Other fishes reflexively shift to an alternative mode of ventilation which eliminates the work requirements of the branchial pumps and is entirely dependent on reaching a critical velocity of forward locomotion. Many near-shore, midwater and pelagic fishes whose life styles include cruise and continuous swimming at moderate to high velocities routinely convert from active branchial to ram gill ventilation (= open-mouth swimming, = ram-jet ventilation) when their forward velocity reaches about 1·5 body lengths/sec ($bl.s^{-1}$) (Roberts, 1975*a*, 1979).

Although the kinematic viscosity (ratio of viscosity to density) of air is 14 times that of water (Alexander, 1968), water has a much lower solubility for oxygen (Randall, 1970). Inertial energy losses occurring during cyclic ventilation from pulsatile ventilatory flow off-set the usually favourable kinematic viscosity of water compared to other liquids. Therefore switching to ram ventilation should be advantageous in terms of metabolic efficiency.

The present study deals with determinations of swimming metabolism of two facultative ram ventilators, striped bass and bluefish, in relation to mode of gill ventilation. In addition, data are presented on the velocity *v*. size dependence for ram adoption. The results demonstrate and characterize energetic advantages in the transfer of ventilatory work from the branchial to the swimming musculature.

MATERIALS AND METHODS

Animal procurement and maintenance

Striped bass (*Morone saxatilis* Walbaum; Percichthyidae) and bluefish (*Pomatomus saltatrix* L.; Pomatomidae) were obtained from waters around Milford, Connecticut, Woods Hole, Massachusetts, Narragansett, Rhode Island and Manor Haven Harbor, Long Island Sound, and transported in aerated coolers to the National Marine Fisheries Laboratory, Milford, Connecticut. Animals were maintained in kilolitre tanks continuously supplied with sand-filtered sea water (25–27 ‰) at 15 °C with ambient water or by mixing ambient water with either chilled or heated sea water, depending on the season. Water was added at one end of the tank resulting in a gentle current in which the fish swam. They were exposed to L:D regimes of 14:10 h and fed chopped clam and mackerel every other day.

Rainbow trout (*Salmo gairdneri* Richardson; Salmonidae) were obtained from the Sunderland State Hatchery, Sunderland, Massachusetts, and The Fish and Water Life Division of the Department of Environmental Protection, State of Connecticut,

Kensington, Connecticut. Animals were maintained (at NMFS) in 300 l tanks continuously supplied with well water at 15 °C. Trout were fed commercial 'trout pellets' every other day during holding periods.

Animals were not fed for 24–36 h prior to experimentation. Survival and health during holding periods of several months was excellent.

Swimming apparatus

A Brett-type swimming respirometer (Brett, 1964) was used for enforced swimming at controlled velocities for the various types of experiments. The stainless-steel respirometer (69·5 l volume) incorporated a cylindrical acrylic fish chamber (16·2 cm bore) with upstream and downstream honeycomb grids to confine the animals to the swimming tube. A centrifugal pump driven by a variable speed 3 H.P. motor produced flow velocities in excess of 200 $cm.s^{-1}$, and temperature was controlled (within 0·2 °C) by refrigerant flow through a counter-current heat exchanger (30·48 m coiled copper tubing) located on the return flow tube of the respirometer. Microturbulent flow with a rectilinear profile was maintained by three nylon mesh screens positioned at the upstream entry to the swimming tube. An Annubar Flowmeter (Ellison Instruments), located in the return flow tube of the respirometer was calibrated with both an impeller knotmeter (Marine Advisers, Inc., Model B-7C) and a movable pitot tube positioned in the fish chamber to measure the pressure profile. Plexiglass 'boxes' with removable flat covers were fitted around the oval-cut access ports of the swimming tube to allow fast debubbling and to provide ports for an oxygen electrode, temperature probe and exit holes for electrode leads and catheters. Black tape was placed on the bottom and sides of an upstream portion of the swimming tube to serve as a visual-motor band which improved station-holding ability of the animals while swimming.

The maximum cross-sectional area of the fish used generally occupied less than 7% of the cross-sectional area of the swimming tube. In a few cases where the '10% rule' was exceeded, velocity corrections were made for solid blocking as described by Webb (1975).

