

MECHANICS OF RESPIRATORY PUMPS

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I. INTRODUCTION

To facilitate oxygen uptake and carbon dioxide excretion, fishes ventilate their gas exchange surfaces with water or air. Because water and air differ substantially in their density, viscosity, and oxygen content, the biomechanical problems associated with aquatic and aerial ventilation also differ. Nonetheless, aerial and aquatic respiratory pumps do share one biomechanical challenge stemming from the fact that muscles only generate force in the direction of shortening (Brainerd, 1994b). It is a simple matter for muscle contraction to generate positive pressure and force fluid out of a cavity, but respiratory pumps also require an expansive phase to refill the cavity with new fluid. Some biomechanical trickery is necessary for muscle shortening to cause the expansion of a cavity and the generation of subambient pressure. This trickery generally takes the form of a lever system or occasionally elastic recoil, as is described for aquatic and aerial respiratory pumps in Sections II and III below.

The primary biomechanical problems in the design of aquatic respiratory pumps stem from the physical and chemical properties of water: high density (1000 kg m^{-3} for fresh water), high viscosity ($1.0 \times 10^{-3} \text{ Pa s}$ for fresh water at 20°C), and low oxygen content (from 0.4% by volume in seawater at 30°C to 1% by volume in fresh water at 0°C when in equilibrium with air). To minimize the work of ventilation, the high density of water dictates that the respiratory medium should undergo as little acceleration and deceleration as possible, the high viscosity dictates that fluid velocities should be low, and the low oxygen content dictates that oxygen extraction efficiency should be high. The unidirectional flow, countercurrent gas exchange system of ray-finned and cartilaginous fishes is well designed to meet these requirements (Hughes and Shelton, 1962). Buccal and opercular pumps, as described in Section II, generally work together to produce unidirectional flow of water over the gills, but some interesting cases of momentary flow reversal have recently been discovered (Summers and Ferry-Graham, 2001).

In contrast to water, air has low density (1.2 kg m^{-3} at 20°C), low viscosity ($0.02 \times 10^{-3} \text{ Pa s}$ at 20°C), and high oxygen content (21% by volume). Aerial gas exchange is a primitive characteristic for ray-finned fishes that was lost in basal euteleosts and that has re-evolved at least 38 times and possibly as many as 67 times within acanthomorph fishes (Liem, 1980, 1988; Graham, 1997). Gas exchange organs include lungs, respiratory gas bladders, skin, gills, and various air-breathing organs (ABOs) such as the labyrinth organs of anabantoids (Liem, 1980; Graham, 1997). The biomechanical challenges for aerial respiratory pumps stem from predation risk (because fishes are vulnerable when they go to the surface to breathe and thus must limit their time there), hydrostatic pressure, buoyancy, surface tension, and mechanical conflicts between breathing and feeding. As described in Section III, the solutions to these problems are diverse.

II. AQUATIC RESPIRATORY PUMPS

In fish gills, the exchange of dissolved gases between water and blood occurs on the surface of tiny, leaf-like projections—the secondary lamellae. Water is pumped over the secondary lamellae in a direction opposite to the direction of the blood moving through the vessels of the secondary lamellae (Hughes and Shelton, 1962). This countercurrent flow of water and blood produces much greater oxygen extraction from the water than would be produced by concurrent flow. When the flow is concurrent, water and blood quickly reach diffusion equilibrium and no more oxygen can be extracted. In countercurrent flow, even though diffusion is occurring, the partial pressure of oxygen in the water is always slightly higher than the partial pressure of

the oxygen in the blood, allowing extraction of a high percentage of the oxygen from the water. Countercurrent gas exchange results in oxygen partial pressures that are higher in the blood leaving the lamellae and entering the body than in the water exiting the gill slits. Fishes are the only vertebrates that can achieve such high percentages of oxygen extraction from their respiratory medium (Piiper and Scheid, 1992).

The efficiency of countercurrent exchange depends on the ability of the aquatic respiratory pumps to produce unidirectional flow of water over the gills. In both actinopterygian and elasmobranch fishes, unidirectional flow is achieved with a two-phase pump system.

A. Two-Phase Pump in Actinopterygian Fishes

The two-phase pump models of aquatic ventilation come from the pioneering work of G. M. Hughes (Hughes and Shelton, 1958; Hughes, 1960a,b, 1966, 1970, 1978a,b; Hughes and Ballintijn, 1965; Hughes and Umezawa, 1968; Hughes and Morgan, 1973). In Hughes's models, the buccal and opercular cavities are depicted as pistons (Figure 1.1). The movement of a piston to increase or decrease the volume inside a chamber mimics the expansion and compression of the buccal and opercular cavities during normal ventilation. In the two-phase model, the suction pump phase begins with the opercular cavity compressed and just beginning to expand, causing the pressure inside to be lower than ambient and somewhat lower than the pressure in the buccal cavity (Figure 1.1, stage 1). This expansion of the opercular cavity results in water being drawn into the mouth, over the gills, and into the opercular cavity. At the start of the pressure pump phase, the buccal cavity begins to compress while the opercular cavity continues to expand (Figure 1.1, stage 2). Subsequently, the buccal cavity reaches

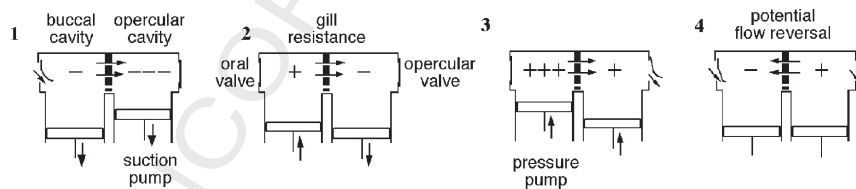


Fig. 1.1. The two-phase pump model of aquatic ventilation as developed by Hughes (1960a,b): stage 1, start of suction pump phase; stage 2, transition from suction to pressure pump; stage 3, pressure pump phase; stage 4, transition from pressure to suction pump phase. During the stage 4 transition, pressure may be momentarily higher in the opercular than in the buccal cavity. Flow reversal may result from the pressure reversal, or adduction of the gill bars may pose enough resistance to block backflow. (Adapted from Ferry-Graham, 1999, Figure 6, p. 1507 and Summers and Ferry-Graham, 2002, Figure 4 p. 96.)

maximal compression before the opercular cavity, thereby maintaining higher pressure in the buccal cavity and maintaining unidirectional flow as water exits the opercular valves (Figure 1.1, stage 3). Just as the pressure pump ends and the suction pump starts again, there is a brief moment of pressure reversal in which opercular pressure is higher than buccal pressure (Figure 1.1, stage 4). This pressure reversal may, in some circumstances, produce brief reversals of flow (see later discussion), but overall the effect of the two-phase pump is to produce flow over the gills that is unidirectional and continuous, albeit highly pulsatile (Hughes, 1960b; Piiper and Schuman, 1967; Scheid and Piiper, 1971, 1976; Malte, 1992; Malte and Lomholt, 1998; Piiper, 1998).

The suction and pressure pumps are powered by abduction and adduction of the opercula, suspensoria, and hyoid apparatus. To generate buccal and opercular expansion and create the subambient pressures of the suction pump, each of these functional units acts as a lever system to convert muscle shortening into abduction of skeletal elements. The motor pattern of the two-phase aquatic respiratory pump is summarized in Figure 1.2 (Liem, 1985). Starting with the pressure phase (P in Figure 1.2) the adductor mandibulae muscle fires (becomes active) to reduce the gape of the mouth, which in many fishes is sealed with a flap-like oral valve that closes in response to superambient pressure in the buccal cavity. Then, the geniohyoideus fires to protract and elevate the hyoid apparatus, and the adductor arcus palatini fires to adduct the suspensorium, thereby compressing the buccal cavity. Increased pressure in the buccal cavity drives water across the gills and into the opercular cavity, and at the end of the pressure pump phase, the adductor operculi contracts and water is forced out the opercular valve. At the beginning of the suction pump phase (S in Figure 1.2), the levator operculi fires to open the mouth by a small amount and the levator arcus palatini fires to abduct the suspensorium. After a slight delay, the dilator operculi fires to abduct the operculum, and the pressure in the opercular chamber falls below buccal pressure and water is drawn over the gills. The branchiostegal rays fan out during opercular expansion to maintain the opercular valve seal. Then the adductor mandibulae fires and the pressure phase starts again.

