

MECHANICS OF VENTILATION IN SWELLSHARKS, *CEPHALOSCYLLIUM VENTRIOSUM* (SCYLIORHINIDAE)

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Accepted 10 March; published on WWW 6 May 1999

Summary

A simple two-pump model has served to describe the mechanics of ventilation in cartilaginous and bony fishes since the pioneering work of G. M. Hughes. A hallmark of this model is that water flow over the gills is continuous. Studies of feeding kinematics in the swellshark *Cephaloscyllium ventriosum*, however, suggested that a flow reversal occurred during prey capture and transport. Given that feeding is often considered to be simply an exaggeration of the kinematic events performed during respiration, I investigated whether flow reversals are potentially present during respiration. Pressure and impedance data were coupled with kinematic data from high-speed video footage and dye studies and used to infer patterns of water flow through the heads of respiring swellsharks. Swellsharks were implanted with pressure transducers to determine the pattern and magnitude of pressures generated within the buccal and parabranchial (gill) cavities during respiration. Pressure traces revealed extended periods of pressure reversal during the respiratory cycle. Further, impedance data suggested that pressures within the buccal and parabranchial cavities were not generated by the cyclic opening and closing of the

jaws and gills in the manner previously suggested by Hughes. Thus, the classic model needs to be re-evaluated to determine its general applicability. Two alternative models for pressure patterns and their mechanism of generation during respiration are provided. The first depicts a double-reversal scenario common in the swellshark whereby pressures are reversed following both of the pump stages (the suction pump and the pressure pump) rather than after the pressure-pump stage only. The second model describes a scenario in which the suction pump is insufficient for generating a positive pressure differential across the gills; thus, a pressure reversal persists throughout this phase of respiration. Kinematic analysis based on high-speed video footage and dye studies, however, suggested that during respiration, as opposed to feeding, distinct flow reversals do not result from the pressure reversals. Thus, water is probably pooling around the gill filaments during the long periods of pressure reversal.

Key words: respiration, behaviour, kinematics, pressure transduction, modelling, elasmobranch, swellshark, *Cephaloscyllium ventriosum*.

Introduction

The mechanics of ventilation in cartilaginous and bony fishes has been fairly well studied and a simple two-pump model, developed from the pioneering work of Hughes (1960b, 1965), has served for years to describe how water is moved into the mouth and subsequently out through the external gill openings (see also Liem, 1985). A key feature of this model is that water flow over the gills is continuous and unidirectional, despite the episodic nature of water entering the mouth and exiting the gills (Hughes, 1965). Benthic fishes, in particular, appear to rely almost exclusively on a system of pumps to generate a continuous respiratory current because they rarely utilize the alternative method of ram-jet ventilation (Hughes, 1960a,b).

Ventilation models infer how water is pumped through the head of a respiring fish on the basis of dynamic pressures within the buccal and parabranchial cavities. Pressures will

oscillate from positive to negative (relative to ambient) as water enters, fills and then is forced out of the respective cavities. When the pressure in the buccal cavity exceeds that in the parabranchial cavity, it is inferred that water is flowing in the anterior to posterior direction (unidirectionally) or from the buccal cavity over the gills and out through the gill openings. If this difference in pressure results from the buccal cavity being more positive than the parabranchial cavity, it is assumed that water is 'pushed' over the gills creating the 'pressure-pump' phase of respiration (Hughes and Shelton, 1958). If the pressure difference occurs because the buccal cavity is less negative than the parabranchial cavity, it is assumed that water is 'pulled' over the gills by the parabranchial pressure, creating the 'suction-pump' phase of respiration (Hughes and Shelton, 1958). These two phases are presumed to occur in an alternating fashion, creating

continuous unidirectional water flow over the gills during normal respiration.

Recently, however, studies of feeding kinematics in the swellshark *Cephaloscyllium ventriosum* suggested that bi-directional flow occurred during prey capture and transport (Ferry-Graham, 1997). Dye studies conclusively indicated that, during feeding, water taken into the buccal cavity actually reversed direction (presumably rebounding off the gillbars) and exited anteriorly, through the open mouth, rather than continuing unidirectionally over the gills (Ferry-Graham, 1997). The swellshark is a member of the catshark family (Scyliorhinidae) and is a benthic shark that is nocturnal and active for only short periods. Since it spends most of its time on the sea floor, it relies heavily on buccal pumping for respiration (L. A. Ferry-Graham, personal observation). As with feeding, buccal pumping may not generate a continuous, unidirectional flow of water over the gills as once thought (see Lauder, 1983).

Given the potential for water flow reversal during respiration, the classic respiratory model needs to be re-evaluated to determine its general applicability to all fishes. In this paper, I describe the pattern of pressure generation in the head of respiring swellsharks. Further, I make inferences regarding patterns of water flow during respiration on the basis of intraoral pressure data and kinematic data. I qualitatively contrast the results with the work of Hughes and his colleagues (see Hughes, 1960b, 1965, 1978; Hughes and Ballintijn, 1965) and refine the classic model of respiratory mechanics for sharks (Hughes, 1965) on the basis of previously unpublished trends discovered in those data sets and the swellshark data presented here.

Materials and methods

Pressure data

Intraoral pressures were recorded from six swellsharks *Cephaloscyllium ventriosum* (Garman) (25.5–30.7 cm total length; *L*) using Millar Mikro-Tip catheter pressure transducers (model no. PR-249; for details, see Lauder, 1984). To record pressures, cannulae were first implanted in the buccal cavity, approximately 3 mm ventral to the spiracle, and in the dorsal portion of the third parabranial cavity, approximately 4 mm dorsal to the gill opening (Fig. 1). Cannulae were implanted in a single individual 3 mm ventral and 3 mm posterior to the spiracle to determine the effect of implantation location on pressure recordings from the buccal cavity. For cannula implantation, sharks were anesthetized in tricane methanesulfonate (MS222) in sea water, and a 12 gauge hypodermic needle was inserted through the skin and musculature. Sections of polyethylene tubing (i.d. 1.40 mm, o.d. 1.90 mm, length 8–12 cm) served as cannulae and were flared at one end, without altering the internal diameter of the tubing, using a warm soldering iron. Cannulae were inserted through the hypodermic needle from inside the cavity starting with the unaltered end and then pulled through the hole such that the flared end ultimately lay flush against the inside of the