Electrode implants for ventilatory and cardiac activity

Insertion of indwelling electrode pairs (0·07 mm diameter, stainless steel, epoxy-coated wire, Johnson Matthey, Ltd) for recording ventilatory and cardiac activity was accomplished using surgical and implantation techniques described in detail by Sutterlin (1969) and Roberts (1975*a*). Animals were anaesthetized (tricaine methanesulphonate, 0·1 $g.l^{-1}$) and placed on an operating table designed to produce a flow of sea water with one-half the initial anaesthetic concentration over the gills so that bipolar electrodes could be inserted in one of the ventilatory muscles (usually the *adductor mandibularis*) and near the heart (pericardial space). Implants were skin-sutured at the entry point and dorsally in two places (just anterior and posterior to the first dorsal fin) to prevent entanglement during swimming activity.

Oxygen uptake during swimming

Individual animals were placed in the respirometer and allowed to recover from handling and surgery for 13–16 h at a flow velocity of 4–6 $cm.s^{-1}$. Most fish began to swim against this slow current within 30 min of recovery. During the second hour they

were trained to swim over a wide range of velocities (0–80 cm.s^{-1} flow rate). Those fish which exhibited erratic swimming behaviour and failed to maintain station during training were not used for experimentation. Oxygen uptake was measured at increasing velocity increments (Brett, 1964). During each 30–40 min swimming bout at a specific swimming speed, the oxygen depletion rate (rate of oxygen uptake) was monitored over a terminal 15 min period, after shut-off of the incoming aerated water supply, with a Fieldlab Oxygen Analyser (Beckman Instruments, Inc.). Oxygen content of the water was maintained above 85% saturation by periodic flushing with aerated water. Increments of flow velocity were designed to allow determinations of oxygen uptake at several swimming speeds below and above ram adoption velocities. At each velocity, ventilatory and cardiac activity were recorded using a multichannel RB Dynograph (Beckman Instruments, Inc.). The same experimental protocol for oxygen uptake rates was used for animals without electrode implants while ventilatory activity was monitored through a one-way mirror; these animals were also acclimated to the respirometer for 13–16 h. The swimming tube was covered with white towelling during the acclimation and experimental periods to reduce external visual stimuli.

Buccal and opercular pressures

Buccal and opercular pressures (pre- and post-branchial) in swimming striped bass were detected via implanted catheters (PE 60, Clay Adams). Two catheters, flared at one end, were inserted into small holes drilled in the buccal cavity dorsally at the mid-line and through a similar hole in the left opercular door midway on the side of the fish. Short, tight-fitting 'collars' formed from PE 190 tubing were slid over the catheters to the skin exit point to insure retention of the flared ends of the catheters against the cavity wall. Catheters were skin-stitched in two places dorsally, led out of the swimming tube and connected to a differential pressure transducer (Hewlett Packard, Sanborn, Model 268B) through a 'plumbing' arrangement similar to that used by Hughes & Roberts (1970). Miniature 3-way valves allowed rapid switching of pressure detection from the pre- or post-branchial catheters, a bath reference (ambient pressure), a calibration manometer and the mean differential pressure (pre-branchial minus post-branchial). These pressure waveforms were monitored with the RB Dynograph using an LVDT coupler (for use with the linear transformer transducers, Sanborn 268B).

Maximum sustainable swimming speeds

Animals were lightly anaesthetized (tricaine methanesulphonate, 0·1 g.l^{-1}), placed in the respirometer for a training and 12–14 h acclimation procedure after which flow was increased in 6 cm.s^{-1} increments until the fish was exhausted. The time to exhaustion at the highest swimming velocity was recorded and the critical swimming speed calculated by adjustment of the last velocity increment in proportion to the length of time which the animals maintained station after that velocity was reached (Brett, 1964). Striped bass and bluefish were subject to 30 and 45 min test periods at each swimming velocity in different experiments.

RESULTS

Gill ventilation and oxygen uptake during swimming

Striped bass and bluefish are facultative ram ventilators (Roberts, 1975*a*) utilizing branchial pumps at rest and at low swimming speeds and routinely relying on ram gill ventilation at moderate and high velocities (Fig. 1). As swimming velocity increases