The slight delay between the start of buccal expansion and the firing of the dilator operculi leads to the potential for a momentary pressure reversal (Figure 1.1, stage 4). The available data to date for teleosts suggest that while pressure reversals do occur, concomitant flow reversals likely do not occur (Hughes and Shelton, 1958; Saunders, 1961). Lauder (1984) demonstrated that the gill bars adduct during the pressure reversal, momentarily increasing the resistance between the buccal and opercular cavities. By placing plastic spacers on the gill bars to prevent them from closing fully during normal

1. RESPIRATION

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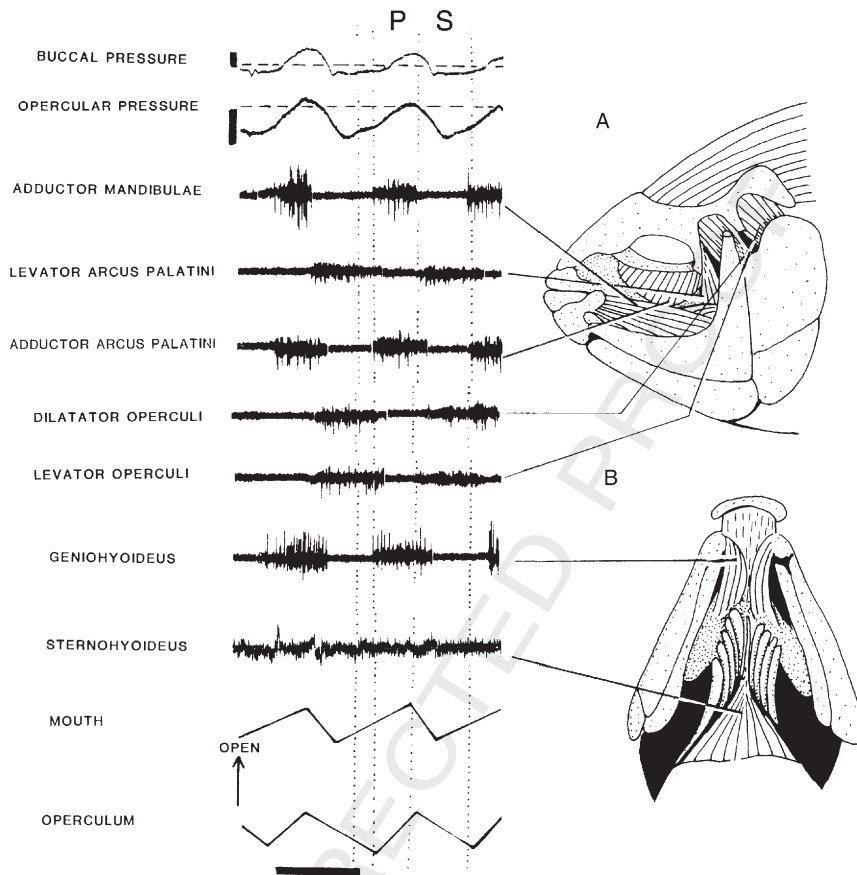


Fig. 1.2. Functional morphology of gill ventilation in an anabantoid, *Heleostoma temmincki*. P, the pressure pump phase (stage 3 of Figure 1.1). Note that buccal pressure always exceeds opercular pressure. S, suction pump phase (stage 1 of Figure 1.1). Note that opercular pressure is lower than buccal pressure. (From Liem, 1985, Figure 11-2, p. 187.)

respiration, Lauder was able to observe flow reversals. When the spacers were absent, flow reversals were not observed (Lauder, 1984).

The two-phase aquatic respiratory pump model has been found to apply to most teleost species studied to date, including the following freshwater fishes: trout *Salmo trutta*, tench *Tinca tinca*, and roach *Leuciscus rutilus* (Hughes and Shelton, 1958); white sucker catfish *Catostomus commersoni* and brown bullhead catfish *Ictalurus nebulosus* (Saunders, 1961); and carp *Cyprinus carpio* (Saunders, 1961; Ballintijn, 1969a,b). Pelagic and semi-pelagic marine species studied include the horse mackerel *Trachurus*

trachurus, herring *Clupea harengus*, whiting *Gadus merlangus*, conger eel *Conger conger*, rockling *Onos mustela*, great pipefish *Syngnathus acus*, and wrasse *Crenilabrus melops* (Hughes, 1960a). Benthic marine species also appear to fit this model: stickleback *Gasterosteus aculeatus* (Anker, 1978; Elshoud, 1978), bullhead sculpin *Cottus bubalis*, butterfly blenny *Blennius ocellaris*, grey gurnard *Trigla gurnardus*, and dragonet *Callionymus lyra* (Hughes, 1960a). Morphological evidence combined with opportunistic observation of live specimens suggests that the two-phase pump is also used by the bowfin *Amia calva* (Liem, 1985) and coelacanth *Latimeria chalumnae* (Hughes, 1995).

Even the morphologically bizarre flatfishes appear to fit this model (Hughes, 1960a; Liem *et al.*, 1985). With one eye having migrated to the opposite side of the head, they rest on the substrate on the “blind side,” which can be either the left or the right side of the body. When flatfishes are at rest and buried in mud or sand, the two-phase pump is modified such that water generally exits from only the eyed side (Yazdani and Alexander, 1967; Kerstens *et al.*, 1979). During activity or when exposed to hypoxia, water exits from both sides (Steffensen *et al.*, 1981a; Liem *et al.*, 1985), and during extreme hypoxia, flatfishes will even raise their heads up above the substrate, presumably to reduce the resistance encountered by the exhaled water (Steffensen *et al.*, 1981a).

For reasons that are unclear, some teleosts have gill slits that are restricted to a small hole; the rest of the opercular valve and the branchiostegal rays are covered with skin. Some of the fishes with tiny gill openings are all tetraodontiforms (pufferfishes, triggerfishes and their allies), some pleuronectiforms (flatfishes), synbranchiform and elopomorph eels, some antennariids (anglerfishes), and some gasterosteiforms (pipefish and seahorses). The puffers, anglerfishes, flatfishes, and seahorses jet water out of their gill openings at the start of locomotion or when handled (Brainerd *et al.*, 1997; E.L.B., personal observation). It is possible that the function of reduced gill slits is to increase the velocity of these water jets, but a more thorough survey of opercular valve morphology and function is needed to draw any firm conclusions.

B. Two-Phase Pump in Elasmobranch Fishes

It was once thought that a countercurrent gas exchange system does not exist in cartilaginous fishes because they often exhibit lower oxygen extraction efficiencies relative to bony fishes (Millen *et al.*, 1966; Piper and Schuman, 1967). Elasmobranchs differ morphologically from actinopterygian fishes in several ways with regard to respiratory features. Most notably, they have five or more gill slits on each side of the head compared with the single opercular opening in ray-finned fishes. The parabranial chambers in

elasmobranchs, which are homologous with the opercular chamber of actinopterygians, are similarly separated by septa along their length internally. Early work by several authors proposed that the septa, to which the lamellae are attached, might interfere with the flow of water and force concurrent exchange during at least part of the respiratory cycle (Hughes and Shelton, 1962; Piiper and Schuman, 1967). Piiper and Schuman (1967) proposed a “multi-capillary” model, much like gas exchange in birds, to explain the observed partial pressures of oxygen in the blood and the ventilatory water. Further work, however, rejected this view on the grounds that the partial pressure of oxygen in the arterial blood was higher than that of the expired water in the *Scyliorhinus stellaris*, as can only be achieved with a countercurrent gas exchange system (Piiper and Baumgarten-Schumann, 1968). Further investigations support the notion of a countercurrent gas exchanger in elasmobranchs (Grigg, 1970; Scheid and Piiper, 1976; De Vries and De Jager, 1984), and the countercurrent exchange model presently serves to describe gas exchange in all aquatic-breathing fishes, even hagfish (Malte and Lomholt, 1998) and lamprey (Mallatt, 1981, 1996).