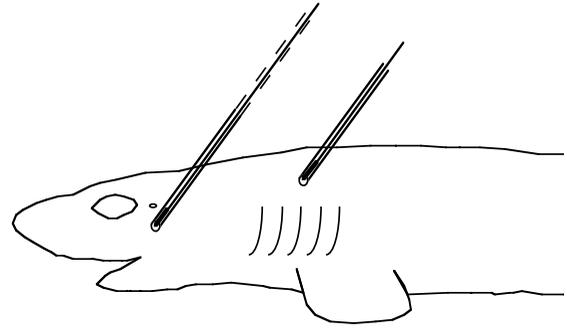


Fig. 1. Diagram of a swellshark indicating where the pressure transducers were inserted. Two catheter-tip pressure transducers were used to record pressure in the buccal and third parabranial cavities simultaneously.

cavity. The hypodermic needle was removed, and a slightly larger piece of polyethylene tubing (i.d. 1.77 mm, o.d. 2.80 mm, length 1–2 cm) was flared, sliced lengthwise and fitted snugly around each cannula on the external surface of the shark to prevent retraction. The pressure transducers were fed through the cannulae from the distal end to the point where they lay level with the epidermis (Fig. 1) such that the pressure-sensitive tips were within 1 mm of the internal buccal and parabranial cavities. The distal ends of the cannulae remained under water, and air bubbles were forced out of the system. A soft rubber sleeve was fitted over the distal end of the polyethylene tubing such that it surrounded the pressure transducer cable, creating a closed system for measuring pressures. Hughes (1960b) recorded pressure in several of the parabranial cavities of small-spotted catsharks (also known as 'dogfish') *Scyliorhinus canicula* (Scyliorhinidae) and found the pressures to be largely the same; thus, the third parabranial cavity was always used in the present study.

Surgery lasted no longer than 20 min, and sharks were allowed to recover in fresh sea water in the filming chamber. The filming chamber used in this study was a 28 cm×28 cm×104 cm acrylic aquarium maintained at $19\pm 0.5^\circ\text{C}$. Sharks were not restrained in any way during recovery or subsequent data collection periods. A small section of cork was attached to the cannulae, causing them to float and thereby preventing them from sinking behind a shark and interfering with normal gill opening and closing as much as possible. Sharks were allowed to recover for 1–5 h, and data were not collected until the shark was resting on the bottom of the tank. Buccal pumping, however, was always very active while the cannulae were in place, and the relaxed, barely perceptible pumping generally observed in inactive swellsharks could not be recorded. The respiratory patterns described here are presumed to be characteristic of active buccal pumping, such as that observed prior to feeding (L. A. Ferry-Graham, personal observation).

Signals from the pressure transducers were amplified 5000× using Grass (P-5 series) pre-amplifiers (low-pass filter of 0.1 Hz, high-pass filter of 0.3 kHz) and recorded onto a TEAC XR-5000 cassette data recorder at 9.6 cm s^{-1} . For analysis,

Table 1. Sample sizes and experiments in which individual sharks were used

Individual	Experiment				
	Pressure	Kinematics		High-speed video	Dye
		Jaw	Gill		
1	x			x	
2	x	x		x	
3	x	x	x ¹		
4	x	x	(x)		
5	x	(x)	(x)		
6	x	(x)	(x)		x ²
7				x	
8				x	
9				x	
10				x	
11				x	

Multiple experiments on an individual were simultaneous except where indicated.

x refers to experiments in which individual sharks were used.

(x) indicates that no data were successfully collected because electrodes became dislodged.

¹Impedance data collected sequentially; gill data first (pressure data collected throughout).

²Conducted several weeks after the pressure/impedance experiments.

signals were played back at 1000 Hz through a Keithley (series 500) analog-to-digital converter and saved. Differential pressure data were calculated from the digital data. For each shark, four separate sequences were downloaded using a custom-designed program (D/A/D; DataCrunch, Inc.) from those sections of tape during which a shark did not change its behavior in any externally detectable way. Sections of tape containing unique patterns of behavior, such as coughs, as verified by either synchronous video recordings or a voice track, were also downloaded. Sequences contained 10 000 data points and represented 10 s of real-time data. The data were compiled and smoothed using IGOR Pro 3.03 for Power Macintosh (WaveMetrics, Inc.).

Ventilatory frequency, estimated from the pattern of positive and negative pressure generation and determined as the number of complete respiratory cycles per second (Hz), was calculated for all individuals.

Kinematic data

Kinematic events that accompanied pressure changes were documented using either impedance recordings or high-speed video footage. Impedance recordings were obtained by implanting unipolar electrodes made of coated stainless-steel wire into the upper and lower jaws, and on either side of the third gill opening ($N=5$ of the six sharks used to collect pressure data; Table 1). Impedance was recorded from one set of wires at a time by connecting the corresponding pair of wires to a Biocom impedance converter (UFI Corporation, model 2991), which played directly into a third channel on the TEAC system detailed above. Impedance data proved quite difficult to obtain in general, as two of the five sharks dislodged all the electrodes prior to beginning any data recording. Two of the

five implanted individuals yielded jaw impedance only (Table 1). For the single individual that retained all four of the electrode implants, impedance was recorded first from the gill openings, and the wires connected to the impedance converter were then switched so that recordings could also be made from the jaws (Table 1).

Synchronized video recordings of respiratory kinematics were obtained for two individuals of the six sharks used to collect pressure data (Table 1). One of these individuals was also used to collect jaw impedance data (Table 1). Impedance recordings were not attempted on the second individual to determine whether there was any obvious effect of the implantation process on the respiratory data as determined by kinematic events compared between individuals. A NAC HSV-500 high-speed video recorder was used to film (at $250 \text{ frames s}^{-1}$) a ventral view of the respiring shark by aiming the camera at a mirror placed at 45° below the filming chamber. A synchronization pulse was recorded simultaneously onto the video footage and onto a fourth channel of the TEAC tape recorder so that pressure data could be matched exactly in time with the corresponding kinematic events.

