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PRESSURE AND WATER FLOW PATTERNS IN THE RESPIRATORY TRACT OF THE BASS (*MICROPTERUS SALMOIDES*)

BY GEORGE V. LAUDER

Department of Anatomy, University of Chicago, 1025 East 57th St, Chicago, Illinois 60637 U.S.A.

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SUMMARY

Instantaneous water velocities in the respiratory tract of bass, *Micropterus salmoides* (Lacepède), were measured using a fast-responding hot-film anemometer. The flow velocity waveform varied within the buccal cavity, with lower peak velocities at the back than at the front. Flow velocity in both the buccal and opercular cavities varied over the respiratory cycle, and 80% of signal power in the velocity waveform was between 1 and 10 Hz. Flow within the buccal cavity reached a maximum velocity of 50 cm s^{-1} and did not decline to zero, even when differential pressure across the gills was negative. Simultaneous measurement of dimensional changes in the branchial apparatus, pressure and velocity fluctuations showed that gill bar adduction coincides both with the pressure reversal across the gills and with maximum flow velocities in the opercular cavity. The movement of the gill bars during respiration causes flow velocity fluctuation just in front of the primary lamellae and may be an important component of intraoral resistance contributing to the phase differences between pressure and velocity waveforms.

INTRODUCTION

The analysis of respiratory mechanisms in fishes over the last 25 years has provided one of the best documented cases of the relationship between structure and function in a countercurrent exchanger, and a comprehensive system for the study of the regulatory responses of respiratory processes to environmental change. The first investigators to apply modern experimental techniques to the study of respiratory dynamics in fishes (Hughes, 1960; Hughes & Shelton, 1957, 1958; Saunders, 1961) demonstrated that the two main divisions of the respiratory tract, the buccal and opercular cavities, displayed coordinated movements and pressure fluctuations that were indicative of continuous water flow over the gills (the double-pump model). This work established the measurement of pressure in the mouth cavity as a useful technique for subsequent analyses of respiratory efficiency (e.g. Hughes & Umezawa, 1968; Jones & Schwarzfeld, 1974), ventilatory mechanics (Burggren, 1978; Freadman, 1981; Roberts, 1975) and cardioventilatory synchrony (Hughes, 1978*a*; Satchell, 1960, 1971; Shelton, 1970).

Key words: Respiration, velocity, fishes.

In 1975, Holeton & Jones published an important and widely cited paper that provided the first (and still the only) direct measurements of flow *velocities* within the respiratory tract of fishes. The major contributions of that paper, a study of the carp *Cyprinus carpio*, were (1) the first direct measurement of flow velocities, (2) the discovery of a phase difference between differential pressure and flow velocity in the buccal cavity, (3) the emphasis on the necessity of making measurements of changes in cross-sectional area within the oral cavity during respiration and (4) the discovery of fluctuations in flow velocity within the buccal cavity providing "a potential for error in many of the previous analyses of 'gill resistance' and energetics of breathing..." (Holeton & Jones, 1975: p. 537). The data of Holeton & Jones (1975, Fig. 2) also clearly indicate that there is a period of zero or even reverse (posterior to anterior) flow within the buccal cavity during normoxic respiration.

The purpose of this study is to provide a detailed analysis of water velocities during respiration in bass (*Micropterus*). In particular, four key problems will be addressed. (1) What is the nature of the water flow close to the primary and secondary lamellae? Holeton & Jones measured flow velocities by introducing an electromagnetic flow probe into the mouth, and were thus not able to record velocities inside the opercular cavity or near the gill lamellae. (2) Is there a reverse flow within the oral cavity at any point during the respiratory cycle? The data of Holeton & Jones show a period of zero and reverse flow in carp, but the experiment of Van Dam (1938) showed a continuous posterior flow of water in a tube connecting the buccal and opercular cavities. (3) Do the ceratobranchial and epibranchial bones supporting the lamellae move during respiration? The gill bars are located anterior to the primary and secondary lamellae and rhythmic adduction and abduction of these structures during respiration could greatly change the flow velocity profile over the gills. (4) Do the velocity waveforms within the oral cavity of other species show the same magnitude of fluctuation reported by Holeton & Jones (1975) for carp? Their finding of large ($38\,cm\,s^{-1}$) and unsteady water velocities has important implications for models of gas exchange, and it is critical to determine if similar results are obtained using techniques that allow velocity recordings near the lamellae.