The respiratory pump in elasmobranchs is a two-phase pump that is very similar to the actinopterygian two-phase pump (Figure 1.3A) (Hughes, 1960b; Hughes and Ballintijn, 1965). Recent work on several elasmobranch species has demonstrated, however, that flow reversals are only partially prevented by the action of the gill bars, and that flow reversals may be widespread among species and body types (Figure 1.3B) (Ferry-Graham, 1999; Summers and Ferry-Graham, 2001, 2002). It is only with the application of technologies recently made available to biologists that we have been able to observe directly the path and pattern of water flow during ventilation. The pioneers in this field had to rely on pressure recordings taken inside the respiratory chambers to infer patterns of water flow. Further, movements of any pertinent anatomical features, because they are internal, could only be inferred from electromyographic recordings indicating when the muscles were electrically active, but not necessarily performing actual movements. The addition of sonomicrometry to this field has allowed the determination of the physical position of important morphological elements. Sonomicrometry, combined with the use of endoscopy to visualize anatomical elements in action and the movement of the ventilatory water, has confirmed that although the core elements of Hughes’s elasmobranch models are correct, small differences exist, at least among the species originally studied and those studied more recently (Ferry-Graham, 1999; Summers and Ferry-Graham, 2001, 2002). The most important of these is the observation that the gill bars do close, but not for the entire duration of the pressure reversal period (Figure 1.4). Thus, water does flow back over the gills and into the oral chamber.

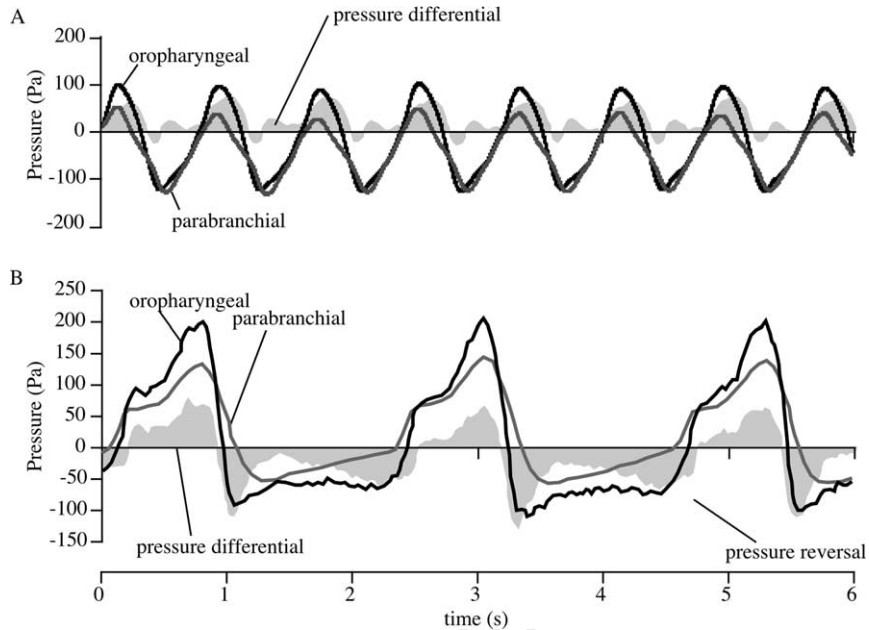


Fig. 1.3. Representative traces showing pressure reversals in (A) *Cephaloscyllium ventriosum* and (B) *Leucoraja erinacea*. The data from *L. erinacea* show much longer pressure reversals (indicated by negative pressure differential). Individuals of *C. ventriosum* also sometimes showed reversals of this magnitude and duration, although they were not as common. *Squalus acanthias* (data not shown) also showed both types of reversal profiles. *L. erinacea* did not exhibit profiles as in (A). Profiles from *C. ventriosum* and *L. erinacea* sometimes lacked a pressure reversal; *S. acanthias* profiles always had a reversal of some nature.

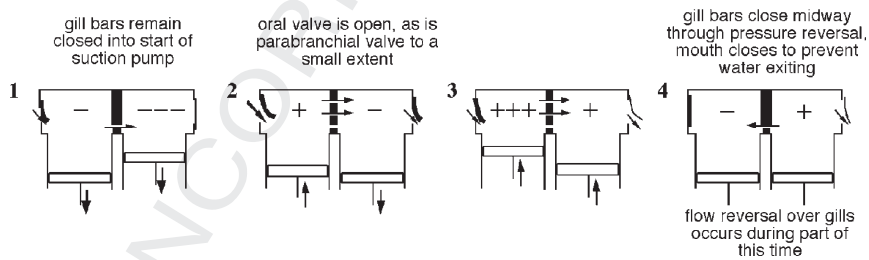


Fig. 1.4. Modifications to the two-phase pump model in elasmobranchs verified by sonometric data and direct observation of anatomical elements and water flow inside the oral and parabranchial chambers using endoscopy (Summers and Ferry-Graham, 2002). Specific modifications are indicated with text on the figures at each time interval. The mouth may be slightly open in stage 4, depending on the species. (Adapted from Ferry-Graham, 1999, Figure 7, p. 1508 and Summers and Ferry-Graham, 2002, Figure 4, p. 96.)

Flow reversals have been difficult to detect since they are typically not apparent externally. Valves normally prevent water from exiting the mouth or entering through the gill slits in most species. Water was never observed exiting the mouth in the swellshark *Cephaloscyllium ventriosum* (Ferry-Graham, 1999; Summers and Ferry-Graham, 2002), and it only rarely exited the mouth in the skates *Leucoraja erinacea* and *Raja clavata* (Hughes, 1960b; Summers and Ferry-Graham, 2001, 2002). Water exited the mouth more frequently in the dogfish *Squalus acanthias*, but not for the entire portion of the pressure reversal period and not during every pressure reversal (Summers and Ferry-Graham, 2002). Water never entered through the gills slits in any species studied. This is likely due to the fact that the reversals are fairly small in nature and short in duration. For example, water did not exit the mouth of most *L. erinacea*, even when the mouth was open and flow reversals were directly observed at the gills (Summers and Ferry-Graham, 2002).

Bidirectional flow has been observed, and tends to be much more obvious, at the spiracles of some elasmobranchs. Spiracles are openings on the dorsal surface of the head that lead directly to the oral chamber and channel water toward the gills. Recent comparative analyses suggest that the spiracle is a derived feature within elasmobranchs (Summers and Ferry-Graham, 2002), but this analysis depends strongly on the placement of the batoids within any given elasmobranch phylogeny, and the position of Batoidea is still in flux (Shirai, 1996; Douady *et al.*, 2003). The presence of the spiracle is not tightly correlated with a benthic habitat, as *C. ventriosum*, a derived carchariform shark, is largely benthic but lacks spiracles, and *S. acanthias*, a basal squaliform shark, spends much of its time in open water and has fairly large spiracles. However, the use of the spiracle as the exclusive ventilatory aperture has been observed only in benthic species.

Water was seen to enter and exit the spiracle in *L. erinacea* when the skate was resting on the bottom (Summers and Ferry-Graham, 2001), and was also seen on occasion in *R. clavata* in earlier studies (Hughes, 1960b). In contrast, no consistent pattern of exclusive spiracular use was observed in the non-benthic dogfish, *S. acanthias*. Skates tend to rest or even bury themselves in the substrate, and thus the mouth is not or cannot be used to draw in a current of water for respiration during these periods of time. Outflow through the gills may be similarly reduced to prevent stirring up sediment upon discharge. Although distantly related, the sturgeon, *Acipenser transmontanus*, provides some evidence for this notion via the evolution of convergent structures. The sturgeon inhabits and forages in largely silty benthic habitats. Despite its reduced spiracles, enlarged openings on the dorsal regions of the gill slits serve to both draw in and expel water for respiration (Burggren, 1978). Other benthic fishes, such as *C. ventriosum*, in which the spiracles are so reduced that they are presumed to be nonfunctional, have been observed propped up on

their pectoral fins or with their neurocrania rotated dorsally during periods of very active buccal pumping, thereby increasing the exposure of the mouth to the surrounding water (L.A.F.G., personal observation).