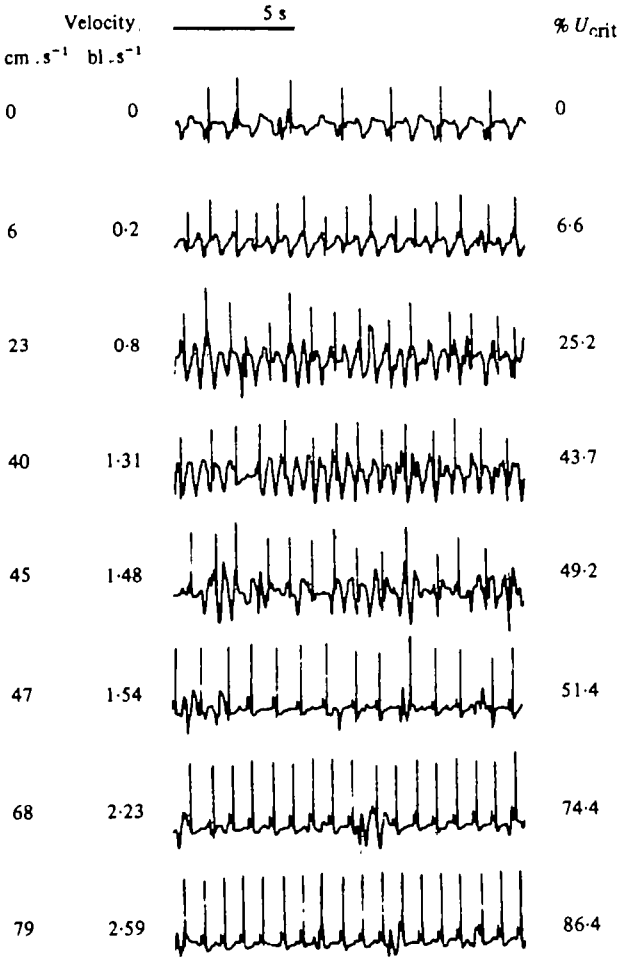

Fig. 1. Ventilatory (slow wave, adductor mandibularis, left side) and superimposed cardiac events in a striped bass (28·80 cm, s.l.) at rest and at imposed swimming speeds to and above ram supporting velocities. % U_{crit} refers to percentage of maximum sustainable swimming velocity.

from rest, ventilatory frequency and amplitude increase but not proportionately with activity. At intermediate velocities, active ventilatory movements are suppressed; small mouth gapes and opercular door slits are maintained and only occasional 'coughs' are evident, indicating the adoption of ram ventilation.

If the transition from cyclic to ram ventilation has metabolic consequences, this should be reflected in oxygen-uptake and swimming-activity experiments. The change

in oxygen uptake with swimming velocity in relation to mode of gill ventilation for a individual striped bass and bluefish is shown in Figs. 2 and 3. Oxygen uptake increases exponentially as the animals utilize cyclic ventilatory movements but when the shift to ram ventilation occurs, this event is always accompanied by a small drop in energy expenditure. Over the next 15 cm.s^{-1} velocity increase, oxygen uptake rises at a shal-

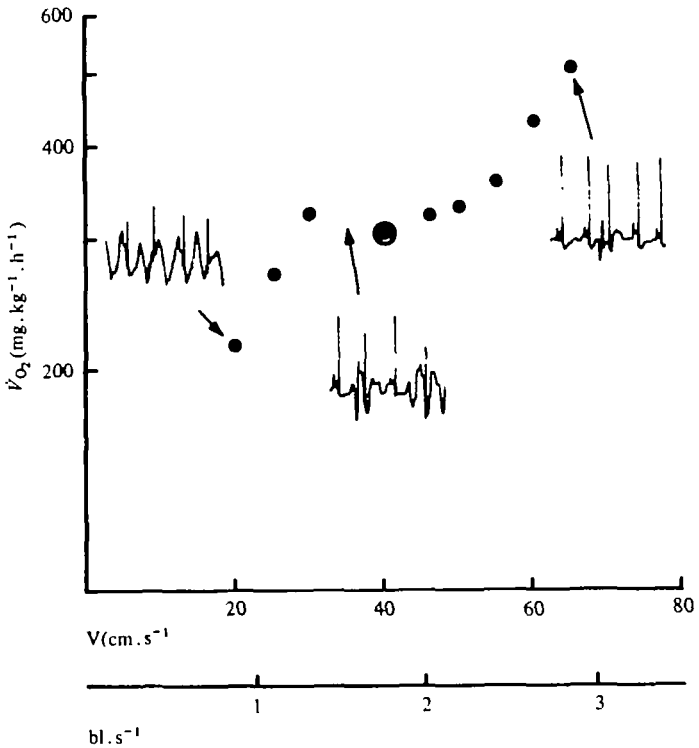

Fig. 2. Oxygen uptake of a striped bass (22·86 cm, s.l., 220·5 g) at enforced swimming velocities in relation to mode of gill ventilation at 15 °C. The circled value at 40 cm.s^{-1} indicates oxygen uptake at a velocity just above adoption of ram gill ventilation. Insets are combined ventilatory and cardiac events at 22, 35 and 65 cm.s^{-1}.

low rate and eventually the animals reach a speed at which energy expenditure increases exponentially once again. In ten replicate experiments with each species, oxygen uptake was never found to depart from an exponential relationship until the animals adopted ram gill ventilation. Animals tested over the same range of swimming velocities without electrode implants to monitor ventilatory activity showed the same relationship of oxygen uptake and swimming speed at characteristic transition velocities between rhythmic and ram modes of ventilation.