In addition, five swellsharks (23.6–37.0 cm L) which were not implanted with pressure transducers or impedance electrodes were video-taped using high-speed video from a simultaneous ventral and lateral view as they actively respired prior to initiating feeding events (Table 1). For each individual, a sequence was downloaded that contained four replicate respiratory cycles and during which no changes in behavior were noted. Sequences were digitized at 12 ms intervals using a custom-designed digitizing program (MTV; DataCrunch, Inc.) to quantify the pattern of expansion of the buccal and

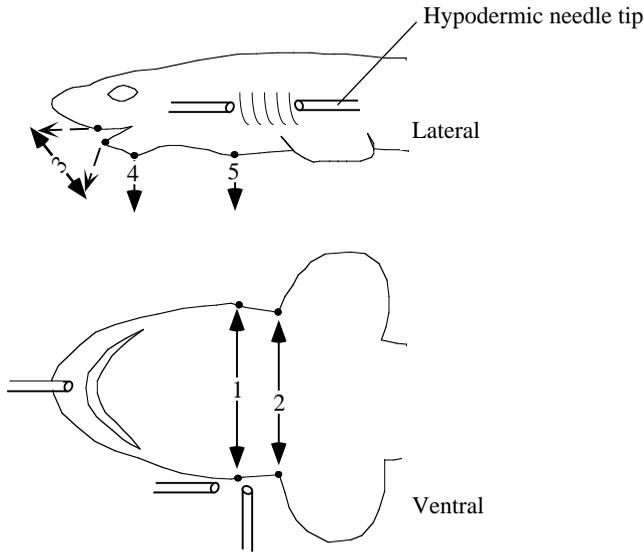


Fig. 2. Digitized points used for estimating the pattern of buccal and parabranchial cavity expansion from high-speed video footage. Measurement points 1–5 are described in the Materials and methods section. Points 4 and 5 have the potential to move both ventrally and posteriorly. Diagrams of a hypodermic needle tip are used to indicate the four positions where dye was ejected relative to the shark's mouth and gill openings for the dye experiments. The tips are pictured to reflect accurately the angle at which the syringe and needle were held relative to the body. The needle positioned directly anterior to the gill slits is pictured twice (in both the lateral and ventral views) to assist in visualizing placement.

parabranchial cavities. The points digitized from the ventral view (Fig. 2) were (1) the gill margin of the first gill opening on either side of the head (to calculate head width, cm, at the first gill opening) and (2) the anterior point of pectoral fin insertion on either side of the head (to calculate head width at the pectoral fin, cm). The points digitized from the lateral view were (3) the anterior tip of the upper jaw and the anterior tip of the lower jaw (to calculate amount of jaw opening, cm), (4) the hyoid as it was depressed and retracted (cm) during respiration, and (5) the center of the region of buccal expansion (cm) that occurred as water was taken into the buccal cavity (Fig. 2). Relevant kinematic variables were compared with analogous variables measured from video tape of sharks with cannulae using a Student's *t*-test to determine any effect of cannula implantation. Ventilatory frequency, estimated from the pattern of gill opening and closing and determined as the number of complete respiratory cycles per second (Hz), was calculated for all individuals. This value was compared using a Student's *t*-test with frequency data from the individuals implanted with pressure transducers to determine any possible effects of the pressure transducers on the frequency of respiration.

Dye experiments were used to visualize the pattern of water flow into and out of the head. For one individual (25.5 cm *L*, also used in the pressure transducer experiments; Table 1), high-speed video was used to film streams of dye as they were

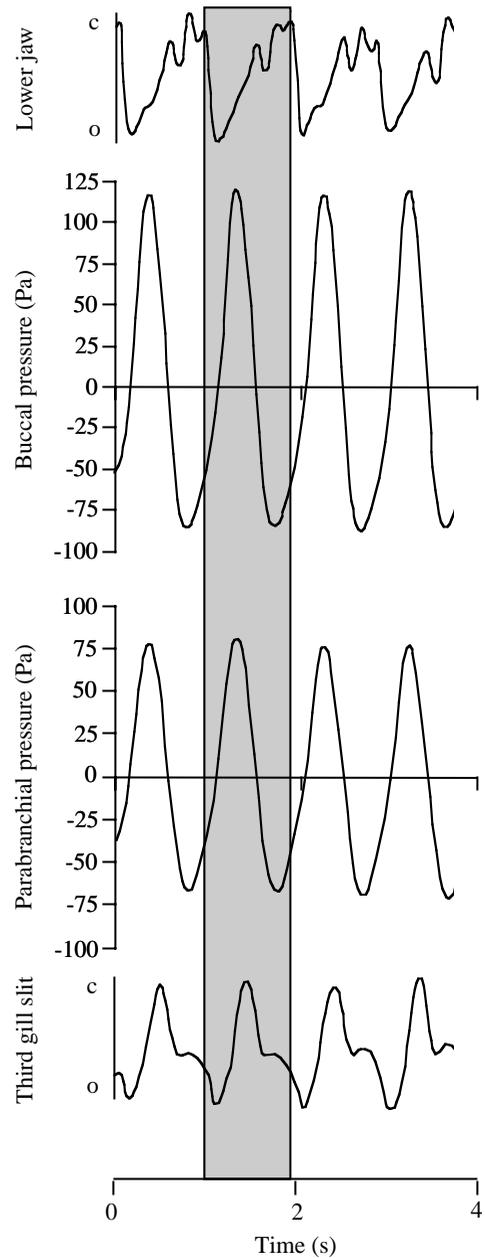


Fig. 3. Pressure data from a representative individual (female, 30.5 cm total length). The kinematic (impedance) traces for the lower jaw and third gill slit are from impedance recordings. The open (o) and closed (c) positions of the jaw and gills are noted. A single respiratory cycle, as indicated by lower jaw opening (from a closed position) and closing again fully, is demarcated by the shaded box. For comparison with previous studies $100\text{ Pa}=1\text{ cmH}_2\text{O}$.

ejected from a small hypodermic needle positioned in front of the mouth and at three positions immediately external to the gill slits: directly anterior and lateral, and directly posterior (Fig. 2).

