

3.2.4. THE EVOLUTION OF CO<sub>2</sub> EXCRETION PATHWAYS IN VERTEBRATES

A comparison of CO<sub>2</sub> excretion pathways across vertebrates as a whole yields some insight into the evolution of the elasmobranch model of CO<sub>2</sub> excretion, despite very limited data on which to base such speculation (see also Tufts and Perry, 1998; Tufts et al., 2003; Gilmour and Perry, 2010). Based on extant agnathans, the ancestral vertebrate likely possessed RBCs that lacked the band 3 anion exchanger and contained low levels of CA activity. The RBCs of both hagfish (Ellory et al., 1987; Peters et al., 2000; Esbaugh et al., 2009) and lamprey (Nikinmaa and Railo, 1987; Tufts and Boutilier, 1989, 1990) lack functional anion exchange and exhibit levels of CA activity that are low relative to values for teleosts (Maren et al., 1980; Henry et al., 1993; Esbaugh and Tufts, 2006a; Esbaugh et al., 2009). The potential for the hagfish RBC to contribute to CO<sub>2</sub> excretion is further limited by a small Haldane effect (Tufts et al., 1998) and the low buffer capacity of its Hb (Nikinmaa, 1997). However, the presence in the hagfish gill of type IV-like and type XV-like CA activities, coupled with relatively high plasma buffer capacity (the buffer capacity of separated plasma equals that of true plasma), and the absence of an endogenous plasma CA inhibitor provide conditions under which plasma HCO<sub>3</sub><sup>-</sup> dehydration can make a substantial contribution to CO<sub>2</sub> excretion (Esbaugh et al., 2009). In agreement with this hypothesis, the majority of the blood total CO<sub>2</sub> load in hagfish is carried in the plasma despite the absence of RBC anion exchange (Tufts and Perry, 1998; Tufts et al., 1998; Esbaugh et al., 2009). A similar pattern is present in elasmobranchs (or at least *Squalus suckleyi*). Although RBC anion exchange appears in this group, other factors limiting RBC contributions to CO<sub>2</sub> excretion remain, including low CA activity and the absence of a Haldane effect, whereas the presence of branchial CA IV together with high plasma buffer capacity allow for a significant contribution of plasma HCO<sub>3</sub><sup>-</sup> dehydration, collectively resulting in dual reliance on both plasma and RBC (see Section 3.2.3). In both hagfish and elasmobranchs then, O<sub>2</sub> transport and CO<sub>2</sub> transport are effectively uncoupled, with O<sub>2</sub> delivery being dependent upon the RBC and CO<sub>2</sub> excretion exhibiting substantial dependence on the plasma.

In the presence of Hb with a strong Bohr-Haldane effect, O<sub>2</sub> and CO<sub>2</sub> transport can be coupled to benefit both O<sub>2</sub> delivery and CO<sub>2</sub> excretion (reviewed by Brauner and Randall, 1998). Addition of CO<sub>2</sub> to the blood in the tissues lowers Hb-O<sub>2</sub> binding affinity (Bohr effect) to enhance O<sub>2</sub> delivery to the tissues, whereas elimination of CO<sub>2</sub> at the gas exchange organ reverses this effect to the benefit of O<sub>2</sub> loading. As O<sub>2</sub> binds to Hb, it drives off oxyliable protons (Haldane effect) that can then be used for HCO<sub>3</sub><sup>-</sup> dehydration to benefit CO<sub>2</sub> excretion, whereas deoxygenation of the blood