MATERIAL AND METHODS

Experimental protocol

Experiments were performed on six largemouth bass, *Micropterus salmoides*, with a mean total length of 22·3 cm. Bass were anaesthetized in tricaine methanesulphonate buffered to neutral pH as described previously (Lauder, 1980). Polyethylene cannulae used to house the recording transducers for pressure and velocity were implanted under anaesthesia in four sites, and in one experiment five cannulae were implanted. For recording flow velocity, a larger cannula size was used (o.d. = 2·8 mm, i.d. = 1·8 mm) than for the pressure sensors (o.d. = 1·9 mm, i.d. = 1·4 mm). Cannulae were implanted in the skull by threading them through a large hypodermic needle so that a flange made on one end of the cannula lay flush against the roof of the mouth. The positions of the velocity cannulae are shown in Fig. 1. The anterior cannula opened into the buccal cavity just lateral to the parasphenoid bone, about 1 cm behind the buccal valve. The pressure cannula and the velocity cannula wer

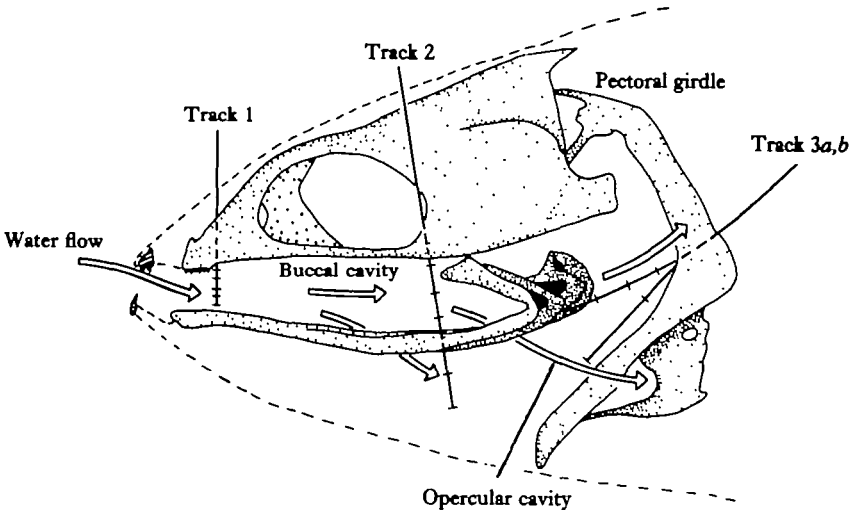

Fig. 1. Schematic section of the head of a largemouth bass, *Micropterus salmoides*, to show the location of sites where instantaneous velocity measurements were made. The three tracks identify the paths taken by the hot-film anemometer as it was advanced through the oral cavity. Short bars across the track lines provide a schematic indication of sites where a measurement was made. Exact descriptions of recording sites are given in the appropriate figure caption. Only two of the three tracks were used on any given individual. Two variations of track three were used, labelled as *a* and *b*. Both buccal and opercular pressures were always measured simultaneously, as was either mouth opening, the distance between ceratobranchials 2 and 3, or opercular movement.

always implanted on opposite sides of the head so that (as nearly as possible) recordings of both variables occurred at the same distance from the mouth opening. The cannula in the posterior portion of the buccal cavity was passed through the skull behind the eye just medial to the joint of the hyomandibula with the skull. The flanged ends of the cannulae on each side were located just anterior to pharyngobranchial three. Opercular cavity cannulae were positioned in the posterior aspect of the cavity (Fig. 1) by drilling a small hole (approximately 2·0 mm in diameter) through the cleithrum. In one experiment, a second pressure cannula was implanted in the dorsal portion of the opercular cavity (under the suprascapular bone) to test for differences in pressure fluctuations within the opercular cavity.

All experiments were conducted in a shallow Plexiglas chamber containing continuously filtered and recirculated water. The experimental fish were not restrained by clamps or other holding devices. Most recordings were obtained within 8 h of cannula implantation, but two experiments were repeated 48 h later on the same individual.

Pressure recordings

In order to avoid the low frequency response associated with fluid-filled pressure transducers (see Lauder, 1980), catheter-tip transducers (Millar model PR-249, Houston, Texas; diameter of the catheter = 0·7 mm) with a frequency response of 0 Hz to 10 000 Hz were used. The catheters were advanced through the cannulae until the tips were within 1 cm of the mouth cavity, and the distal ends of the cannulae were

then plugged with silicone sealant. The signals were amplified with Grass P511J (Quincy, Massachusetts) preamplifiers (low pass filter of 0·1 Hz, high pass filter of 300–1000 Hz), recorded on a 7-channel Bell & Howell (Pasadena, California) 4020A FM tape recorder at 37·5 cm s^{-1} and played back on a rectilinear Gould 260 chart recorder at 4·7 cm s^{-1}. The pressure recordings were calibrated after each experiment both by applying a known pressure head to the transducers and by using the internal transducer calibration that had been checked previously for accuracy. Buccal and opercular pressures were always recorded simultaneously. The effective frequency response of all chart records was 1000 Hz, although frequencies up to 3000 Hz were recorded faithfully on the tape recorder (these data were used for computer analysis).

