VENTILATORY MODES OF ELASMOBRANCHS

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Aquatic vertebrates are faced with one of two options for respiration: physically moving their gills through the water ("ram"), or actively pumping water over their gills via "buccal pumping". The current model of the mechanics of respiration was described over 40 years ago by Hughes (*J. exp. Biol.* 37, 11-27, 1960), and has been incorporated into textbooks and physiological literature alike. It was suggested that alternating "suction" and "pressure" pumps allowed for the continuous and unidirectional flow of oxygenated water over the gills. This unidirectional flow of water is important for setting up and maintaining the counter-current oxygen exchange mechanism prevalent in fishes. This method of exchange facilitates an extremely efficient transfer of oxygen to the blood, and allows more oxygen to be extracted from the water than could be if the flow were not continuous (Piiper and Scheid, *Handbook of Physiology 13, Comparative Physiology*, 309-356, 1997).

Using pressure transducers implanted into the oral and gill cavities, we previously found patterns of pressure generation that are inconsistent with a constant flow hypothesis in swellsharks (*Cephaloscyllium ventriosum*; Ferry-Graham, *J. exp. Biol.*, 202, 1501-1510, 1999) and little skates (*Leucoraja erinacea*; Summers and Ferry-Graham, *J. exp. Biol.*, 204, 1577-1587). We repeated these experiments with six actively respiring dogfish (*Squalus acanthias*) during October of 2000. Consistent among all three species were high magnitude pressure reversals during portions of the respiratory cycle (Fig. 1). If the pressure is reversed, flow will also be reversed over the gills if morphological elements do not prevent it.

Video data showed that the gills, mouth, and spiracle (spiracle in skates and dogfish only) are open during some portion of the pressure reversal period. However, dye and particle studies revealed that water rarely flows externally in a reversed direction. Specifically, water does not exit the mouth or spiracle or enter through the gills of swell sharks (Ferry-Graham, *J. exp. Biol.*, 202, 1501-1510, 1999), but water can exit the large spiracle in little skates, and occasionally exited the mouth in one experimental animal (Summers and Ferry-Graham, *J. exp. Biol.*, 204, 1577-1587). Water sometimes exited through the mouth in the dogfish. In other words, either the pressure reversals indicate flow reversal that are completely contained within the head, or the pressure reversals do not lead to flow reversals because the internal gill bars prevent back flow.

The gill bars, found between the parabranchial chambers and the buccal chamber, have the potential to block flow reversals by closing together during periods of pressure reversal (Lauder, *J. exp. Biol.* 104, 1-13, 1983). Sonomicrometry of morphological elements in the little skate previously suggested that movements of the gill bars may stop, or slow, the flow reversal expected for the observed pressure reversals (Summers and Ferry-Graham, *J. exp. Biol.*, 204, 1577-1587). Endoscopic data from little skates showing movement of particles in seawater in the gill cavity revealed that flow over the gills is not continuous. Flow can halt or even reverse during consecutive respiratory cycles where pressure reversals are consistently observed.

Our results suggest that respiration is not as efficient as once presumed. This presents a problem for physiological models that rely on optimization, presumably through natural selection, as a guiding principle. Elasmobranchs may be an example where performance is comprised by other demands on the same morphological elements, such as feeding. Models that are incorrect undermine our ability to relate organismal physiology to ecology. For example, sluggish sharks like the swellshark, may be limited in their activity patterns by an inefficient ventilatory mechanism. We do not know if this is the case, or even which factor is the cause and which might be an effect in such a scenario. However, a better understanding of basic physiological principles is needed to begin to determine the answer.

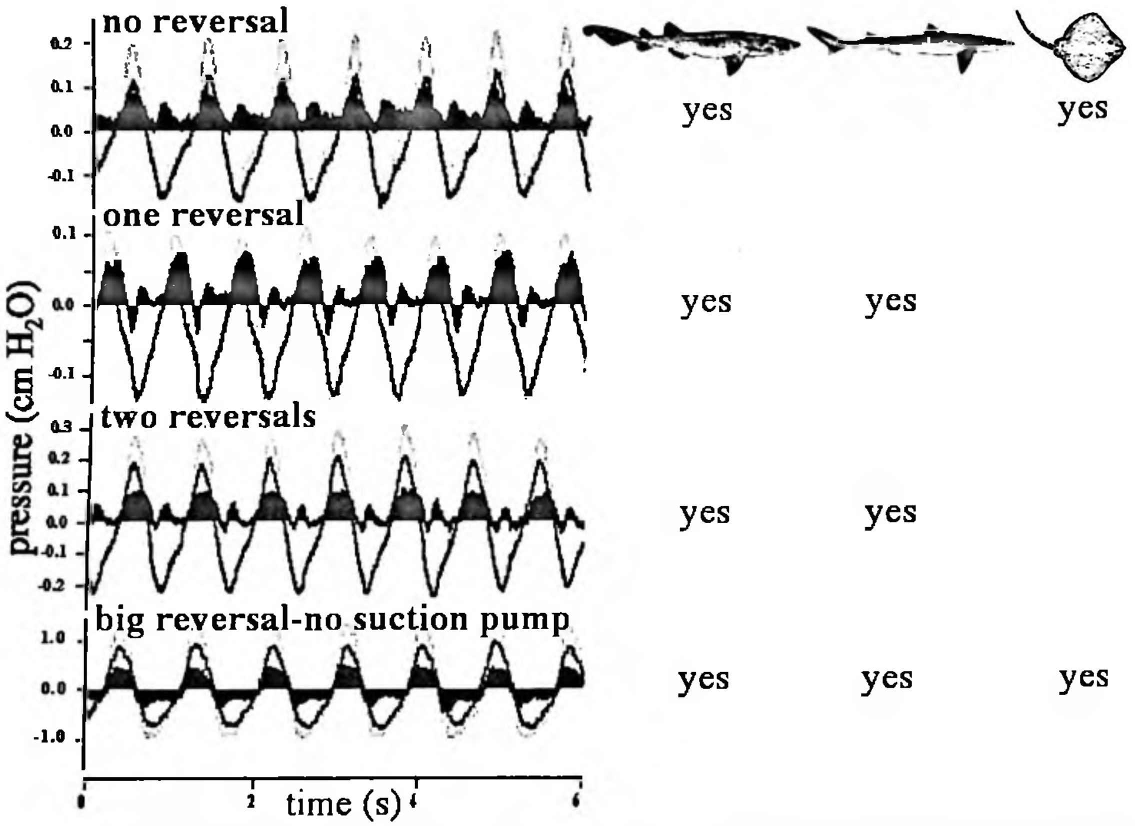

Figure 1. Breathing patterns exhibited by the swellshark (*Scyliorhinus canicula*), the spiny dogfish (*Squalus acanthias*), and the hedgehog skate (*Leucoraja erinacea*) depicted from left to right.

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