Results

Individuals with pressure transducers had a significantly

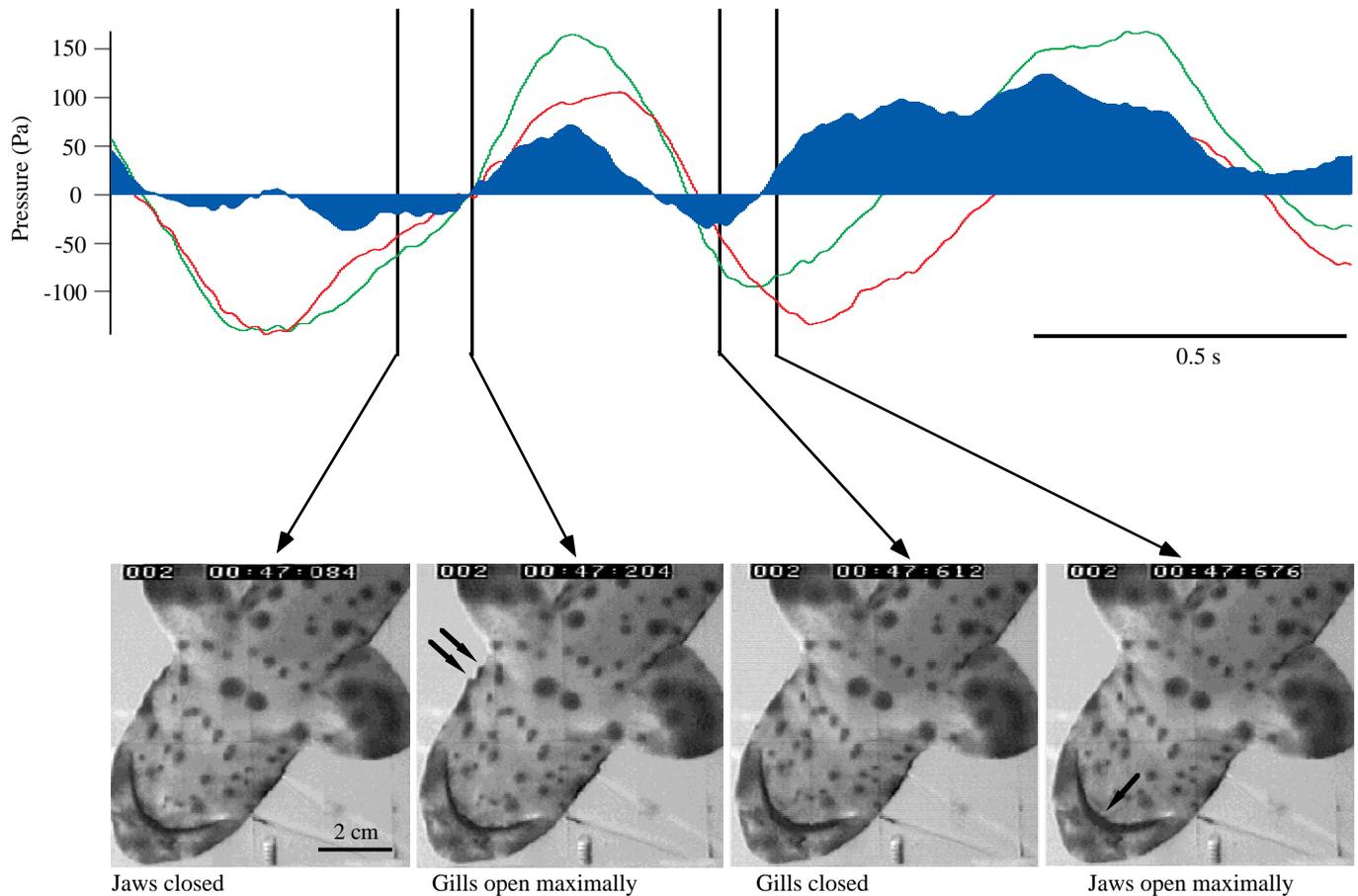


Fig. 4. Still images from a high-speed video recording showing a ventral view of a respiring shark (female, 29.0 cm total length) at the times indicated on the pressure trace. Time is indicated on the still images in min:s:ms. Note that the movement of the lower jaw is slight, but that the opening of the gill slits is easily detected from this view (arrows in second frame). Also visible are the cannulae containing the pressure transducers inserted into the buccal and parabranchial cavities. The corresponding buccal pressure trace (green), parabranchial pressure trace (red) and resulting differential pressure (area beneath curve filled in blue) are shown. According to convention, periods of positive differential pressure are times during which the pressure in the buccal cavity is greater than the pressure in the parabranchial cavity. Similarly, periods of negative differential pressure, or pressure reversals, are times during which the pressure in the parabranchial cavity exceeds that in the buccal cavity. When both the buccal and parabranchial cavity pressures are positive relative to ambient pressure, and the differential pressure between them is positive, the 'pressure-pump' phase of respiration is achieved (Hughes and Shelton, 1958). During periods when pressures in both the buccal and parabranchial cavities are negative, but the differential pressure is still positive, the 'suction-pump' phase of respiration is created (Hughes and Shelton, 1958).

faster frequency of ventilation than individuals without surgery (Student's $t=3.192$; $P=0.011$; d.f.=9), although the mean frequencies were still rather similar at 1.106 ± 0.097 Hz and 0.931 ± 0.082 Hz (means \pm s.d.) respectively. There were no significant differences in the degree of gill opening and head expansion (points 1 and 2 on Fig. 2; the most mobile and therefore the most accurately digitized points on the sharks' heads) to indicate that implantation impaired the sharks' ability to move water into and out of the head (Student's $t=0.173$ and 0.278 , respectively; $P>0.50$; harmonic $N=2.66$; power 72% and 45%, respectively). Thus, it is reasonable to assume that ventilation was more rapid as a result of the implantation of pressure transducers, but that ventilation was not intrinsically different, as indicated by head expansion and therefore the amount of water transported, between implanted and non-

implanted individuals. The implantation of impedance electrodes did not apparently differentially affect the kinematics of the individual examined.

For all individuals implanted with pressure transducers, an oscillatory pattern of pressure generation was recorded as the pressure in both the buccal and parabranchial cavities oscillated from positive to negative and back again together with mouth and gill opening and closing events (Fig. 3). No apparent effect of implantation location (in the shark buccal cavity) on the pressure data was detected. The pressure in the buccal cavity typically oscillated between $+161.7\pm 77.6$ Pa and -98.3 ± 51.2 Pa relative to ambient pressure. In the third parabranchial cavity, pressure typically reached $+96.7\pm 54.7$ Pa and fell to -110.0 ± 59.7 Pa (means \pm s.d.) during the respiratory cycle.

A slight time lag existed between the buccal and parabronchial pressure cycles such that the pressure in the buccal cavity changed from negative to positive, and later from positive to negative, slightly before the pressure in the parabronchial cavity changed sign (Fig. 4). Thus, there existed a pressure gradient from one cavity to the other. This gradient can be shown most easily by plotting differential pressure, or the difference in pressure between the buccal and parabronchial cavities (Fig. 4). The differential pressure traces show that the gradient was typically positive: pressure was higher in the buccal cavity than in the parabronchial cavity. A reversal in pressure, however, was nearly always present where the parabronchial pressure exceeded that of the buccal cavity (Fig. 5; for the exception, see Fig. 5A). The magnitude and duration of the pressure reversal were variable among and sometimes within individuals (Fig. 5B–D). The ‘classic reversal’ that occurs during the transition from the pressure-pump to the suction-pump phase of respiration is often of much greater magnitude than described previously (Fig. 5B). Further, reversals occurred not only during the transition from the pressure-pump to the suction-pump phase of respiration (see legend to Fig. 4), but also during the transition back to the pressure-pump phase, creating a ‘two-reversal’ scenario (Fig. 5C). In extreme cases, this can lead to a period of pressure reversal that is extended such that the suction-pump phase of respiration may not occur at all; the ‘ineffective suction-pump’ scenario (Fig. 5D).