The physiological consequences of flow reversals, whether the reversals be inadvertent, as during the switch from pressure to suction pump, or apparently deliberate, as in spiracular breathing, may not be as grave as some researchers have suggested. Most species can tolerate large, experimentally induced inefficiencies in gas exchange (Malte, 1992), and it is likely that natural flow reversals decrease as oxygen demand increases and the respiratory pumps work harder.

The kinematics of ventilation in elasmobranchs are highly variable (Hughes, 1960b, 1978a; Hughes and Ballintijn, 1965). Much of this variation may be driven by physiological requirements, such as oxygen demand. For example, increases in ventilatory stroke volume are likely achieved by increases in the compression and subsequent expansion of the oral and parabranial chambers. When a fish is at rest and the oral and parabranial chambers are compressed to a lesser degree, the two-pump system can break down. Several scenarios have been documented, ranging from double pressure reversals to a complete failure of the suction pump to operate. Figure 1.5 depicts a scenario in which the pressure reversal is extreme. Sonometric and endoscopic data show that the gill bars are closed during stages 1 and 2 of such sequences, preventing prolonged reversals in water flow. However, water is also not flowing from anterior to posterior, as the suction pump is insufficient to generate flow. Variations of this pattern exist such that pressure reversals are seen at stages 4, 1, and 2 (Summers and Ferry-Graham, 2002), and just 4 and 2 (Ferry-Graham, 1999), whereby the suction pump presumably manages to create some anterior-to-posterior flow between pressure reversals.

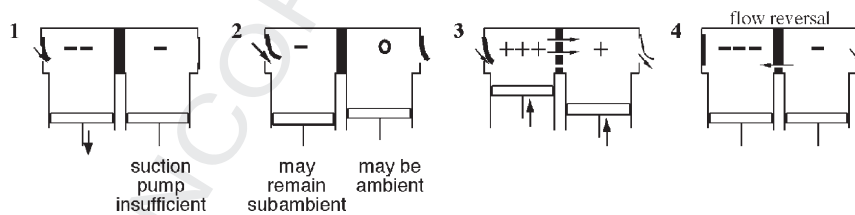


Fig. 1.5. A general scenario depicting a complete failure of the suction pump to generate anterior-to-posterior water flow verified by sonometric data and direct observation of anatomical elements and water flow inside the oral and parabranial chambers using endoscopy (Summers and Ferry-Graham, 2002). The mouth may be slightly open in stage 4, depending on the species. (Adapted from Ferry-Graham, 1999, Figure 7, p. 1508 and Summers and Ferry-Graham, 2002, Figure 4, p. 96.)

C. Ram Ventilation

During ram ventilation, a respiratory current is generated by the locomotor efforts of the fish. In fast-swimming fishes, water enters the oral cavity and passes over the gills as long as the fish holds its mouth and opercular valves open.

Many fishes are able to buccal pump when needed but switch to ram ventilation at appropriate swimming speeds. Facultative ram ventilation has been documented in paddlefish *Polyodon spathula* (Burggren and Bemis, 1992; Sanderson *et al.*, 1994), sandtiger sharks *Odontaspis* (= *Eugomphodus* or *Carcharias*) *taurus* (von Wahlert, 1964), leopard sharks *Triakis semifasciata* (Hughes 1960b), a variety of salmonids (Roberts, 1978; Steffensen, 1985), several pelagic species such as mackerel *Scomber scombrus*, blue runner *Caranx crysos*, bluefish *Pomatomus saltatrix*, scup *Stenotomus crysops*, and the halfmoon *Medialuna californica* (Roberts, 1975), and shark-suckers *Echeneis naucrates* and remoras *Remora remora* when attached to a fast-swimming shark or aquatic mammal (Muir and Buckley, 1967; Steffensen and Lomholt, 1983; Steffensen, 1985). Interestingly, a number of species, including some that routinely move into open water habitats, never switch to ram ventilation. An apparent inability to perform ram ventilation has been documented in the striped mullet *Mugil cephalus* and in basses and rockfishes of the genera *Paralabrax* and *Sebastes* (Roberts, 1975). In facultative ram ventilation, the switch from buccal pumping to ram ventilation is triggered by a mechanoreceptor that is stimulated by flow velocity (Roberts and Rowell, 1988); benthic fishes may lack this reflex altogether (Roberts, 1978). Switching from active pumping to passive ram ventilating is estimated to save about 10% of the total energy expenditure during high-speed locomotion, although these calculations are only rough estimates (Brown and Muir, 1970; Roberts, 1978; Steffensen, 1985).

In contrast, pelagic fishes such as the scombrids (tuna and mackerel, primarily tuna), istiophorids (sailfish), and xiphiids (swordfish) are obligate ram ventilators. Their branchial anatomy is so severely reduced that they cannot generate a sufficient respiratory current using the buccal pump. There is a great deal of fusion of both the gill filaments and the lamellae in all of these families of fishes as well as in the dolphinfish *Coryphaena hippurus* (Muir and Kendall, 1968). Lamellae on adjacent filaments may be fused to one another along their facing edges, and in some adjacent filaments may even be fused along part of their length. Water passes through small slits or openings where fusion is incomplete. The reason for the fusion is not entirely clear, but it occurs widely among fast-swimming oceanic fish, and there appears to be greater fusion in more-derived species. Possible advantages of fusion include (1) restricting access by parasites to the gill tissues,

(2) increasing the rigidity of the structure so that it does not collapse and can therefore extract the greatest amount of oxygen possible, and (3) reducing the velocity of water flow over the lamellae to increase oxygen extraction (Muir and Kendall, 1968). Interestingly, similar fusion is found in *A. calva*, which lives in stagnant marshes, further suggesting that enhanced oxygen extraction may be a primary function of the fusion (Bevelander, 1934).

D. Gill Ventilation in Lamprey and Hagfish

In the two groups of extant jawless fishes, the anatomy of the respiratory pumps is markedly different from that of gnathostome fishes. Nonetheless, water flow through the oropharynx in lampreys and hagfishes is largely unidirectional and countercurrent gas exchange occurs (Mallatt, 1981, 1996; Malte and Lomholt, 1998).

The respiratory structures of hagfishes consist of pairs of sacs or pouches, anywhere from 6 to 14 depending on the species, that house the gill lamellae. The lamellae are the primary gas exchange surfaces (Malte and Lomholt, 1998). The skin of the hagfish is also quite permeable, but, except when scavenging on carcasses and other large food falls, hagfish are largely buried in the sediment with only their nostrils and tentacles exposed (Steffensen *et al.*, 1984). Water reaches the pouches through afferent ducts originating in the posterior portion of the pharynx and exits through efferent ducts that lead to external gill openings on either side of the animal. In some species, the efferent ducts fuse to form one common opening to the surrounding medium. Water enters the pharynx through the mouth or the nostril and is pumped into the afferent ducts by the action of the velum (Malte and Lomholt, 1998). The velum is a muscular structure situated at the dorsal midline of the rostral portion of the pharynx that serves to contract the chamber and pump water posteriorly. As a result, the flow entering the nostril is pulsatile and the frequency is highly variable, ranging from 0.01 to 1.3 Hz (Steffensen *et al.*, 1984), with the higher frequencies recorded from hagfish under warmer experimental conditions.