at the tissues increases the proton-binding capacity of Hb to the benefit of CO<sub>2</sub> loading into the blood. The large Haldane effect of lamprey Hb is critical for effective CO<sub>2</sub> transport by the blood (Tufts and Perry, 1998). Membrane-associated CA activity does not appear to be present in the lamprey gill (Henry et al., 1993), which precludes a role for catalyzed dehydration of HCO<sub>3</sub><sup>-</sup> in the plasma, and the absence of functional RBC anion exchange (Nikinmaa and Railo, 1987; Tufts and Boutilier, 1989, 1990) leaves the RBC as the site of CO<sub>2</sub> transport in the blood (Tufts and Boutilier, 1989). Proton removal via the pronounced Haldane effect and a secondarily active Na<sup>+</sup>/H<sup>+</sup> exchanger allow CO<sub>2</sub> to be loaded into the blood while HCO<sub>3</sub><sup>-</sup> ions are retained within the RBC (reviewed by Nikinmaa et al., 1995; Nikinmaa, 1997; Tufts and Perry, 1998). The tight linkage between O<sub>2</sub> and CO<sub>2</sub> transport is retained in teleosts. Again, the gill appears to lack membrane-associated CA activity (Henry et al., 1988, 1993; Henry et al., 1997; Gilmour et al., 1994, 2001, 2002; Stabenau and Heming, 2003; Georgalis et al., 2006), which places reliance for catalyzed HCO<sub>3</sub><sup>-</sup> dehydration solely on the RBC. Rapid anion exchange at the RBC membrane (Cameron, 1978; Romano and Passow, 1984; Jensen and Brahm, 1995) allows efficient utilization of the plasma for CO<sub>2</sub> carriage, while the benefit of the marked Haldane effect (Jensen, 1991) is maximized by high RBC CA activities (Maren et al., 1980; Henry et al., 1997; Esbaugh et al., 2004) that ensure rapid CO<sub>2</sub> hydration/HCO<sub>3</sub><sup>-</sup> dehydration reactions with proton production/consumption in close proximity to Hb. It is this pattern of CO<sub>2</sub> excretion that appears to have been largely retained through the tetrapods. Although pulmonary capillary endothelial CA IV is present in tetrapods (Whitney and Briggie, 1982; Zhu and Sly, 1990; Waheed et al., 1992; Stabenau and Heming, 2003), the RBC dominates CO<sub>2</sub> excretion owing to high RBC CA activity and buffer capacity (Henry and Swenson, 2000; Swenson, 2000).

Thus, two basic strategies for CO<sub>2</sub> excretion appear to be present among vertebrates. In one, represented in hagfish and elasmobranchs, the Bohr-Haldane effect is small or absent, O<sub>2</sub> and CO<sub>2</sub> transport are uncoupled, and CO<sub>2</sub> excretion relies to a significant extent on dehydration of HCO<sub>3</sub><sup>-</sup> in the plasma catalyzed by branchial extracellular CA activity. The second strategy is utilized by lamprey, teleost fish, and tetrapods, and relies on RBC CA to catalyze CO<sub>2</sub> hydration/HCO<sub>3</sub><sup>-</sup> dehydration reactions; CO<sub>2</sub> excretion is tied to the RBC by coupling it to O<sub>2</sub> uptake. However, with only a handful of species having been studied in any detail, such inferences about patterns of CO<sub>2</sub> excretion and the evolution of CO<sub>2</sub> excretion pathways across vertebrates broadly and fish in particular must remain speculative.

#### 4. CONCLUSIONS AND PERSPECTIVES

Gas transport and exchange have been most thoroughly investigated in just a few, small, sedentary elasmobranch species. Consequently, models of O<sub>2</sub> transport and CO<sub>2</sub> excretion are largely based on information from the so-called “dogfish” sharks, *Scyliorhinus canicula*, *Scyliorhinus stellaris*, *Squalus acanthias*, and *Squalus suckleyi*. Larger and more active elasmobranchs are often dangerous and difficult to use in experiments, and thus data collection from these species has been largely opportunistic. In recent years, researchers have been able to maintain juveniles of large shark species in a laboratory setting, allowing more in depth analysis of the respiratory characteristics of the shortfin mako, *Isurus oxyrinchus*, and sandbar sharks, *Carcharhinus plumbeus* (e.g., Sepulveda et al., 2007; Brill et al., 2008; Wegner et al., 2012). Field physiology (see Bernal and Lowe, 2015) is likely to prove an important tool for future investigations into the respiratory physiology of large elasmobranchs. An excellent example of direct physiological measurements carried out on juveniles and field physiology studies of adults is provided by recent work on the infamous white shark, *Carcharodon carcharias*, a large, regionally-heterothermic shark that does not fare well in aquaria. The O<sub>2</sub> consumption rates of juvenile white sharks were measured (Ezcurra et al., 2012), and a field physiology study was used to estimate routine metabolic rates and feeding requirements of adult white sharks (Semmens et al., 2013), providing great insight into this shark’s ecophysiology.