Despite the prominence of pressure reversals, kinematic analysis of the buccal region (see Fig. 2, points 4 and 5) and subsequent dye experiments failed to indicate any time at which water actually exited the open mouth or entered the parabronchial cavities through the gill slits.

Discussion

Ventilation models

During periods when pressure is higher in the buccal cavity than in the parabronchial cavity, water presumably flows unidirectionally from the buccal to the parabronchial cavity. During the periods of pressure reversal, water flow may also reverse, flowing from the parabronchial to the buccal cavity. Although identification of this pressure reversal in respiring sharks is not unique, the timing, duration and magnitude of the reversal are unique. Despite the failure to detect flow reversals externally, it seems unlikely that continuous unidirectional water flow over the gills could persist given such long and large pressure reversals. Of the pressure reversals shown here, some look exactly like those described as occurring occasionally by Hughes (1960b). However, in swellsharks, it appears that such reversals nearly always occur. Further, they occur with greater frequency, magnitude and duration than described by Hughes (1960b, 1965) and Hughes and Shelton (1965).

The ‘classic reversal’ seen in Fig. 5B is often of larger magnitude than previously shown because parabronchial pressure is generally not positive relative to ambient pressure (see Fig. 7A; step 4). Rather, the parabronchial pressure is

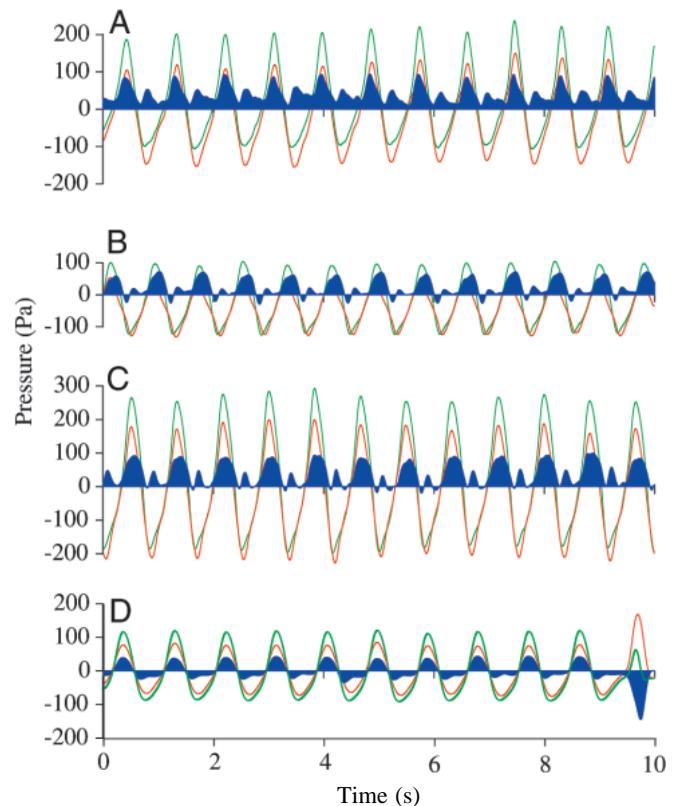


Fig. 5. Representative pressure traces from three individuals (two traces, B and C, are from one individual) indicating the variations observed in differential pressure pattern. The buccal pressure trace (green), parabronchial pressure trace (red) and resulting differential pressure (area beneath curve filled in blue) are overlaid in each plot. Note that the y-axis is scaled differently in each part. The last cycle in D is a cough. Of the patterns shown, one individual consistently exhibited pattern A, one exhibited pattern B, one exhibited pattern C and two exhibited pattern D. A sixth individual alternated between patterns B and C with equal regularity.

negative (see Fig. 7B; step 4), while the buccal cavity pressure is extremely negative. The mouth is closed (necessary to create such a strong negative pressure), and the gills are just closing or even already closed as the pressure in the parabronchial cavity becomes negative (note that dye studies indicated no influx of dye at the gills; thus, the parabronchial valves must be closed even if the external gill slits appear slightly opened).

The ‘two-reversal’ pattern particularly evident in Fig. 5C was also present in the data of Hughes (1960b), although he did not discuss it. Thus, the ventilation model can be modified to describe variation in respiration in catsharks (Scyliorhinidae) more precisely. The phases of respiration indicated in the piston model (Fig. 6A) should represent discrete moments in time taken from real data. Fig. 6B suggests that such discrete intervals do not exist when trying to contrast the model of Hughes (1965) with one sample of actual data from small-spotted catsharks (from Hughes and Ballintijn, 1965). Fig. 7A,B indicates the modifications to Hughes’s model that are necessary to create such snap-shots in