Based on anatomical studies, it was long thought that the velum alone was responsible for generating the respiratory current, and hagfish had little ability to alter the path of water once in the head. One of the first studies to examine hagfish anatomy in action was a cineradiographic study (Johansen and Hol, 1960). In this study, the researchers used barium and hypaque dyes that fluoresce under radiographic light to follow the path of the respiratory currents in live animals after introducing the contrast agents at either the mouth or the nostril. This foundational, and unequalled, study revealed that hagfish do use pumping of the velum to generate respiratory water flow through the head. However, the gill pouches themselves are muscular and

also pump water through the system. Flow is further modified by the active control of sphincters located at both the afferent and efferent ends of the gill ducts. The sphincters open and close rhythmically during normal respiration, but this pattern can be altered as conditions require. The barium solution, for example, rarely entered the gill ducts and instead was routed directly from the esophagus to the gill openings, frequently by extreme expansion of the esophagus. Presumably, overfilling this chamber allowed for the forceful ejection of the offending material through the gill openings, and barium was prevented from entering the gill pouches by the sphincters. If a small amount of barium did enter the pouches, it was ejected back into the esophagus rather than continuing through the efferent gill ducts, where the maintenance of unidirectional flow is assisted by peristaltic-type contractions (Johansen and Hol, 1960). Clearly, hagfish can determine the water quality and/or particle sizes entering the head and alter the path of respiratory water accordingly to avoid contact with gas exchange surfaces.

Similar to hagfish, larval lamprey, or ammocetes, primarily use the action of a velar pump to generate a respiratory current (Rovainen, 1996). Ammocetes are suspension feeders, and thus ventilation and feeding are coupled and rely on a unidirectional current (Mallatt, 1981). The gill pouches are located within the pharynx (Mallatt, 1981), also referred to as the branchial basket (Rovainen, 1996). The velum has flaps that come together to form a seal during contraction, presumably preventing the flow of water back out the mouth. The velum moves posteriorly and the branchial basket contracts to produce an expiratory current, although the contribution of basket compression to expiration seems to be directly and positively related to activity or oxygen demand (Mallatt, 1981; Rovainen, 1996).

The inspiration of water back into the pharynx is powered primarily by elastic recoil of the branchial basket (Mallatt, 1981; Rovainen, 1996). During inspiration, water enters the mouth, passes through the velum and into the pharynx and gill sacs, and then exits via the branchiopores. Valves over the branchiopores reduce the influx of water during expansion of the branchial basket, but Mallatt (1981) noted that they function imperfectly and water is often drawn into the pharynx through the branchiopores during the inspiratory phase.

Mallatt (1981) suggested that the combined action of the velum and the branchial basket in ammocetes is sufficient to generate a two-phase pump as seen in actinopterygians and elasmobranchs. Contraction during expiration forces water laterally over the gill filaments and out the branchiopores and constitutes the first phase of the pumping cycle, the pressure pump phase. Elastic recoil of the basket during inhalation draws water in through the mouth via suction and constitutes the second phase of the pumping cycle. During ventilatory cycles in which only velar pumping is used and contraction

of the basket does not contribute to water flow, the suction pump is not sufficient to generate substantial lateral flow across the gills. As noted previously, there is detectable backflow during the suction pump phase where water is drawn in through the branchiopores. This backflow period can be lengthy, persisting for up to half of the complete ventilatory cycle.

During metamorphosis from ammocete larva to adult lamprey, the velum is extensively remodeled. Many adult lamprey are parasitic, feeding by attaching their rasping mouth parts onto the sides of fishes with a sucker-like structure. Therefore, the mouth and anterior portions of the head are largely unavailable for respiration, and water both enters and exits the gill sacs via the external branchiopores. In adults, the velum presumably functions to prevent the rostral flow of water and maintain ventilation separate from feeding, while contraction and elastic recoil of the branchial basket exclusively generate the respiratory current (Mallatt, 1981; Rovainen, 1996).

III. AERIAL RESPIRATORY PUMPS

A. Evolutionary History and Biomechanical Challenges

Lungs are present in basal members of Actinopterygii and Sarcopterygii but not in Chondrichthyes; therefore, it is most parsimonious to conclude that lungs arose in stem osteichthians and have been retained as a primitive character in actinopterygians and sarcopterygians. Within Actinopterygii, paired lungs are present only in Polypteriformes, and an unpaired lung, homologous with paired lungs and termed a gas bladder, is present in other basal actinopterygians (Liem, 1988; Graham, 1997). The pneumatic duct connecting the gas bladder to the pharynx was lost in euteleosts, probably in stem acanthomorphs, and buoyancy control became the primary function of the gas bladder. Thus, the physoclistous swim bladder of euteleosts is homologous with the physostomous gas bladders of basal actinopterygians and with the lungs of tetrapods.

The physostomous gas bladder lost and regained its respiratory function several times in the evolutionary history of basal actinopterygians and teleosts (Liem, 1989b). However, once the pneumatic duct was lost, the swim bladder did not regain its respiratory function in any euteleosts. Instead, various other kinds of ABOs evolved, such as the suprabranchial chambers of *Channa* and *Monopterus*, the branchial diverticulae of *Clarias* and anabantoids, and the stomach and intestinal modifications of some siluriforms (Graham, 1997).

All air-breathing fishes are bimodal or trimodal breathers (Graham, 1997). They retain gills as important sites of CO₂ excretion and ion

exchange, and the gills also absorb oxygen when the water is not hypoxic. In addition, the skin is often an important site of gas exchange, both in water (Steffensen *et al.*, 1981b) and when fishes emerge during “terrestrial trespassing” (Liem, 1987). In severely hypoxic water, some air-breathing fishes may actually lose oxygen to the water through their gills and skin if the oxygen derived from air breathing causes the blood to have a higher oxygen tension than the surrounding water. This apparent inefficiency results from the fact that blood from most ABOs flows back to the heart and gills before being redistributed to the rest of the body. This seemingly maladaptive system is one of several lines of evidence that led to the myocardial oxygenation theory (Farmer, 1997), in which selection for increased oxygen delivery to the heart muscle is proposed as a primary selection force in the evolution of air breathing.

Aerial respiratory pumps face biomechanical challenges that result from the interaction of air and water. Within lungs and gas bladders, pressure generated by aerial pumps must overcome the surface tension of the air-liquid interface. However, surface tension is probably quite low, as surfactants are produced by the epithelia of gas bladders and lungs (Liem, 1988). Hydrostatic pressure also affects aerial respiratory pumps. If a fish takes an air breath with its body at an angle with the surface of the water, as is usually the case, then the aerial pump pressure must exceed the hydrostatic pressure at the deepest part of the gas-filled space (Figure 1.6). On the other hand, hydrostatic pressure may also assist breathing by contributing to exhalation.

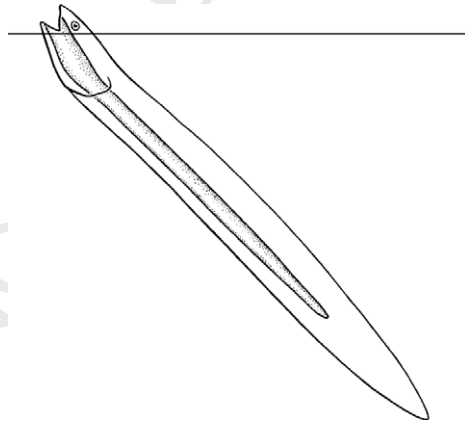


Fig. 1.6. The effect of hydrostatic pressure on air breathing. When a fish approaches the surface at an angle, hydrostatic pressure at the caudal end of the lungs or gas bladder may assist expiration but will also oppose inspiration.

Air breathing strongly affects the buoyancy of fishes, and this coupling between respiration and buoyancy places a constraint on the volume of air that can be held in a gas exchange organ. Fishes are vulnerable to both aerial and aquatic predators when they come to the surface to breathe (Kramer and Graham, 1976). Presumably there is selection to breathe as infrequently as possible, which should favor high-volume gas exchange organs. However, too much air would result in positive buoyancy—a condition that traps fishes on the surface and increases their vulnerability to predators. Therefore, the upper limit on the size of aerial gas exchange organs is constrained by the need to avoid positive buoyancy.¹ In addition, air-breathing fishes have fine control over their gas volume and manage their buoyancy at slightly negative, neutral, or slightly positive, depending on their behavioral needs at any given moment in time (E.L.B., personal observation). In most cases, total gas volume is probably regulated on the basis of buoyancy, whereas tidal volume and breath frequency vary with metabolic needs.