Velocity recordings

Instantaneous velocities within the respiratory tract were measured with a TSI hot-film anemometer (St Paul, Minnesota; Model 1465J; sensor length = 0·5 mm, sensor diameter = 0·7 mm; catheter diameter = 1·2 mm) modified to be sensitive to flow at 90° to the catheter axis. This anemometer was calibrated by the manufacturer over a flow range of 0–10 m s^{-1} in a flow tank and provided with circuitry that linearized the relationship between flow velocity and output voltage. The frequency response of the anemometer is flat from 0 to 10 000 Hz. The anemometer output was recorded directly on the FM tape recorder, as described above, to preserve the frequency response of the signal. Instantaneous velocity was recorded only at one site at a time, and at each location the velocity catheter was advanced known increments through the implanted cannula during steady respiration. This produced a series of tracks through the mouth cavity outlined in Fig. 1. By advancing the velocity catheter through the opercular cavity cannula, it was possible to record velocities between adjacent primary lamellae, and between adjacent gill bars (ceratobranchials). The latter location could also be reached by passing the anemometer vertically through the posterior buccal cavity cannula. It was not possible to measure velocities between adjacent *secondary* lamellae because of the small distance between them and the relatively large anemometer diameter.

Special care was taken to ensure that accurate levels of zero velocity were determined. Flow velocities within a small container of still water were measured to ensure that zero velocity was indicated by the transducer. During each experiment, as well as before and after every velocity track through the respiratory tract, flow velocity was recorded within the cannula to provide a zero level. This value was compared to flow velocities obtained while the fish was still anaesthetized, and in every case comparable zero levels were indicated.

The hot-film anemometer used for these experiments is maximally sensitive to flow at 90° to the catheter axis, but only a 10% reduction in response occurs for flows at a 30° angle to the long axis. The anemometer is not sensitive to reverse flows, and cannot directly indicate bidirectional flow. However, a flow reversal cannot occur without velocities first falling to zero, a condition that did not occur.

A Fourier analysis of the water velocity waveforms was conducted to provide a quantitative measure of signal oscillation. Velocity waveforms were digitized from the tape recorder at 8-bit accuracy with a frequency of 1000 Hz. Portions of the digitized data were used in a 1024 point Fast Fourier Transform (Cooley-Tukey algorithm)

that calculated the proportion of signal power at 1-Hz intervals from 1 to 500 Hz. The signal power provides a measure of the proportion of total energy in a fluctuating signal at each frequency. Three power spectra were calculated from different data for each velocity location and the resultant transforms averaged to increase accuracy.

Distance measurements

A Biocom impedance converter (model 2991, UFI Corporation, Morro Bay, California) was used to transduce the distance between selected parts of the mouth cavity. Unipolar steel alloy electrodes were implanted in the skin overlying the premaxilla and mandible, in the tissue of ceratobranchials 2 and 3, and in the skin of the posterior opercular margin and pectoral girdle. The distance between each of these pairs of sites was recorded serially and simultaneously on the tape recorder with