The results do not reflect effects of restless behaviour at lower swimming velocities for several reasons. Animals were well trained and subject to a long adjustment period to the swimming tunnel. They were observed visually during an experiment for erratic swimming and readily adopted ram ventilation without thrashing or darting. Furthermore, similar experiments with rainbow trout (N = 7) using the same apparatus and experimental protocol reveal an exponential relationship between oxygen

uptake and swimming effort (Fig. 4) with values of expenditure essentially the same as those determined by Rao (1968). Hatchery reared trout were used for comparison since they rely on active branchial ventilation over their entire sustainable swimming speed range. Long-term, hatchery selection of non-anadromous *S. gairdneri* has resulted in a race of fish that will not resort to the ram transition except with periods of training for high-speed stream swimming (Roberts, 1975*b*).

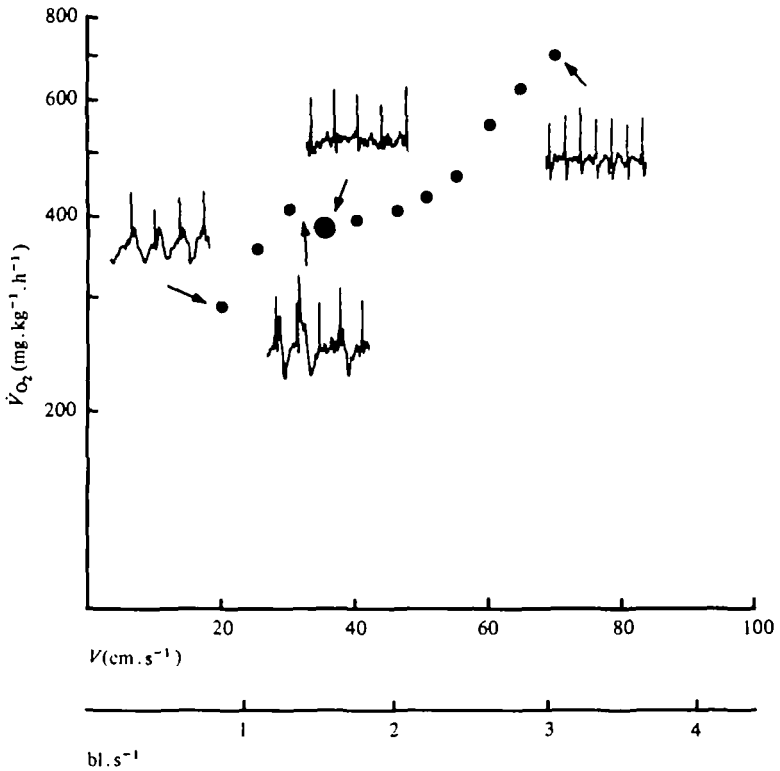

Fig. 3. Oxygen uptake of a bluefish (22·86 cm, s.l., 217·2 g) at enforced swimming velocities at 15 °C. The circled value at 35 cm.s^{-1} indicates oxygen uptake at a velocity just above that required for ram ventilation. Insets are combined ventilatory and cardiac activity at 20, 32, 35 and 70 cm.s^{-1}.

Respiratory pump pressures during swimming

The minimum requisite pressure developed between the mouth and the opercular door openings for ram ventilation has been estimated to be 1·8 cm water for *Remora remora* (Muir & Buckley, 1970) and 0·8 cm water for skipjack tuna (Brown & Muir, 1970). Buccal, opercular and differential pressures measured during active and ram ventilation in striped bass ($N = 5$) indicate the requisite trans-gill pressure to be 0·5 cm water (Fig. 5), a value in agreement with that of an engineering model based on an impact-reverse pitot tube proposed by Roberts (1975*a*). During active ventilation the relative contribution of the two pumps appears to be equal, judged by analysis of areas of the corresponding phases of the differential pressure record. Pressure fluctuations at ram supporting velocities unavoidably appear in the record. These are directly

related to cyclic tail movements which produce side-to-side head movements from body recoil which thus bend the catheters and raise or lower the pressure and induce lateral, inertial pressure changes in the ventilatory stream. That is, because of the high density of the respiratory stream, pressure changes also reflect the side-to-side acceler-