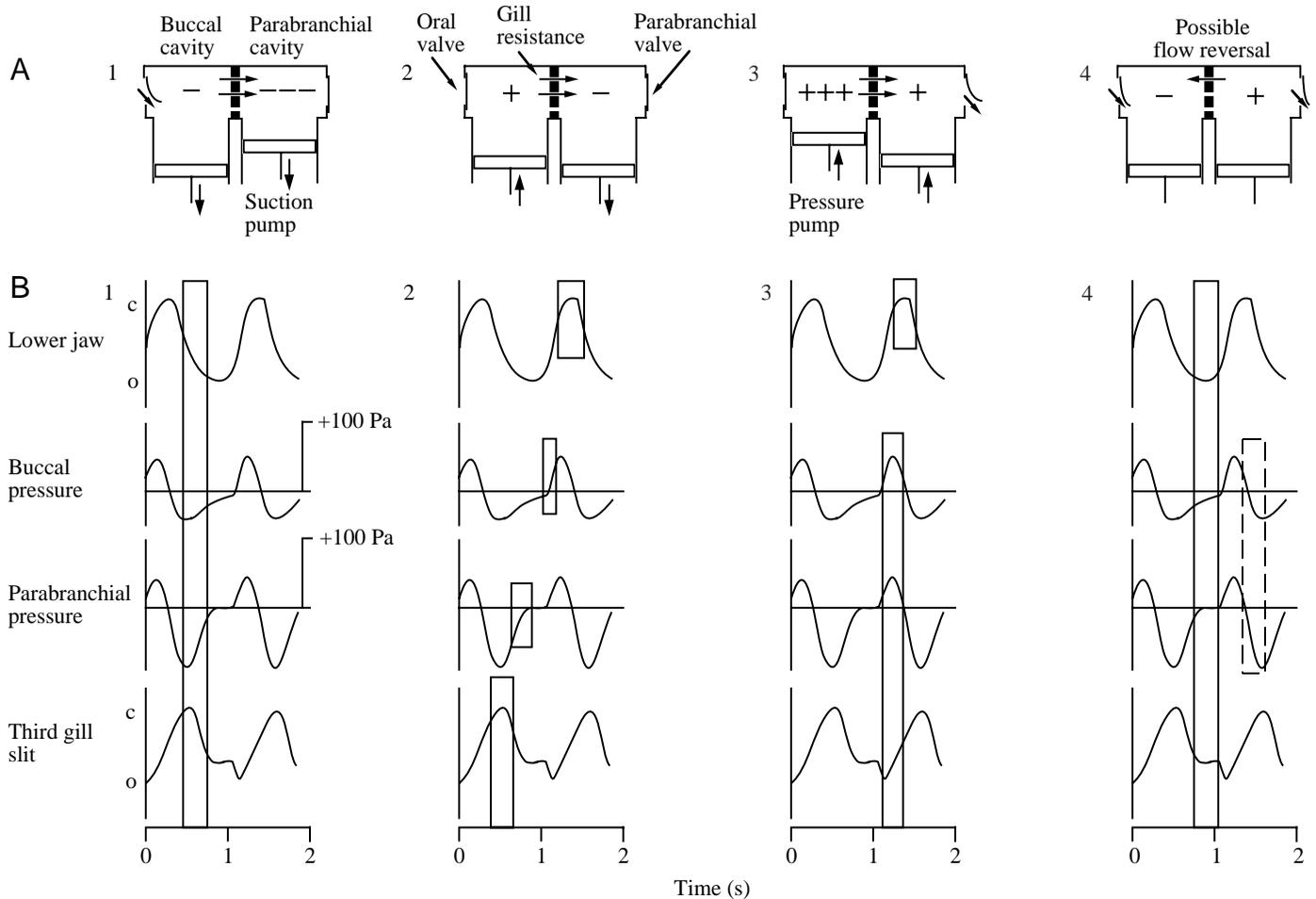


Fig. 6. Hughes' (1965) classic model of fish respiration using a system of pistons to represent the expanding and contracting buccal and parabranchial cavities (A). In B, some of Hughes' (1960b) data for *Scyliorhinus canicula* are shown. On the vertical axes, c refers to closed and o refers to open. The boxes in B demarcate the periods in the pressure and impedance data that are represented by the piston model in A. Note that, in the first step of the model (1; far left), there is clearly a period during which the model describes precisely all aspects of respiration measured. However, in the second step (2), the positions of the pistons and valves represent several different instants in the data, not a single instant. Note in step 4 (panel B) that the primary reversal in pressure (parabranchial pressure > buccal pressure) occurs before the pressure-pump phase, not after as noted in Hughes' model (step 4; A). The dashed box indicates where the reversal should be if Hughes' model fit the data more precisely.

time. In particular, the mouth is generally still open during the transition to the pressure-pump phase (Fig. 7B; step 2), and the gills are starting to open in cases where two reversals exist. The pressure differential is such that the pressure in the buccal cavity is still negative (persisting from the suction-pump phase in step 1) and the parabranchial cavity is at ambient pressure (see alternative pressures provided in Fig. 7B; step 2).

The 'ineffective suction pump' scenario seen in Fig. 5D is most clearly understood using a further modification of the classic piston model of Hughes (1965) (Fig. 7C). On the basis of data from the swellshark (see Fig. 5D), the suction pump is ineffective when buccal pressure remains very negative beyond the classic single reversal that follows the pressure pump (transition from step 4 to step 1 in Fig. 7C). If buccal pressure does not change from negative to positive quickly enough (Fig. 7; step 1), the buccal pressure remains much more negative than the parabranchial pressure throughout the suction-pump phase.

These changes are further supported by data from the present study because the revised model also corresponds to distinct periods within a generalized swellshark sequence (Fig. 8).

Modeler's dilemma

Choosing whether or not to accept the classic model of Hughes (1965) of fish respiration for elasmobranchs becomes something of a modeler's dilemma. Such a dilemma exists regardless of whether the model pertains to population dynamics or to physiological mechanisms; one always faces the decision to develop either a simpler model with broader applicability or a more precise model that fits only particular situations. The trade-off between precision and generality plagues modelers from all disciplines.

Taking the work of Hughes (1960b) and Hughes and Shelton (1965) into account, together with the present study, it would seem that the double-reversal scenario applies at least to the