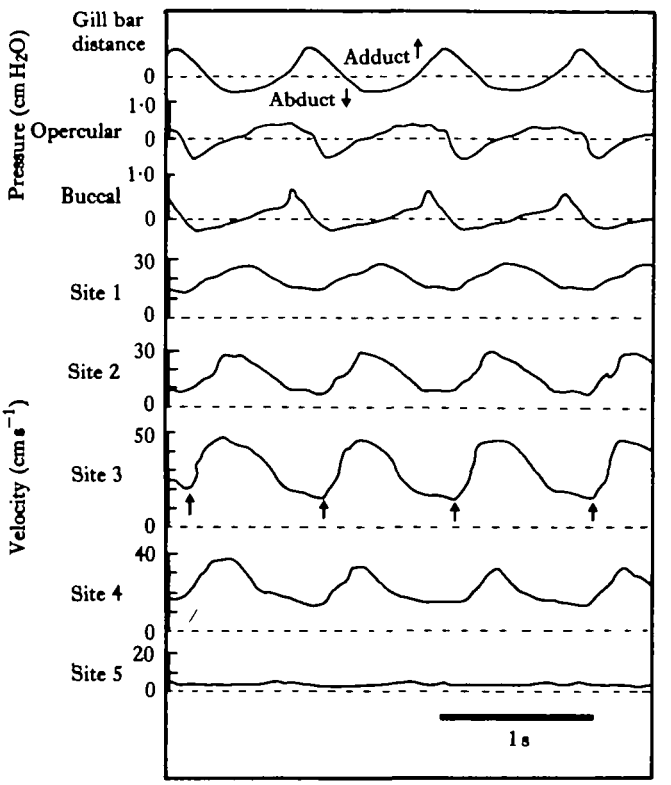

Fig. 2. Patterns of flow velocity within the anterior portion of the buccal cavity. See Material and Methods and Fig. 1 for the location of the vertical track (track 1) along which velocities were measured. Opercular and buccal pressures were recorded simultaneously, as was the distance between ceratobranchials 2 and 3 and the velocity at one site. The anemometer was advanced along the track and readings were taken at each location. The dashed line indicates zero velocity, resting pressure, or the distance between the gill bars when the fish is anaesthetized (2·0 mm). Arrows below the site 3 record define arbitrary respiratory cycles. Site 1, 2·0 mm ventral to the roof of the mouth; site 2, 5·0 mm ventral to the roof of the mouth; site 3, centre of the buccal cavity; site 4, 3·0 mm from the floor of the buccal cavity; site 5, 1·0 mm from the floor of the buccal cavity, dorsal to the basihyal bone.

pressure and velocity recordings. Zero values were established with the fish under anaesthesia either before the experiment was begun, afterwards, or both. This technique was used only to provide information on whether adjacent structures were adducting or abducting and a general indication of distance between them. The most common experimental procedure was to record buccal and opercular pressures continuously, and for each site at which velocities were measured, to record all three distances (each over about ten ventilatory cycles) by changing the leads into the impedance converter.

RESULTS

Water velocity along the anterior track in the buccal cavity (see Fig. 1) was oscillatory and reached peak values of almost 50 cm s^{-1} in the centre of the mouth cavity (Fig. 2, site 3). Flow velocity never declined to zero within a respiratory cycle and the lowest velocities in the centre of the buccal cavity averaged nearly 12 cm s^{-1}. Velocity waveforms differed with location along the anterior track through the buccal cavity (Fig. 2). Within 2 mm of the roof of the mouth, fluctuations in flow velocity were apparent, and these increased with depth in the mouth cavity (Fig. 2). Peak velocities were obtained in the centre of the mouth, while oscillation was least within 1 mm of the buccal floor (Fig. 2, site 5). This pattern was extremely repeatable among experimental animals. Maximum buccal velocity was correlated with neither maximum nor minimum buccal pressure and consistently occurred as buccal pressure reached ambient levels.

Along a vertical track through the posterior portion of the buccal cavity (Fig. 1), pressure fluctuations were smaller than those occurring anteriorly (Fig. 3) and showed little variation among sites. In the posterior portions of the buccal cavity, maximum velocity tends to coincide with gill bar adduction. In contrast, water velocities along the anterior track peak as the gill bars near maximal abduction.

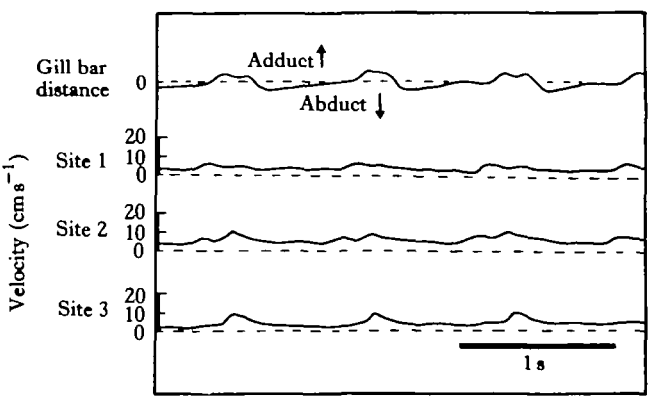

Fig. 3. Patterns of flow velocity within the posterior portion of the buccal cavity recorded relative to the distance between ceratobranchials 2 and 3. Conventions as in Figs 1 and 2. Site 1, 2·0 mm below the roof of the posterior aspect of the buccal cavity; site 2, in the middle of the posterior buccal cavity, about 5·0 mm superior to the opening between ceratobranchials 2 and 3; site 3, 2·0 mm superior to the opening between ceratobranchials 2 and 3. Note that this is the location where water leaves the buccal cavity, and passes between the gill bars to flow over the gills.