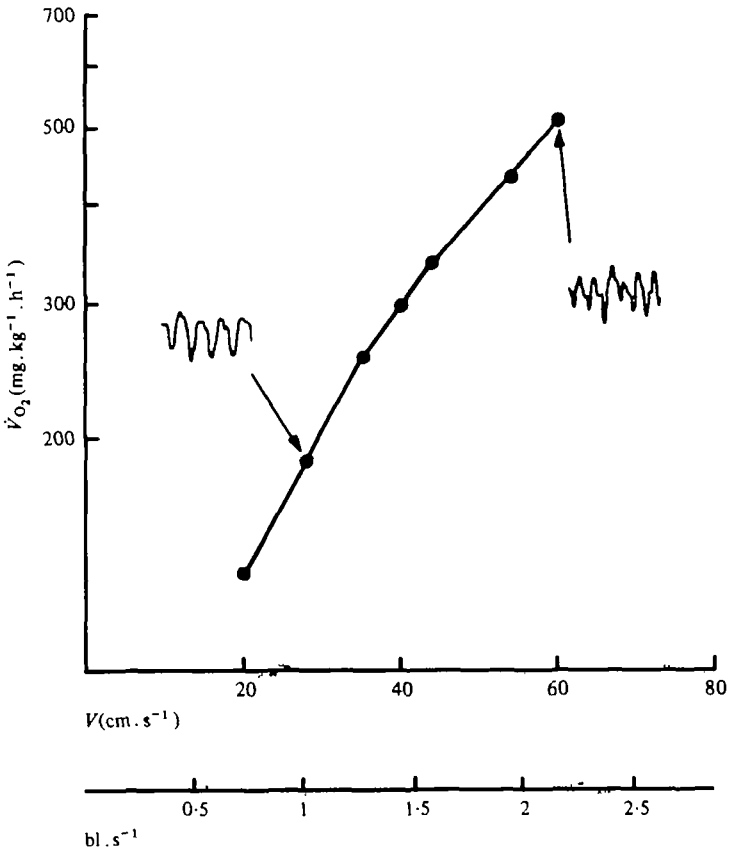

Fig. 4. Oxygen uptake of a rainbow trout (27·94 cm, s.l., 309·7 g) at imposed swimming velocities at 15 °C. The insets of ventilatory activity at 28 and 60 cm.s^{-1} indicate that the animal utilizes active branchial ventilation over its entire sustainable swimming range.

ation changes in the ventilatory stream. Some low amplitude anterior body movements are expected in striped bass since they swim in the subcarangiform mode. Similar oscillations are evident in records of buccal pressure during ram ventilation in sockeye salmon (Smith, Brett & Davis, 1967).

The ventilation pressure differential of 0·5 cm water is similar to the values found in different teleosts at rest (Hughes, 1960), but at rest buccal and opercular pumps generate the pressure, whereas during ram gill ventilation the swimming musculature takes over this role.

Velocity v. *size dependence for ram adoption*

The adoption of ram ventilation occurs as a swimming fish accelerates to a velocity at which the differential pressure developed between the mouth and gill cover margins rises enough to overcome the gill curtain resistance. To test the hypothesis that the transition is a velocity-dependent phenomenon, striped bass and bluefish of many