B. Air Ventilation Mechanics

Unlike ourselves and other amniotes, fishes lack the intercostal and/or diaphragmatic muscles necessary for aspiration breathing. Instead, almost all air-breathing fishes use buccal pump breathing, in which expansions and compressions of the buccopharyngeal cavity ventilate the gas exchange organs (Liem, 1985). As described previously for aquatic ventilation, the hyoid apparatus and suspensorium act as lever systems to convert muscle shortening into buccal cavity expansion, thereby generating subambient pressure and drawing air in through the mouth. As the mouth closes, the hyoid protracts and the suspensorium adducts, generating superambient pressure and forcing air into the gas exchange organ. Aquatic ventilation, suction feeding, and aquatic coughing all involve buccopharyngeal expansion and compression, and the evolution of aerial buccal pumps appears to have occurred by modifying and combining these basic behaviors (McMahon, 1969; Liem, 1980, 1985; Brainerd, 1994a).

AU1

In most basal actinopterygian and basal teleost fishes, the respiratory gas bladder is ventilated with a four-stroke buccal pump, named by analogy with the piston movements in four-stroke internal combustion engines (Brainerd *et al.*, 1993; Brainerd, 1994a). A four-stroke air breath begins as the fish approaches the surface and transfers gas from the gas bladder into the buccal cavity. Hydrostatic pressure, elastic recoil of the gas bladder or

¹One could imagine a scenario in which fishes might experience selection for added bone mass to offset a larger lung, if selection for infrequent air breathing were sufficiently strong. One possible group in which to look for this effect would be the armored catfishes.

body wall, and active expansion of the buccal cavity, thereby sucking gas out of the gas bladder, may all contribute to the transfer phase of expiration (Liem, 1988; Brainerd, 1994a). After gas transfer, the buccal cavity compresses and expired gas is expelled either out the mouth (*Amia*) or out the opercular valves (all others). With the fish still at the surface, the mouth then opens and the buccal cavity expands to inspire fresh air, whereupon the mouth closes and the buccal cavity compresses to pump the fresh air into the gas bladder. Thus, the four strokes of this buccal pump are (1) gas transfer, (2) expulsion, (3) inspiration, and (4) compression (Figure 1.7). Four-stroke breathing has been observed in basal actinopterygians, *Amia* and *Lepisosteus*, and in basal teleosts, *Arapaima*, *Gymnarchus*, *Notopterus*, *Pangasius* (Rahn *et al.*, 1971; Liem, 1988, 1989b; Brainerd, 1994a), and *Megalops* (E.L. B., personal observation).

In contrast to the four-stroke buccal pump of actinopterygians, lepidosirenid lungfishes ventilate their lungs with a two-stroke buccal pump² (Bishop and Foxon, 1968; McMahon, 1969; Brainerd *et al.*, 1993; Brainerd,

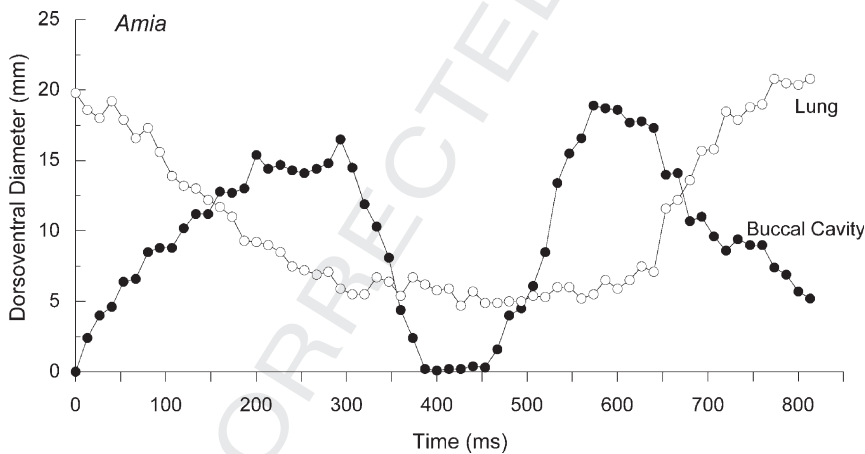


Fig. 1.7. Kinematics of four-stroke breathing in *Amia calva*. Changes in the maximum diameter of the buccal cavity and gas bladder were measured in lateral projection x-ray videos. Note that gas bladder diameter decreases during the first buccal expansion, and then the buccal cavity compresses to expel all of the expired air. Then the buccal cavity expands to draw in fresh air and gas bladder diameter increases as the buccal cavity compresses for the second time. (From Brainerd, 1994a, Figure 2, p. 291.)

²No data are available on air ventilation in the only extant, non-lepidosirenid lungfish, *Neoceratodus*, but observations of an Australian lungfish taking air breaths in a public aquarium suggest that they may use a four-stroke pump (E.L.B., personal observation).

1994a). With the snout of the lungfish protruding slightly from the surface of the water, the mouth opens and the buccal cavity expands to draw in fresh air. While the buccal cavity is expanding, exhalation of air from the lungs begins, driven by hydrostatic pressure, elastic recoil of the lungs and body wall, and possibly the contraction of smooth muscle in the lung walls. Neither buccal suction nor contraction of body musculature contributes to expiration (Figure 1.8). Buccal expansion generally continues beyond the end of expiration, and then buccal compression forces gas into the lungs (Figure 1.9). Because the buccal cavity does not compress after exhalation in two-stroke breathing, expired gas mixes with fresh air in the buccal cavity, and then this mixed gas is pumped into the lungs. In contrast, all of the expired gas is expelled from the buccal cavity in four-stroke breathing before fresh air is inspired and pumped into the gas bladder (Figure 1.7).

The two-stroke buccal pump is present in amphibians as well as in lepidosirenid lungfishes (Brainerd *et al.*, 1993), whereas the four-stroke buccal pump is typical of actinopterygian fishes. This phylogenetic pattern indicates that two-stroke breathing is the ancestral condition for Sarcopterygii, whereas four-stroke breathing is the ancestral condition for Actinopterygii. The ancestral condition for Osteichthyes cannot be determined, because no extant outgroups to Osteichthyes breathe air (Brainerd, 1994a).

The kinematics of the two- and four-stroke buccal pumps resemble kinematics associated with gill ventilation, suction feeding, and aquatic coughing (Brainerd, 1994a). Four-stroke breathing, suction feeding, and

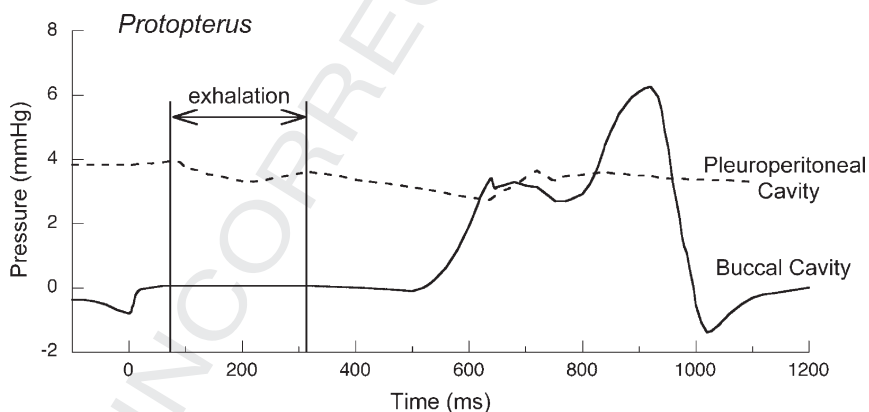


Fig. 1.8. Buccal and pleuroperitoneal (abdominal) pressure during an air breath in *Protopterus aethiopicus*. Note that pleuroperitoneal pressure decreases during exhalation, indicating a slight contribution of body wall elastic recoil to exhalation, but buccal pressure does not decrease, indicating that buccal expansion does not contribute to exhalation. (From Brainerd *et al.*, 1993, Figure 8, p. 176.)