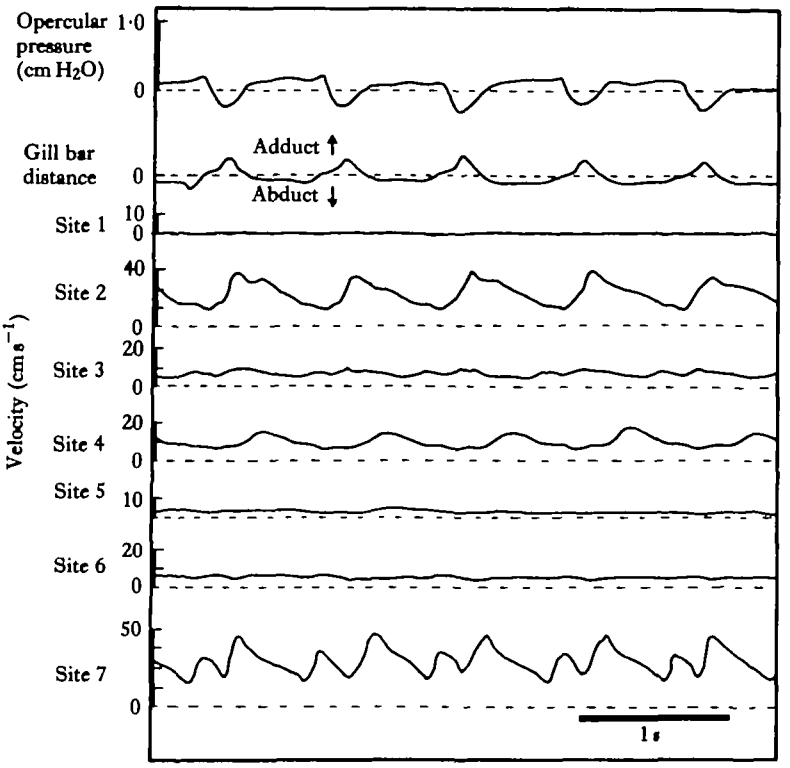

Fig. 4. Patterns of flow velocity within the opercular cavity measured relative to gill bar distance and pressure. The location of the track along which velocities were measured is shown in Fig. 1. Conventions as in Fig. 2. Site 1, 1·0 mm within polyethylene cannula, to show zero velocity; site 2, 1·0–2·0 mm posterior to the tips of the primary lamellae of ceratobranchials 2 and 3. The lamellae were separating slightly for a brief part of the respiratory cycle; site 3, 2·0 mm posterior to ceratobranchial 2, in between the primary lamellae; site 4, between ceratobranchial 1 and the side of the head; site 5, 1·0 cm posteroventral to the suboperculum. The anemometer tip was located outside the opercular cavity and the recorded velocity may have been influenced by surrounding water movement; site 6, between ceratobranchials 2 and 3, just anterior to the primary lamellae; site 7, anteroventral portion of opercular cavity, lateral to the sternohyoideus muscle.

Flow velocity within the opercular cavity showed considerable spatial variation (Fig. 4) although it never fell to zero. The maximum opercular velocities (40 cm s^{-1}) were recorded 1–2 mm posterior to the tips of the primary lamellae, when the adducted lamellae separate briefly allowing water to bypass the secondary lamellae (Fig. 4, site 2). This brief 'shunting' of respiratory flow occurred commonly during quiet respiration. A minimum flow of 10 cm s^{-1} was recorded even when the primary lamellae were adducted. At other sites near the gill filaments, oscillation of flow was less than it was posterior to the primary lamellae. Between the gill bars, maximum velocity was rarely more than double the minimum value (Fig. 4, sites 4 and 6). The most oscillatory flows were recorded in the anteroventral portion of the opercular cavity, about 2 mm lateral to the sternohyoideus muscle (Fig. 4, site 7). At this location, a double peak was observed and the velocity waveform showed no period of steady flow.

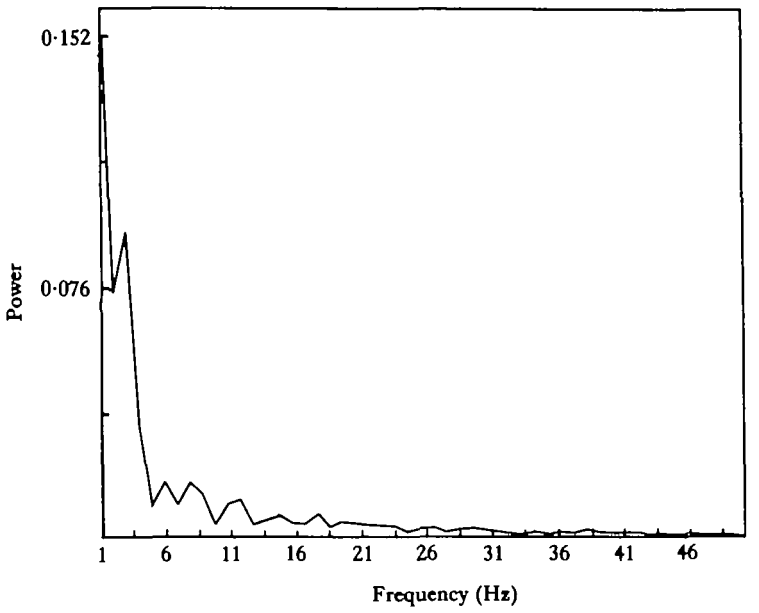

Fig. 5. Fourier transform of the opercular velocity waveform recorded posterior to the primary lamellae. Transforms of velocities at other sites were very similar. Three 1024-point Fast Fourier Transforms were calculated for different points and averaged to increase accuracy at the 1-Hz interval chosen for power calculation.