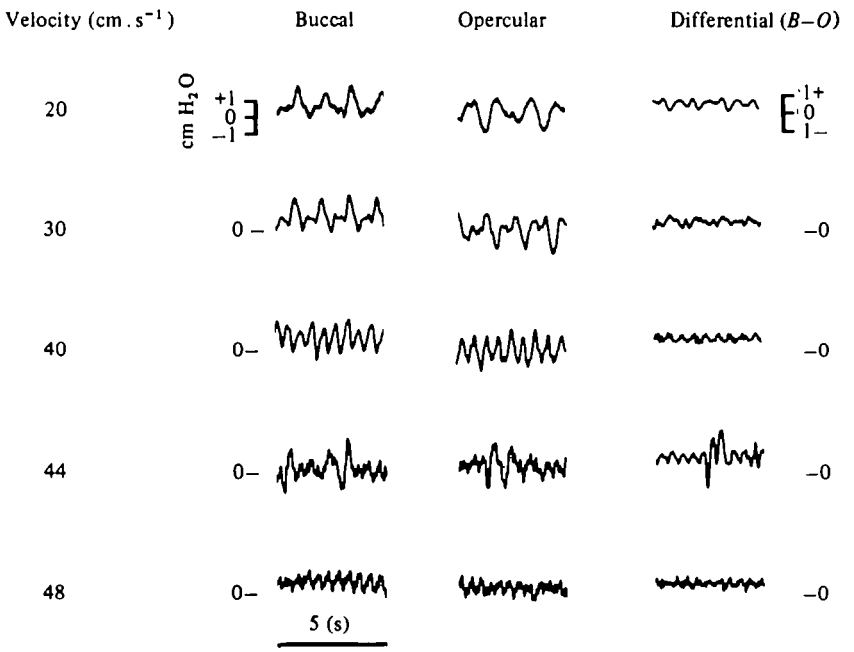

Fig. 5. Sequentially recorded buccal, opercular and differential (buccal minus opercular) pressure waveforms from a striped bass during active and ram ventilation at 15 °C. Oscillations in the records at ram supporting velocities are attributable to side-to-side head movement from body recoil during forward locomotion. Zero is the ambient pressure.

different weights were forced to swim at velocities just over the transition. Striped bass ranging in weight from 28 to 837 g adopt the ram mode at a mean velocity of 45·6 cm.s^{-1} (N = 47) which for all the bass tested in equivalent to 1·36–3·14 bl.s^{-1} (largest to smallest fish) (Fig. 6*a*). Visual observations of ventilatory activity and stopwatch estimations of swimming velocity of larger striped bass, 122 cm, standard length (s.l.), swimming in large round tanks at the University of Rhode Island Marine Experiment Station, indicate that these larger animals ram ventilate at about the same mean velocity determined in the present study.

Bluefish ranging in weight from 26 to 336 g complete the transition at a mean velocity of 33·4 cm.s^{-1} (N = 31) which is equivalent to a specific swimming velocity of 0·87–2·23 bl.s^{-1} (largest to smallest fish) (Fig. 6*b*). This ram adoption velocity is lower than that reported by Roberts (1975*a*), probably due to the more extensive training and respirometer acclimation procedures used in the present study.

A linear regression of ram adoption velocity (Y) on weight (X) (least-squares method)

of pooled data for each species (striped bass $Y = 42{\cdot}34 + 0{\cdot}01X$; bluefish $Y = 31{\cdot}32$ $0{\cdot}11X$) was tested against the null hypothesis that there is no weight effect on the ram adoption velocity. In both cases, the effect of animal size on ram adoption velocity was not statistically significant ($P > 0{\cdot}05$, F test).