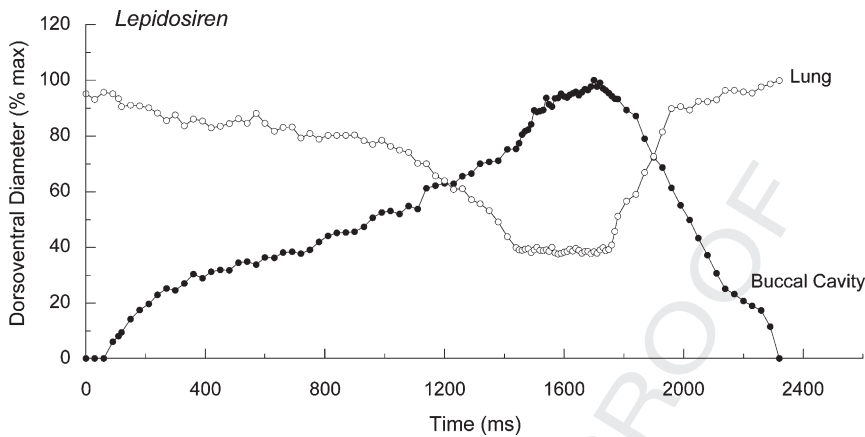


Fig. 1.9. Kinematics of two-stroke breathing in *Lepidosiren*. Changes in the maximum diameter of the buccal cavity and gas bladder were measured in lateral projection x-ray videos. Note that, in comparison to four-stroke breathing (Figure 7), the buccal cavity expands and compresses only once, and therefore some of the expired air is pumped back into the lungs. (From Brainerd, 1994a, Figure 3, p. 293.)

aquatic coughing are all fast movements. The two complete buccal expansion–compression cycles of four-stroke breathing occur in under 1 s, with some fishes completing each cycle in less than 100 ms. The gas transfer and expiration phases may have arisen by modification of the aquatic cough, in which the buccal cavity is expanded with the mouth closed. The inspiration and compression phases may have arisen by modification of the movements associated with suction feeding.

The two-stroke buccal pump of lungfishes more closely resembles the aquatic ventilatory pump in its movements and timing (McMahon, 1969; Brainerd, 1994a). In four-stroke breathing, gill ventilation stops well before each air breath, but in lungfishes, gill ventilation continues as the fish approaches the surface of the water, and the buccal expansion associated with the air breath follows smoothly from the previous gill ventilation cycle (Brainerd, 1994a). The buccal cavity expands more during an air breath than during an aquatic breath, but otherwise the movements are very similar (McMahon, 1969). Aquatic breathing resumes immediately after the buccal compression phase of the air breath, without missing a beat in the aquatic ventilatory rhythm (Brainerd, 1994a).

Although the four-stroke buccal pump is typical for actinopterygians, two alternative ventilatory mechanisms have been described. In polypterid fishes, the patterns of buccal expansion and air transfer are similar to four-stroke, but elastic recoil of the ganoid scale jacket produces subambient

AU2

pressure in the body cavity whereby air is aspirated into the lungs (Figure 1.10) (Brainerd *et al.*, 1989). Two euteleosts, *Gymnotus* and *Hoplerythrinus*, ventilate their gas bladders in a manner that is completely different from any other actinopterygians (Farrell and Randall, 1977; Liem, 1989b). An air breath starts with a large buccal expansion at the surface of the water (Figure 1.11). Then the fish sinks below the surface and compresses the buccal cavity to pump the air into its esophagus, which expands greatly, and the esophagus gradually empties into the gas bladder through the

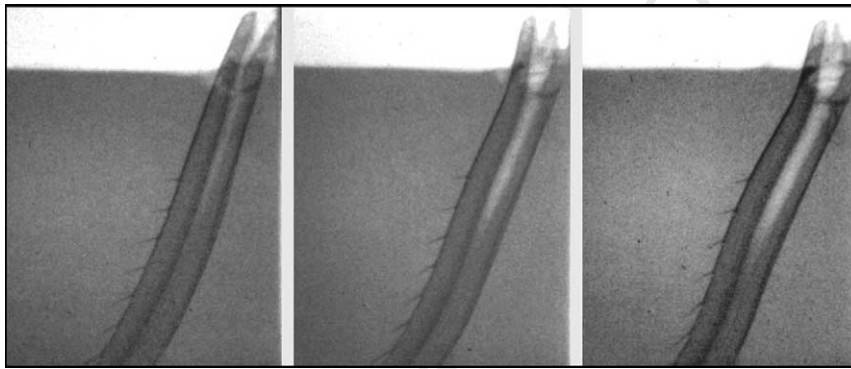


Fig. 1.10. Recoil aspiration in *Polypterus*. Frames from an x-ray video of lung ventilation in *Polypterus senegalis*, lateral projection. The left frame is at the end of expiration, and the middle and right frames show inspiration. Note that the mouth is wide open as the lungs refill with air, indicating that the fish is inhaling by aspiration breathing, rather than buccal pumping (a mouth seal is necessary for buccal pumping).

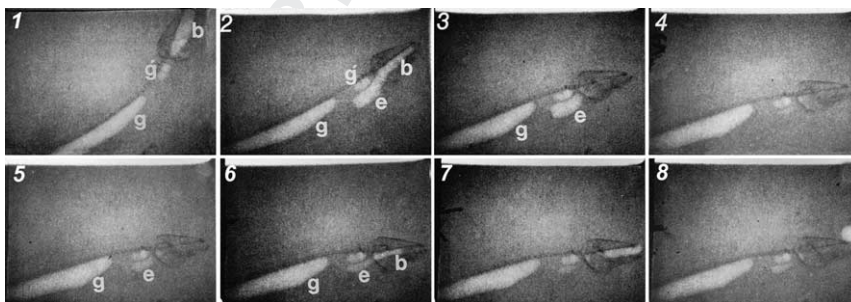


Fig. 1.11. Esophageal pump in *Gymnotus carapo*. Frames from an x-ray video of lung ventilation in lateral projection. Frames 1–4 show inspiration and frames 5–8 show expiration. See text for explanation. Abbreviations: b, buccal cavity; e, esophagus; g, gas bladder; g', anterior chamber of the gas bladder. (Adapted from Liem, 1989b, Figure 8, p. 346.)

pneumatic duct. The fish remains submerged and expiration ensues in reverse of inspiration; gas moves first into the esophagus and then into the buccal cavity and finally is released as bubbles. This mechanism results in relatively small tidal volumes (Figure 1.11), whereas two- and four-stroke breathing and recoil aspiration exchange between 50 and 100% of the gas bladder volume with each breath.

The loss of the pneumatic duct in stem acanthomorphs, presumably through lack of selection for air breathing, apparently produced an evolutionary constraint that prevented the subsequent recruitment of the swim bladder for gas exchange. Nonetheless, air breathing has evolved many times in higher teleosts, most commonly through the use of relatively unmodified buccal, opercular, pharyngeal, and/or branchial surfaces for gas exchange. In these cases, slight modifications of the expansive phase of the aquatic respiratory pump or suction feeding pump are used to draw in a bubble of air at the surface, and then the buccal and/or opercular cavities remain expanded to retain the bubble after submergence (Graham, 1997).

In some teleosts, more elaborate ABOs have evolved. A common theme is the evolution of a suprabranchial chamber (SBC) that may be a relatively simple space dorsal and caudal to the opercular cavity, as in *Monopterus*, or that may contain elaborate structures that increase the surface area for gas exchange, such as the labyrinth organ of anabantoids, the respiratory tree of *Channa*, and the respiratory fans and trees of *Clarias* (Graham, 1997). The dorsal location of the SBC makes biomechanical sense since inspired air will tend to rise up into the chamber and displace the gas or water that is present.