Fourier analysis of opercular velocity waveforms (Fig. 5) indicated that nearly all signal power was below 50 Hz, and that most of the energy in the velocity signal was between 1 and 10 Hz. Similar results were obtained in analyses of waveforms at other sites within the mouth cavity.

The overall pattern of pressure change and water velocity within the respiratory tract in relation to the dimensional parameters studied is summarized in Fig. 6. The differential pressure between the buccal and opercular cavities is predominantly positive, with buccal pressure exceeding that in the opercular cavity. A phase of pressure reversal is clearly evident and comprises 15% of a respiratory cycle on average. The maximum negative differential pressure slightly precedes maximum gape, peak buccal cavity flow velocity, maximum opercular flow velocity at the site posterior to the primary lamellae, and near maximal adduction of the operculum. The gill bars are also maximally adducted and thus branchial resistance is at its highest level. During the period of positive differential pressure, opercular and buccal cavity velocities have reached a minimum, and the gill bars and operculum are abducted.

DISCUSSION

The most noteworthy result of these experiments is the finding that water velocity near the gill lamellae is unsteady, and that a major cause of this unsteady flow is the rhythmic movement of the gill supports during ventilation. In addition, flow velocity in the opercular cavity was found to vary temporally.

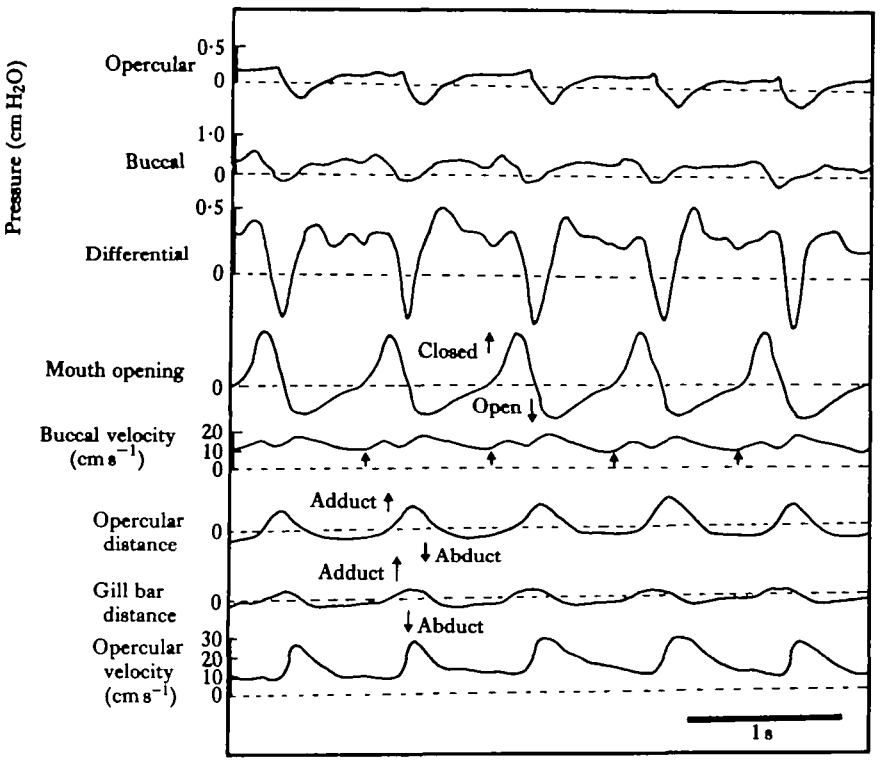

Fig. 6. Summary of buccal and opercular velocity waveforms relative to mouth cavity pressures, differential pressure (buccal minus opercular) across the gills (obtained by digitizing the buccal and opercular pressure signals and subtracting), and three dimensional changes in the respiratory tract: mouth opening, the distance between the operculum and the pectoral girdle, and the distance between ceratobranchials 2 and 3. Note that the time when the differential pressure is negative corresponds to gill bar adduction and near maximal buccal and opercular flow velocities.