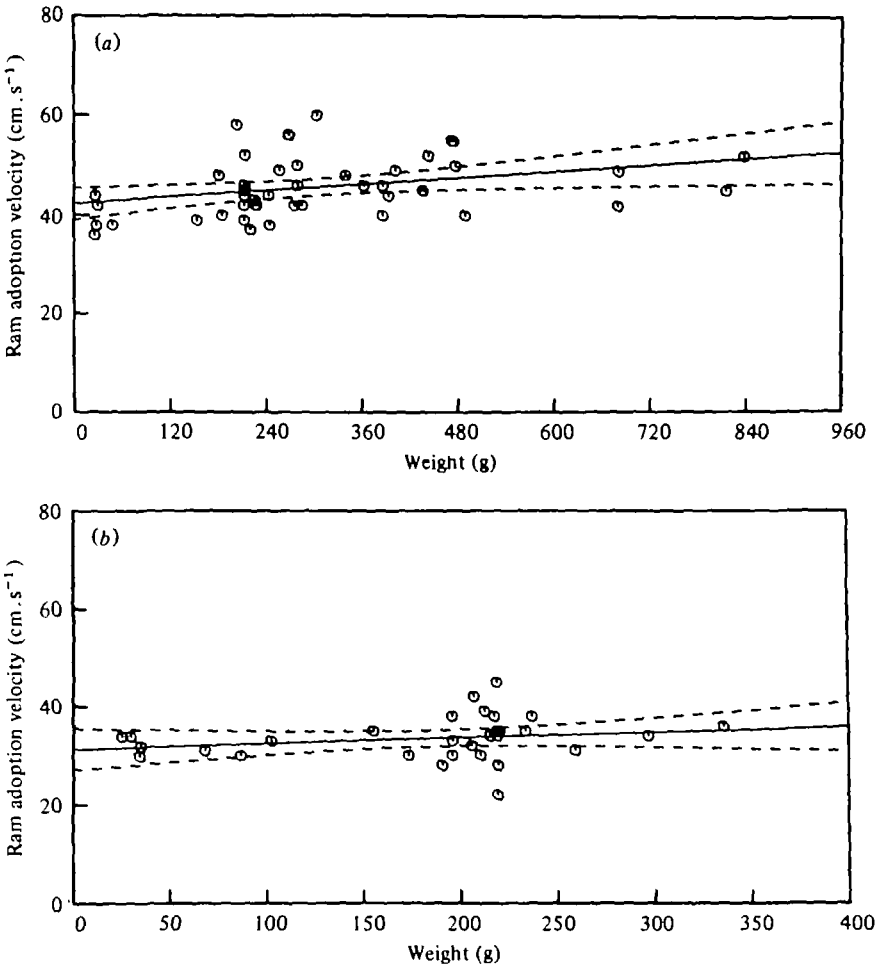

Fig. 6. Ram adoption velocities of different weight striped bass (*a*, $N = 47$) and bluefish (*b*, $N = 31$). The regression lines and 95% confidence intervals were calculated by the least-squares regression method.

Maximum sustainable swimming velocities

To gain impressions of cruising velocities and swimming endurance, determinations of critical swimming speeds for 30 and 45 min swimming bouts in an increasing velocity increment test were performed. Values of U_{crit} for striped bass are 2·9–3·3 bl.s^{-1} but reach 4·0–4·6 bl.s^{-1} for bluefish, indicating that both species are fairly strong swimmers (Table 1). At velocities just over the ram transition point, both species can maintain station for well over 10 h, suggesting that the transition velocities are well within their cruising-speed ranges.

DISCUSSION

The metabolic requirements of swimming in fishes place a great demand on circulatory and ventilatory systems. Circulatory accommodations for activity are thought to be mediated partly by changes in cardiac output with about equal contributions from an increased heart rate and stroke volume (Randall, 1970). Compensations involving

Table 1. *Maximum sustainable swimming velocities* (± 1 S.E.) *of striped bass* (24·13–29·21 *cm, s.l.,* $N = 6$ *for each test*) *and bluefish* (17·78–25·41 *cm, s.l.,* $N = 6$ *for each test*) *in* 30 *and* 45 *min increasing velocity increment tests at* 15 °*C*

	U_{crit}			
	30 min bouts		45 min bouts	
	cm.s^{-1}	bl.s^{-1}	cm.s^{-1}	bl.s^{-1}
Striped bass	86·0 ± 2·5	3·28 ± 0·13	76·0 ± 2·9	2·90 ± 0·14
Bluefish	101·9 ± 2·1	4·61 ± 0·17	84·0 ± 5·3	4·01 ± 0·08

cyclic ventilation include increased rate and amplitude of ventilation and possibly positional changes of the gill filaments (Ballintijn, 1972), but external energy losses resulting from the pumping action during forward locomotion and a drop in utilization percentage (Piiper *et al.* 1977) become significant at moderate and high swimming velocities. Fishes whose life habits include more continuous swimming suppress active ventilatory movements and shift to ram ventilation at intermediate swimming speeds. While the transition may appear to be a subtle change in respiratory behaviour, the results of the present study indicate that substantial metabolic advantages accrue when the swimming musculature performs the ventilatory work. The cost of ram gill ventilation becomes equal to a small and probably negligible expenditure for the 'tonic drive' of the branchial muscles and the resistivity of the gill curtain.

Although the mechanics of active ventilation are reasonably well understood, the energetics are a matter of disagreement. Experimentally derived values of the proportionate cost of rhythmic pumping range from 0·5 to 70% at rest depending on activity and technique used for study (Cameron & Cech, 1970). The most commonly accepted values range from 10 to 20%. A fascinating analysis by Brown & Muir (1970) utilizing the theory of ram-jet mechanics revealed that the gill resistance in a ram-ventilating skipjack tuna (*Katsuwonus pelamis*) moving at 66 cm.s^{-1} was 7% of total swimming drag, which translates to a small expenditure of 1–3% of total metabolism. The very act of swimming seems to modulate the metabolic cost and work requirements of the branchial pumps so the cost does not increase proportionately with swimming up to ram ventilation velocities. In striped bass (Fig. 1) and bluefish, ventilation amplitude and rate increase as swimming activity increases but these do not continue to rise with swimming work, due to pressure rise at the mouth which probably reduces the work load of the buccal fore-pump (Roberts, 1975*a*). The opercular pump may also be aided during active ventilation by post-branchial aspiration (Hughes, 1960) as water passes the opercular doors, although cyclic abduction and adduction of the doors should reduce this effect somewhat. When the transition to ram

ventilation occurs, positive pressures are recorded in the opercular cavity. The venturi effect could be more effective in drawing water through the opercular chamber during ram ventilation since the ventilatory flow should be of more constant velocity than during cyclic gill irrigation, when the ventilatory excurrent stream would be of rhythmically varying velocity, thereby reducing the effectiveness of post-branchial aspiration.