Generally, elasmobranch Hbs exhibit a high intrinsic affinity for O<sub>2</sub>, a high buffering capacity, and weak to moderate cooperativity. There appears to be a division between species in which Hb displays little to no sensitivity to allosteric effectors, and those that exhibit marked Bohr effects and sensitivities to ATP. A high Hb-O<sub>2</sub> affinity causes the O<sub>2</sub> capacitance of the blood ( $\Delta\text{CO}_2/\Delta\text{PO}_2$ ) to be steep and spread over a smaller range at a low  $\text{PO}_2$ . Consequently, elasmobranchs tend to work within a wide portion of the oxygen equilibrium curve, drawing from venous O<sub>2</sub> stores during increased aerobic demand. There are exceptions to this general model (e.g., *Negaprion brevirostris*) and further research into cardiorespiratory adjustments during exercise in elasmobranchs is needed, especially in the high performance lamnid sharks. Elasmobranch RBCs are large, appear to maintain a steady-state volume through exceptional sodium pump activity and RVD mechanisms, and do not possess adrenergic RBC pHi regulation. However, evidence indicates that not all elasmobranchs adhere to this model of RBC function and pH regulation (e.g., *Carcharhinus plumbeus*), clearly warranting research in a wide phylogenetic range of elasmobranchs, as well as in hypoxia- and anoxia-tolerant elasmobranchs.

The blood respiratory properties and Hb-O<sub>2</sub> binding characteristics have been thoroughly investigated for only a few elasmobranchs (e.g., *Squalus acanthias* and *Carcharhinus plumbeus*), but a complete picture of O<sub>2</sub> flux in these species has yet to be composed. A recent resurgence in O<sub>2</sub> equilibria studies has updated standard methods to incorporate modern technology, which in turn has allowed the development of high resolution and high-throughput systems to generate oxygen equilibrium curves on microvolumes of blood (Clark et al., 2008; Lilly et al., 2013; Oellermann et al., 2014). It is hoped that this development will lead to further phylogenetic analyses of Hb function and the elasmobranch Bohr effect. A careful hypothesis-driven investigation of the evolution of the “stingray Bohr effect” in the myliobatid rays is clearly worthy of attention.

As with blood respiratory properties and Hb-O<sub>2</sub> binding characteristics, CO<sub>2</sub> excretion has been thoroughly investigated in only a handful of elasmobranch species, with the most information being available for dogfish. Several lines of evidence suggest that CO<sub>2</sub> excretion in dogfish relies on HCO<sub>3</sub><sup>-</sup> dehydration in both plasma and RBCs passing through the gill, a strategy that differs from the essentially exclusive reliance on RBCs in other vertebrates, including teleost fish. In dogfish, dehydration of HCO<sub>3</sub><sup>-</sup> in the plasma is catalyzed by branchial CA IV, with the requisite proton supply being assured by the substantial plasma buffering found in elasmobranch fish. At the same time, the capacity of the RBC to contribute to HCO<sub>3</sub><sup>-</sup> dehydration is constrained by low RBC CA activity and the absence of a Haldane effect. Clearly there is a pressing need to determine whether this ‘dogfish’ model of CO<sub>2</sub> excretion applies to other elasmobranch species. Molecular and biochemical characterization of branchial and RBC CA isoforms, evaluation of the Haldane effect, and quantification of plasma buffering in a range of elasmobranch fish will be important first steps in determining how likely it is that elasmobranchs beyond dogfish rely on dual plasma and RBC HCO<sub>3</sub><sup>-</sup> dehydration.

Despite the central roles of O<sub>2</sub> uptake and CO<sub>2</sub> excretion in the success of elasmobranchs, our knowledge of these processes in elasmobranchs as a group has been defined by the thorough investigations carried out in just a few species. The grand challenge ahead lies in achieving a more representative understanding of gas transport and exchange in elasmobranchs as a group.

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