The results of these experiments on bass provide no evidence that flow velocity during normoxic ventilation ever drops to zero, or that a reverse flow occurs within the oral cavity as a consequence of a reversal in pressure gradient between the buccal and opercular cavities. This result contrasts with the findings of Holeton & Jones (1975) on carp, *Cyprinus*. The difference is unlikely to result from differences in patterns of pressure change in the two species, as the absolute magnitudes and waveforms of the pressure changes in the buccal and opercular cavities were similar, and the range of differential pressures was similar. Two alternative interpretations of the discrepancy between the two investigations are possible. First, carp and bass may show distinct patterns of change in the cross-sectional area within the respiratory tract, and some morphological or size-related feature of the head causes differences in flow velocity. Secondly, the experimental conditions used by Holeton & Jones (1975) may have induced an abnormal velocity profile. The carp used in that study were held in a head clamp, were lightly anaesthetized and were housed in water to which 3 g l^{-1} of salt had been added. A probe was introduced into the mouth cavity,

and remained there during respiration, to measure velocity. Any of these conditions may have altered the flow velocity pattern.

Three similarities between the results of Holeton & Jones (1975) and those obtained here are noteworthy. (1) The peak velocities recorded in the buccal cavity of bass and carp are similar (about 40 cm s^{-1}). Thus, flow in both species reaches values that indicate a significant contribution of fluid inertia to respiratory dynamics. The combination of fluid inertia and gill bar movement (which increases water velocities near the lamellae) causes continuous water flow in the oral cavity despite a pressure reversal. (2) In both species, the peak velocities declined along an anterior to posterior track so that velocity waveforms recorded near the back of the buccal cavity were less pulsatile than those near the mouth. Finally, (3) the velocity and differential pressure waveforms in both bass and carp are not in phase. However, Holeton & Jones (1975) found that peak differential pressure *preceded* the maximum buccal velocity by about 12% of a respiratory cycle (calculated from their Fig. 4), while in bass peak velocity *lags behind* the maximum differential pressure by 70–90% of a respiratory cycle.

The significance of both the finding of relatively large oscillations in the intraoral velocity waveform and the phase lag between the maximum differential pressure and peak flow velocity lies in the accuracy of assumptions that form the basis of models of gas exchange and gill irrigation. Models of branchial resistance and gill water flow usually assume that a constant pressure gradient exists across the gills and that flow over the lamellae is steady (Langille, Stevens & Anantaraman, 1983; Scheid & Piiper, 1976). A resistant element, such as the gill filaments and supporting bars, interposed between two sites where pressures are measured, will introduce a disparity between the differential pressure between these two sites and the flow through the mouth. Furthermore, the gill bars are rhythmically closing and opening throughout respiration so that pulsatile velocities are recorded even within 1 to 2 mm of the primary and secondary lamellae. If flow at the entrance to the channels between secondary lamellae is also pulsatile (as suggested by the velocity profiles for the bass), then peak Reynolds numbers for flow may be greater than have been supposed, and the boundary layer at the opening to the secondary lamellae may be of a different thickness than has been assumed on the basis of steady flow considerations. Quantitative models will be necessary to appraise the precise effect of unsteady flow, as trade-offs may occur between the effect of unsteady flow on the interlamellar boundary layer (which may be thinned), and gas exchange efficiency (which may be decreased if lamellar blood flow and interlamellar water velocities are out of phase).

If flow were steady and exhibited no fluctuation with time, then the spectral energy in the velocity waveform (as determined by the Fourier transform) would be maximum at 0–1 Hz with no energy at higher frequencies. The presence of higher frequencies in the velocity waveform suggests that models of gas exchange and respiratory efficiency may more accurately depict the actual process of respiration if time-dependent water velocities are incorporated with frequency components in the 1–30 Hz range. Scheid & Piiper (1976, p. 36), in a discussion of factors that may limit gas exchange in fish gills, note that 'unsteady water or blood flow or both is expected to cause inefficiency of gas exchange much like an unequal distribution in space of ventilation, blood flow, and diffusing capacity'. Future work will be needed to demonstrate

whether the magnitude of fluctuations recorded here have an appreciable effect on the efficiency of gas exchange.