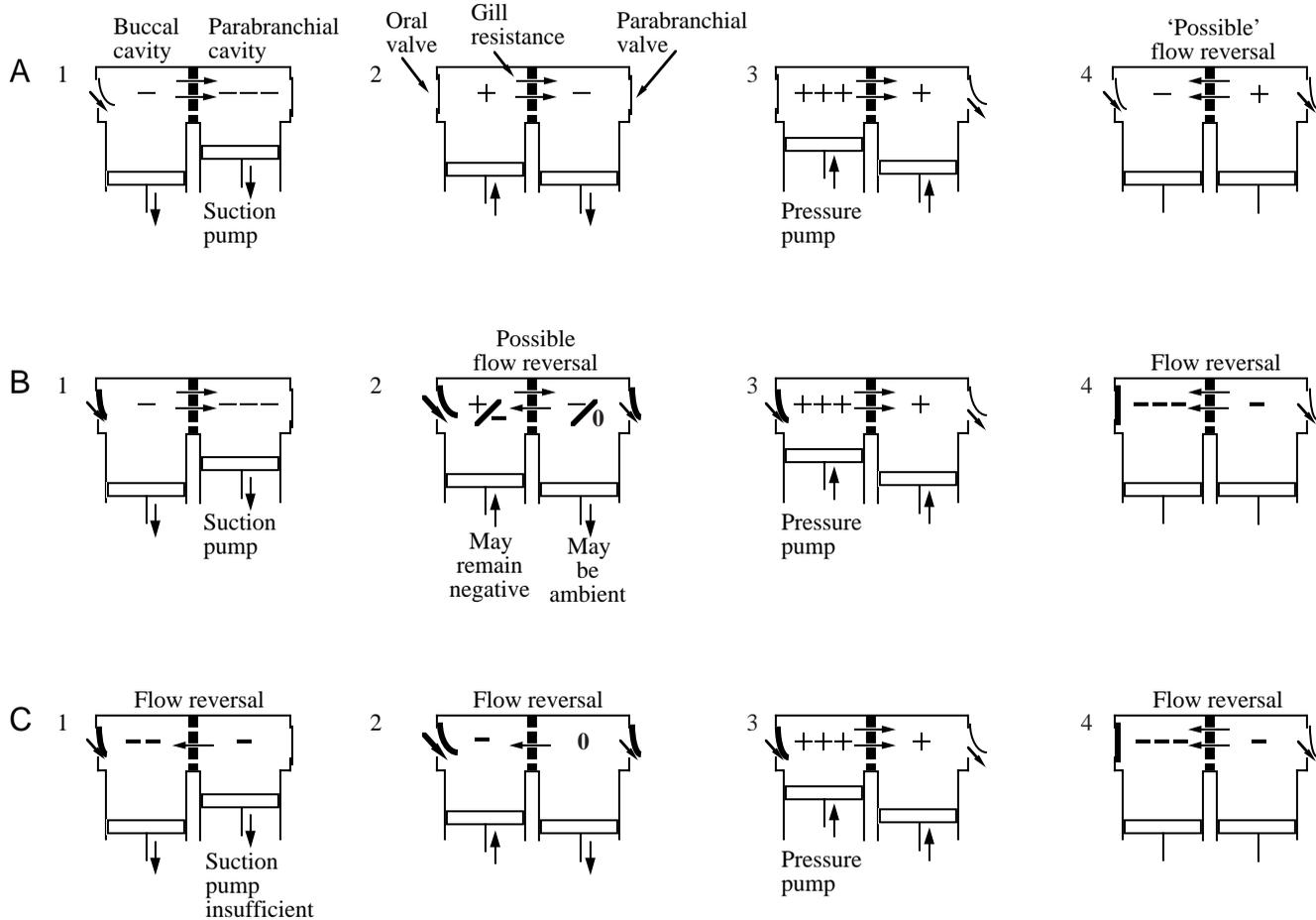


Fig. 7. Hughes' (1965) classic model of fish respiration (A), with changes in the model to fit Hughes's (1965) data and swellshark data containing two reversals (B), and the data from the present study for times when the suction pump is insufficient and pressure reversals persist throughout the period of negative buccal and parabranial pressure (C). Changes to both pressures (relative to ambient) and kinematics are indicated in bold type. For example, when the oral valve is in a position different from that indicated by the classic model (A), it is shown by a thicker line (see B, step 1). The possible flow reversal identified in A was described initially by Hughes (1965). The word 'possible' is placed in quotation marks because swellshark data indicate that it is virtually always present.

catsharks in general (Scyliorhinidae). The occasional absence of a suction pump has not been described for other catsharks, but is probably not unique to the swellshark. The applicability of the extreme reversal models (the double-reversal and ineffective suction pump models) to all elasmobranchs is uncertain, although it would appear that reversals of any kind are rare in skates and rays (Hughes, 1960b, 1978). Further, reversals appear to be rare in the flatfishes (Pleuronectidae) that have been studied (Hughes, 1960a; Liem et al., 1985); thus, extreme reversals are apparently not characteristic of benthic fishes in general. Similarly, although not explicitly investigated by researchers to date, extreme reversals have apparently not been detected in other teleosts whose respiratory mechanics have been studied (Hughes and Shelton, 1958; Hughes, 1960a; Lauder, 1984; Liem, 1985). Thus, the characteristics of extreme pressure reversal and the potential effects on water flow may apply only to benthic sharks.

The duration of the pressure reversals, sometimes exceeding 0.5 s (see Fig. 5D), would suggest that inertia

cannot maintain continuous flow over the gills. Thus, water flow must reverse in response to the pressure reversals if morphological elements do not prevent it. Lauder (1983) has shown that, in teleosts, the gill bars can form an effective barrier between the buccal and opercular (gill) cavities. Therefore, flow reversals may be prevented by active modulation (abduction and adduction) of the gill bars. On the basis of water velocity measurements in and around the gill cavities of a teleost, Lauder (1984) found no evidence for flow actually reversing during periods of pressure reversal. Although sharks clearly possess branchial musculature, it is not known whether they can actively move the gill bars to form a barrier to reversals in water flow. On the basis of the anatomical data of Hughes and Ballintijn (1965) and swellshark dissections (L. A. Ferry-Graham, personal observation), a muscle exists that could be responsible (based on insertions and general location) for drawing the gill arches together to form a barrier to flow reversals: the interarcualis dorsalis. Careful examination of the electromyographic data

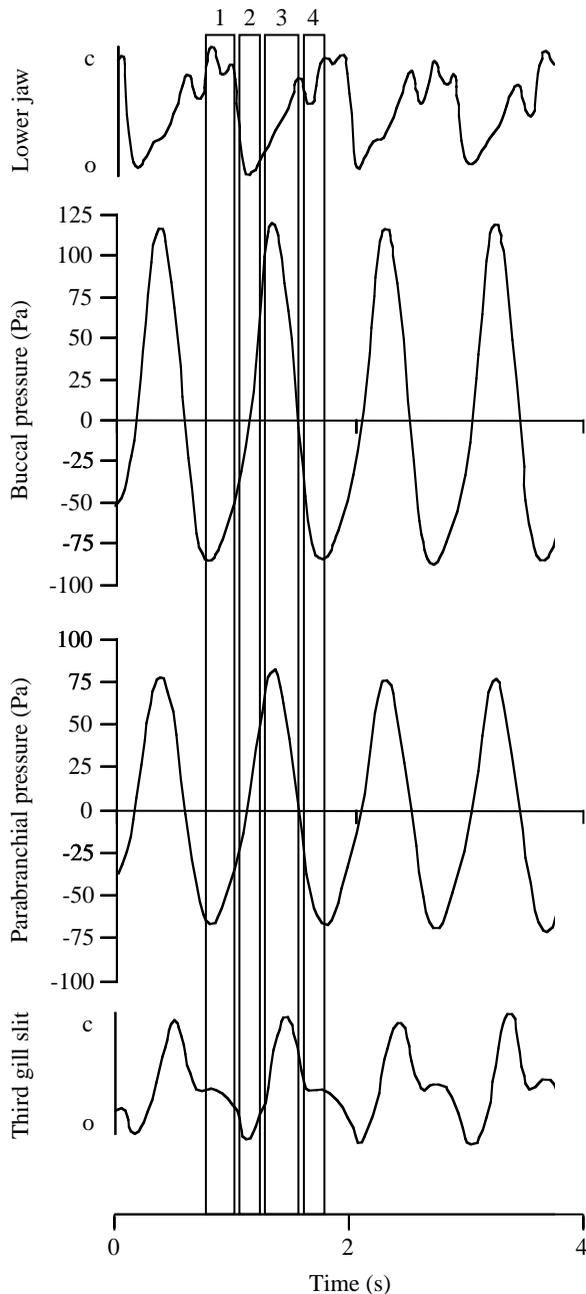


Fig. 8. Times during which the snapshots in Fig. 7C apply to ventilation data from the swellshark. On the vertical axes, c refers to closed and o refers to open. Step 1 of the series indicates a period during which the suction pump is ineffective because of the negative pressure in the buccal cavity. Thus, the reversal in step 4 continues throughout step 1, and positive pressure exists only during the pressure-pump phase, step 3. Differential pressure traces for these data look like those in Fig. 5D.