Ventilation of the suprabranchial chamber is accomplished by one of two mechanisms, named monophasic and diphasic by Peters (1978), and re-named triphasic and quadruphasic by Liem to reflect the number of phases recognizable with EMG and cineradiography (Liem, 1980, 1985, 1989a). Triphasic ventilation is effective when the SBC has both anterior and posterior openings, as in anabantoids. The three phases are as follows: (1) a preparatory phase in which the buccal cavity compresses to expel water, (2) an expansive phase in which the buccal cavity expands to draw in fresh air through the mouth, and (3) a compressive phase in which the buccal cavity compresses to force fresh air into the SBC. The SBC is a rigid structure encased in bone, so the addition of fresh air forces the old gas out of the chamber, thus creating a unidirectional draft of air through the SBC (Liem, 1980).

Muscle activity during the triphasic pump is nearly identical to activity during suction feeding. The levator operculi (LO), levator arcus palatini (LAP), and sternohyoideus (SH) are active during expansion, and the adductor arcus palatini (AAP), adductor mandibulae (AM), and geniohyoideus (GH) are active during compression. One interesting difference is that

AU3

the dilator operculi (DO) is active during the expansive phase of suction feeding but only becomes active at the end of the compressive phase of triphasic ventilation when bubbles are released through the opercular valve (Liem, 1985).

Quadruphasic ventilation is more complex and is bidirectional (Liem, 1980). The four phases are as follows (Figure 1.12): (1) a preparatory phase in which the buccal cavity compresses to expel water, (2) a reversal phase in which activity in the DO abducts the operculum rapidly, activity in the SH

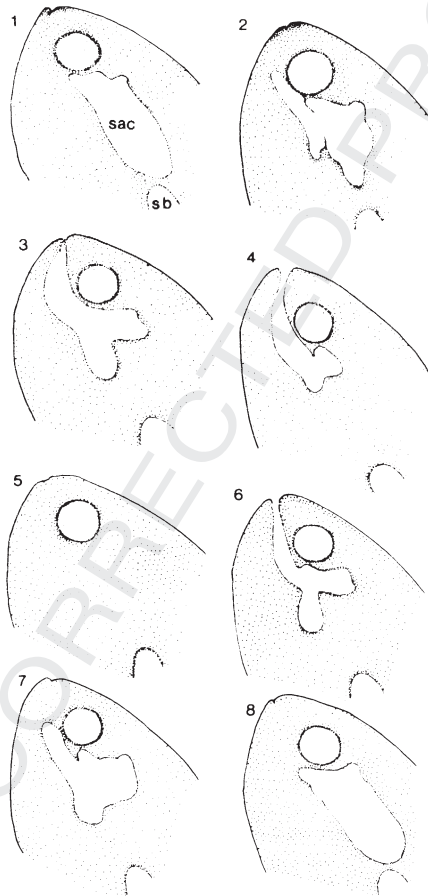


Fig. 1.12. Quadruphasic ventilation of the SBC in an anabantoid, *Heleostoma temminckii*. Drawings traced from an x-ray video of lung ventilation in lateral projection. See text for explanation. Abbreviations: sac, suprabranchial air chamber; sb, swim bladder. (From Liem, 1980, Figure 5, p. 66.)

retracts and depresses the hyoid apparatus, and a current of water is drawn into the posterior opening of the SBC, forcing gas forward through the anterior opening of the SBC and into the buccal cavity whence it is expelled, (3) an expansive phase in which the buccal cavity expands to draw in fresh air through the mouth, and (4) a compressive phase in which the buccal cavity compresses to force fresh air into the SBC. Muscle activity in phases 3 and 4 is identical to suction feeding, including the activity of the DO during expansion. The muscle activity of the reversal phase is identical to muscle activity during the aquatic cough, which is normally used to create a rostral current of water to clear debris from the gills (Liem, 1980).

AU4 Most species of air-breathing fishes with an SBC use either triphasic or quadruphase ventilation, but anabantoids are able to use both (Liem, 1989a). The quadruphase pump relies on a current of water for expiration, so this pump works only when fishes are submerged; the triphasic pump works when fishes are in or out of water. Most air breathers that use buccopharyngeal surfaces or an SBC for gas exchange either expel the air bubble before feeding or lose the air bubble in the process of feeding. In anabantoids and clariids, however, air is not lost from the SBC during feeding. Valves separate the SBC from the buccal and opercular cavities, effectively decoupling feeding and air breathing. Liem (1989a) proposed this decoupling as an explanation for the relatively diverse types of food items eaten by anabantoids and clariids, compared to the limited diets of channids and synbranchiforms.

AU5 Some air-breathing teleosts, particularly the catfishes and loaches, specialize parts of the digestive tract for gas exchange. In loricariid and trichomycterid catfishes, part of the stomach is thin walled and highly vascularized, and air breathing has been described for loricariids (Gradwell, 1971). Loricariids release air from their stomachs while resting on the bottom; the air escapes either out the mouth or out from under the operculum. Soon thereafter, the fish darts to the surface and grabs a bubble of air in the buccal cavity and forces it into the stomach. Loaches, family Cobitidae, and armored catfishes in the family Callichthyidae use the intestine for gas exchange. In both groups, the region of the intestine just proximal to the anus is thin walled and vascularized. Armored catfishes have been demonstrated to ventilate the intestine unidirectionally (Gee and Graham, 1978). A fish darts to the surface and grabs a bubble of air, and as it forces the air into the esophagus, a bubble emerges simultaneously from the anus. The armor of the catfish may play a role in this simultaneous expulsion of air. It is highly unlikely that air just pumped into the esophagus

AU6 travels to the distal end of the GI tract that quickly, but the armor may limit the total volume of the body to the extent that air forced in the front end increases the pressure in the whole peritoneal cavity, thus forcing air out the

anus. Air presumably is then transported by peristalsis to the distal intestine for gas exchange.

IV. FUTURE DIRECTIONS

Work to date has yielded a fairly complete understanding of the functional morphology and basic mechanics of aquatic and aerial respiratory pumps in fishes, but many rich and interesting areas for future research remain. Most of the work reviewed here was done before the experimental techniques of sonomicrometry and endoscopy became available. Application of these techniques to the study of water flow in the pharynx has yielded some unexpected results, such as the discovery of substantial flow reversals during gill ventilation in elasmobranchs (Ferry-Graham and Summers, 1999) and the discovery of crossflow filtration in suspension feeding fishes (Sanderson *et al.*, 2001). Further application of sonomicrometry to quantify shape changes of the pharynx and endoscopy to measure fluid flow could yield the data necessary for the production of more sophisticated and quantitative models of gill ventilation and gas exchange.

Sonomicrometry could also be applied to study the length changes of respiratory muscles during gill ventilation. Most work on whole muscle function has focused on high-performance locomotor activities (reviewed in Biewener, 2002). The study of cranial muscles during gill ventilation could yield information on the behavior of muscles when the strongest selection is likely to act on energetic efficiency rather than on maximizing force or power. This work may also relate to the function of muscles that perform multiple tasks with markedly different performance requirements. The muscles of the gill ventilation pump are also used for suction feeding, a function that presumably requires high power output from the muscles (because the muscles do work to accelerate water into the mouth). Are breathing and suction feeding achieved by different muscle fiber types? How are these fiber types activated? Does the presence of a large volume of inactive fast fibers in a dual-use muscle reduce the energetic efficiency of gill ventilation (due to the inertia and viscosity of the extra muscle mass)? Might this be a source of balancing selection on the size of muscles used for suction feeding?

Finally, as in almost all areas of fish biomechanics, studies of ventilation have focused primarily on adult fishes, with little attention paid to development and ontogeny. At small body sizes, water flow across the gills will be dominated by viscous forces (due to low Reynolds number), which will increase the work of breathing and also decrease the convective transport of oxygenated water to the surfaces of the secondary lamellae. However, this effect is balanced by the efficacy of diffusion over small distances. Small fish

AU7

larvae absorb oxygen across their body and yolk sac surfaces; only at larger sizes do fish need gills at all. Mathematical modeling, combined with morphological and kinematic data, may provide the most insight into changes in the biomechanics of ventilation over the lifetimes of fishes.

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