The role of gill resistance has been stressed by many authors (e.g. Hughes, 1976; Hughes & Morgan, 1973; Jones & Schwarzfeld, 1974) as an important parameter underlying the relatively high cost of ventilation in fishes and the mechanics of the dual pumping mechanism. It has not been generally recognized that the gill bars themselves are capable of contributing significantly to the resistance of the branchial apparatus (see Holeton & Jones, 1975; Hughes, 1972, Fig. 2 for exceptions), and that this resistance will vary temporally through a respiratory cycle as the gill bars are adducted and abducted. The results obtained here clearly document variation in distance between the gill bars during respiration. Furthermore, the period of pressure reversal during which opercular cavity pressure exceeds buccal pressure coincides with the time when the gill bars are maximally *adducted*. Many species, including bass, possess gill rakers that alternate in position on adjacent arches. As the gill bars are adducted, adjacent rakers interlock forming an impediment to flow through the mouth cavity (Lauder, 1983). The changing area of the gill sieve (= the pore area, through which water flows) during respiration has an effect on flow velocity, for as this area decreases, flow velocity over the respiratory surface increases. Depending on the relative magnitude of the change in gill sieve area as compared to changing dimensions of other areas of the respiratory tract, modifications of gill bar distance and rate of movement (under active control of the branchial musculature) could explain much of the fluctuation in flow velocity over the gills.

Although the maximum velocities within the buccal cavity decrease from the mouth to the area anterior to the gills, it is not true that this decrease can be extrapolated back to the secondary lamellae allowing the conclusion to be drawn that flow over the respiratory surface is constant. Gill bar movement causes changes in the cross-sectional area of the mouth cavity just in front of the gills, and the recordings of water velocity at this site indicate that flow velocity is highest as the gill bars adduct. Furthermore, movements of the gill bars also cause the attachments of the primary lamellae to move, thus changing the volume of water contained in the space between adjacent holobranchs. The velocity waveforms recorded in the opercular cavity, both posterior to the tips of the primary lamellae and lateral to the lamellae, clearly indicate that flow is not steady.

Many investigators have measured volume flow through the respiratory tract, and with the addition of data on cross-sectional area, it is possible to calculate the mean linear flow velocity for the site where the cross-sectional area is measured (Table 1). Inter-lamellar linear flow velocities for all species in Table 1 range from 2·0–51 cm min^{-1}, considerably less than the 10–15 cm s^{-1} velocities recorded from the buccal cavity. The reduction in flow rate reflects the increase in cross-sectional area within the respiratory tract – approximately 2–5 cm^2 in the buccal cavity to 20–25 cm^2 at the gills. It is difficult to relate quantitatively instantaneous velocities measured within the buccal cavity to volume flow determinations, because of the extensive variation in magnitude of peak velocities within the respiratory tract, and the variation in velocity with time. However, the results of this study strongly indicate that flow within the space delimited by the gill bars anteriorly, and the hemibranchs of adjacent arches laterally, is pulsatile and perhaps turbulent.

Table 1. *Velocities in the respiratory tract of fishes*

Velocity	Reference	Location	Species	T	Weight	Notes
5·7 cm min^{-1}	Scheid & Piiper, 1976	Interlamellar	*Scyliorhinus stellaris*	17 °C	2·2 kg	Mean velocity over a respiratory cycle
6·5 cm min^{-1}	Hughes, 1966	,,	*Micropterus dolomieu*	——	0·83 kg	Assumed basal value of 150 cm^3 min^{-1} kg^{-1} for $\dot{V}g$
2·0 cm min^{-1}	Saunders, 1962	,,	*Cyprinus carpio*	20 °C	0·18 kg	With minimum $\dot{V}g$ for resting fish
17·7 cm min^{-1}	,,	,,	,,	,,	,,	With maximum $\dot{V}g$, assuming no shunt between primary lamellae
2·6 cm min^{-1}	,,	,,	*Catostomus commersoni*	,,	0·2 kg	With minimum $\dot{V}g$ for resting fish
51 cm min^{-1}	,,	,,	,,	,,	,,	With maximum $\dot{V}g$
2·1 cm min^{-1}	,,	,,	*Ictalurus nebulosus*	,,	0·16 kg	With minimum $\dot{V}g$
26·2 cm min^{-1}	,,	,,	,,	,,	,,	With maximum $\dot{V}g$
35 cm s^{-1}	Holeton & Jones, 1975	3 cm deep in buccal cavity	*Cyprinus carpio*	19–22 °C	3·0 kg	Peak value recorded with electromagnetic flow probe
9·0 cm s^{-1}	,,	8 cm deep in buccal cavity	,,	,,	,,	Mean value at this site
18 cm s^{-1}	Hughes, 1978*b*	Not given	*Salmo gairdneri*	——	——	Peak value recorded with a Doppler flow meter

Values for interlamellar flow have been calculated from volume flow determinations in the literature.
Buccal cavity water velocities have been measured directly.

An important area for future study will be the relationship between dimensional changes along the respiratory tract, instantaneous velocities, and volume flow over the gills. Simultaneous measurement of all these parameters will provide a comprehensive basis for analysing respiratory dynamics in fish and for assessing the relationship between oscillation in water flow and patterns of gill blood flow (Hughes *et al.* 1981).

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