of Hughes and Ballintijn (1965) combined with simultaneous pressure recordings in the buccal and parabranchial cavities suggest that this muscle is active just prior to and during the early portion of a pressure reversal in the small-spotted catshark. Experimental manipulation of the gill bars or direct measurement of water flow is necessary to confirm the

specific function of the interarcualis dorsalis hypothesized here (see Lauder, 1983, 1984).

The kinematic data serve to infer what is happening to water flow during these periods of pressure reversal. Patterns of expansion of the dorsal surface of the buccal region can indicate when water is entering and exiting the buccal cavity. Such expansion was an accurate indicator of flow in a previous study of feeding in this species (see Ferry-Graham, 1997): the buccal region was expanded when filled with water and compressed as the water exited the cavity. Posterior-to-anterior movement of the expanded portion of the buccal region accurately indicated posterior-to-anterior movement (i.e. flow reversal) of water during feeding in the earlier study (Ferry-Graham, 1997). However, such movement was not detected during respiration. During extensive pressure reversals, it would seem that detectable flow reversals are being prevented and that water must be stalled for some period at the gills. Regardless of whether flow is reversed or stalled, flow through the head of catsharks must be episodic.

Implications for oxygen extraction

If water flow actually reverses direction within the head of respiring swellsharks, even to a small degree that is not detected externally, there would be consequences. Gas exchange over the gills of swellsharks is presumed to occur in accordance with the currently accepted model for most elasmobranchs and fishes; a counter-current transfer system (Hughes and Morgan, 1973; Scheid and Piiper, 1976, 1997). Thus, at the site of gas exchange, the secondary lamella, oxygenated water and deoxygenated blood are flowing in opposite directions. Therefore, a diffusion gradient exists allowing for effectively continuous transfer of oxygen to the blood in the secondary lamella (Piiper and Scheid, 1992). In studies of teleosts, the efficiency of oxygen extraction (% U) decreased from 80% to 10% when water flow was experimentally reversed over the gills [$%U = (P_{IO_2} - P_{EO_2}) / P_{IO_2}$; see Hughes, 1965; Hughes and Morgan, 1973]. The high oxygen extraction efficiency of fishes is generally attributed to the counter-current flow system.

Even if the water is merely held stationary, or pooled around the gills during the periods of pressure reversal, the duration of the reversal events suggests that this should have negative consequences. The reversals during periods of ineffective suction pumping in swellsharks persist for 0.5 s or more, as opposed to short pressure reversals recorded for teleosts of 0.1 s or less (Hughes and Shelton, 1958; Hughes, 1960a; Lauder, 1984; Liem, 1985). Estimates of the efficiency of oxygen extraction for the 'pooled-flow' model (i.e. the mammalian lung; see Scheid and Piiper, 1997) will depend on features such as tidal volume and respiratory rate; however, organisms that rely on the pooled-flow model face limitations to diffusion as the oxygen-containing medium at the diffusion interface becomes desaturated. If water pools around the gills of the swellshark during the periods of pressure reversal, the water immediately adjacent to the secondary lamella may become oxygen-depleted and serve as a barrier to further oxygen extraction.

It is quite possible that extreme pressure reversals, particularly the periods of ineffective suction pumping, contribute to a reduced oxygen extraction efficiency. In contrast to teleosts and some sharks, the nursehound ('dogfish') *Scyliorhinus stellaris* (Scyliorhinidae) and the small-spotted catshark have reported efficiencies of oxygen extraction of approximately 50% (Piiper and Schuman, 1967; Hughes and Umezawa, 1968), which decrease to as low as 20% when flow rates of water over the gills are increased (Hughes and Umezawa, 1968). These sharks are not only closely related to the swellshark phylogenetically but are also ecologically similar (Compagno, 1984). It is reasonable to assume that the swellshark's efficiency of oxygen extraction is equally low. Past studies have attributed a low oxygen extraction efficiency to diffusion resistance at the secondary lamella (due to the properties of both the membrane and the water medium; see Piiper and Schuman, 1967; Scheid and Piiper, 1971, 1976); however, the persistence of pressure reversals might also contribute, because fluctuating water velocities are expected to decrease oxygen extraction efficiency further (Scheid and Piiper, 1971, 1976).

Hughes (1960a,b) carefully pointed out that the degree of development of the suction pump may vary among species, but he also noted that the suction pump mechanism should be the most developed in benthic species that live in nearly stationary water. Data for swellsharks refute this assumption and suggest that the suction pump is apparently not required for generating an adequate respiratory current. Extended pressure reversals prevent the action of the suction pump from contributing to the maintenance of a respiratory current. Individuals of this benthic species achieve sufficient oxygen extraction, as necessary for survival, solely on the basis of the pressure pump.

What remains to be determined is the persistence of pressure reversals in response to increased oxygen demand. Presumably, oxygen extraction, and therefore water flow, should become much more efficient and/or continuous in response to hypoxia or following activity. However, if the findings of Hughes and Umezawa (1968) are correct and further generalized to include the swellshark, reductions in oxygen extraction efficiency with increased flow rates suggest that pressure reversals are potentially enhanced, rather than inhibited by, increased flow over the gills. It is further possible that the active ventilation by swellsharks recorded in the current study represents a condition of enhanced pressure reversal despite kinematic comparisons with unmanipulated animals that suggest otherwise. Pressure reversals during respiration may be a general characteristic of a stress response in species such as the swellshark. However, if this were the case, one would expect pressure reversals to occur more prominently in the dataset of Hughes and Ballintijn (1965) because their animals were severely restrained during experimentation. Further studies of the ventilation mechanics in elasmobranchs are warranted to determine the generality of these findings across physiological conditions and taxa.

I gratefully acknowledge G. Lauder, C. Farmer, and two anonymous reviewers for their comments and improvements to this manuscript.

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