Conversion from active branchial to ram gill ventilation results in improved overall efficiency during swimming in striped bass and bluefish at velocities well within their cruising ranges. For example, a 22·23 cm striped bass swimming at 1·35 $bl.s^{-1}$ (30 $cm.s^{-1}$) expends 322 mg $O_2.kg^{-1}.h^{-1}$. While on the move at the ram supporting velocity of 2·47 $bl.s^{-1}$ (55 $cm.s^{-1}$) the rate of oxygen uptake increases to only 360 mg $O_2.kg^{-1}.h^{-1}$, an increase in metabolism of only 11·8% for an increase in velocity of 83·3%. It is tempting to assign the metabolic savings found with the adoption of ram flow to the operational cost of the buccal and opercular pumps. Differences in $\dot{V}_{O_2}$ at high swimming speeds between a line drawn through an expected exponential relationship (over the active ventilation range) and a line joining points at higher ram supporting velocities are about 30%, a value too high for branchial pump operation during swimming. The data, therefore, strongly imply a favourable change in the hydrodynamic characteristics of the flexing hydrofoils with the shift in ventilatory modes. Other experiments with striped bass and bluefish in which oxygen uptake was determined in the same animal under normoxic oxygen conditions (7·7–8·7 ppm O_2) and 24 h later under hyperoxic oxygen conditions (16–20 ppm O_2) revealed that oxygen uptake was reduced by about 20% during active ventilation. The decrease was mediated by lower ventilatory and heart rates; however, the shift in metabolism with ram ventilation still occurred, suggesting that there was a change in overall body drag.

Transfer to open-mouth swimming in striped bass and bluefish is a velocity-dependent phenomenon and appears to be independent of size, at least over the range tested. Adoption of ram ventilation by *Remora remora* when attached to a respirometer tunnel seems to follow the same trend (Muir & Buckley, 1967). A 9 cm, 25·6 g bluefish adopts the ram mode at 35 $cm.s^{-1}$ or 3·78 $bl.s^{-1}$, whereas a 30·5 cm, 336 g bluefish reflexively shifts ventilatory modes at 36 $cm.s^{-1}$ or 1·18 $bl.s^{-1}$. These two fishes have different swimming energetics but the metabolic consequences of the ventilatory shift should be the same.

A possible alternative explanation for the reduced metabolic expenditure with the shift in ventilatory modes, is that striped bass and bluefish resort to the use of white muscle at intermediate swimming velocities. If this were the case then white-muscle contributions to thrust would not be reflected in oxygen uptake determinations since this muscle type shows a greater capacity for anaerobic metabolism (Bilinsky, 1975). Completed experiments (Freadman, 1978) indicate that in both species, lateral red muscle alone is responsible for slow and cruise swimming at velocities well above those required to support ram gill ventilation.

The metabolic cost for movement of the external medium across the respiratory surface can be estimated by determining oxygen uptake at different ventilatory rates. For a voluntary human subject, this estimation is relatively easy and yields values of 1–2% of total metabolism (Otis, 1964; Glauser, Glauser & Rusy, 1967). 'Persuading' a fish to increase its ventilatory rate without influencing other factors leading to in-

reased oxygen demand is a problem. A facultative ram-ventilating fish represents a natural situation in which ventilatory movements are suppressed. Therefore, it should be possible to estimate the oxidative cost of ventilation from oxygen uptake and swimming activity experiments. However, since the reduced metabolic expenditure that follows the adoption of ram gill ventilation probably includes a hydrodynamic component, this aspect must be evaluated before an estimate of ventilation cost can be made for the striped bass and the bluefish.

This work is a portion of a dissertation submitted in partial fulfilment of the requirements for the degree of 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 laboratory for use of the respirometers and bench space. Dr A. B. DuBois and Mr C. S. Ogilvy (John B. Pierce Foundation and Yale University, New Haven, Conn.) reviewed a manuscript for this paper. 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, Narrangansett, Rhode Island), B. Young (N.Y.S. Department of Environmental Conservation, Stony Brook, N.Y.), M. Vernisoni (Connecticutt Department of Environmental Protection, Kensington, Conn.) and the Sunderland State Hatchery (Sunderland, Mass.).

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