Review

The functional ontogeny of the teleost gill: Which comes first, gas or ion exchange? ☆

Peter Rombough

Department of Zoology, Brandon University, Brandon MB Canada R7A 6A9

Abstract

For most of the last century, the need to obtain sufficient oxygen to meet the respiratory requirements of the tissues was viewed as the primary selective pressure driving gill development in teleost fish. Recently, however, it has been suggested that ionoregulatory pressures may actually be more important. This manuscript reviews the theoretical and empirical evidence dealing with the functional ontogeny of the gill in the context of the oxygen and ionoregulatory hypotheses. Gas and ion exchange are subject to similar geometric constraints in developing fish. Both initially are exclusively cutaneous but shift to the gill with tissue growth because of declining surface-to-volume ratios. Based on the appearance of mitochondria-rich cells (MRCs), ionoregulatory activity shifts to the gill in advance of gas exchange. In every species examined to date, MRCs appear on the developing gill in advance of secondary lamellae, the definitive gas exchange structure of the adult gill. Biochemical and histochemical studies indicate that these early branchial MRCs are actively involved in ion exchange. In some cases, the specific activity is many times greater than in the adult gill. In contrast, O_2 microelectrode and hemoglobin ablation experiments suggest that the early gill contributes little O_2 to the general systemic circulation. Any oxygen taken up appears to be consumed locally. Functional ablation experiments with zebrafish indicated that the larval gill became essential for ion balance well before it was needed for O_2 uptake. Similar experiments with rainbow trout, however, found that the gill became essential in terms of gas and ion exchange at about the same time. On balance, the evidence appears to favour the ionoregulatory hypothesis but the oxygen hypothesis cannot be absolutely rejected without more information. Some of the major deficiencies in our knowledge regarding the transition from cutaneous to branchial gas and ion exchange are highlighted and potential implications of the ionoregulatory hypothesis are discussed.

Contents

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1. The oxygen hypothesis

The fish gill is a multifunctional organ involved in gas exchange, ionoregulation, osmoregulation, acid–base balance, ammonia excretion (reviewed in Evans et al., 2005), hormone production (Zaccone et al., 1996), modification of circulating metabolites (Olson, 1998) and immune defense (Dos Santos et al., 2001). Of these functions, gas exchange, in particular oxygen uptake, is the most immediately critical. Adult fish typically die from hypoxemia within a few minutes of being placed in anoxic water. This observation has led to the perception that the primary selective pressure driving gill development during embryonic and larval life must be the need to supply the rest of the body with oxygen. On the face of it, there appear to be sound theoretical reasons to believe that this is the case.

Body size places severe constraints on how organisms obtain oxygen from the environment (e.g. Krogh, 1941; Cameron, 1989; Burggren and Pinder, 1991). Developing fish initially have no gills. They, like many other small organisms, are initially able to obtain sufficient oxygen to meet their metabolic demands by simple diffusion across their skin. Relative to their body mass, small organisms have large surface areas. However, as they grow surface area tends to expand at a slower rate than body mass. Assuming geometric similitude, surface area should expand at a rate proportional to body mass$^{2/3}$. If one also assumes that metabolic rate is directly proportional to body mass (i.e. $\sim$ body mass$^{1.0}$), then surface area per unit O_2 uptake should gradually decline and eventually become limiting as an organism increases in size. This geometric argument, and variants of it, have been used to explain metabolic scaling (Rubner, 1883), the maximum size organisms can achieve without specialized respiratory structures (Harvey, 1928) and why developing fish need to form gills (Krogh, 1941; Hughes, 1984; Blaxter, 1988; Varsamos et al., 2005).

In reality, the situation is not as straight forward as the principle of geometric similitude would suggest. Metabolic rate is rarely directly proportional to body mass and body surface area does not always scale to body mass$^{2/3}$. In fish larvae there is considerable variation among species in how metabolic rate scales with body mass. Rombough (1988a) surveyed the literature and found values for the metabolic mass exponent (b_r) ranging from 0.42 to 1.33. The mean value ($\pm$95% CI, $n=47$) was 0.90 ± 0.05. A similar survey by Post and Lee (1996) yielded values ranging from 0.55 to 1.13 with two modes, one near $b_r=1.0$ and one near $b_r=0.8$. There are fewer reports of how cutaneous surface area scales with body mass. Rombough and Moroz (1997) surveyed the literature and found mass exponents for surface area (b_{sa}) ranging from 0.26 to 0.81 with a mean ($\pm$95% CI, $n=6$) of 0.58 ± 0.20. In all six species, the mass exponent for surface area was lower than the corresponding mass exponent for metabolic rate. Overall, the difference was highly significant (paired t-test, $t=-3.94$, $P=0.01$). On this basis, it would appear that the basic assumption of the geometric argument, that surface area expands at a slower pace than metabolic rate, holds for most fish larvae (leptocephali and other larvae with unusual body shapes or life histories may not fit this pattern). Whether oxygen uptake is the first process to become limiting as the result of this decrease in the relative surface area of the skin is another matter.

2. Problems with the oxygen hypothesis

Recently, cracks have begun to appear in the oxygen hypothesis. In particular, fish seem to begin to develop gills well before they are needed for oxygen uptake. In juvenile and adult fish which rely on gills for the bulk of their oxygen uptake, metabolic rate and respiratory surface area expand at approximately the same rate with increasing body mass (Rombough and Moroz, 1997). This is not the case for embryos and larvae prior to gill development. As mentioned in the previous section, the average mass exponent for oxygen consumption by embryos and larvae is slightly less than unity (i.e. $b_r \approx 0.9$) while the typical mass exponent for skin surface area (b_{sa}) is only about 0.6. The net result is that respiratory surface area per unit O_2 uptake declines with tissue growth (Fig. 1). Rombough and Moroz (1997) used the empirical relationship between skin surface area per unit O_2 uptake and body mass for several species of marine and freshwater fish (mean incubation temperature 10 °C) to estimate when cutaneous gas exchange should become limiting. Based on the assumption that the efficiency of cutaneous gas exchange in larvae was similar to the efficiency of cutaneous gas exchange in adult fish, they estimated that O_2 uptake across the skin should become limiting at a body mass of about 100 mg (Fig. 1). This estimate is probably conservative as the skin of larvae is considerably thinner than that of adult fish (e.g. 20 μm vs. 100 μm in Atlantic salmon *Salmo salar*; Wells and Pinder, 1996a) which, all other things being equal, should result in higher larval exchange efficiencies. The problem in terms of the oxygen hypothesis is
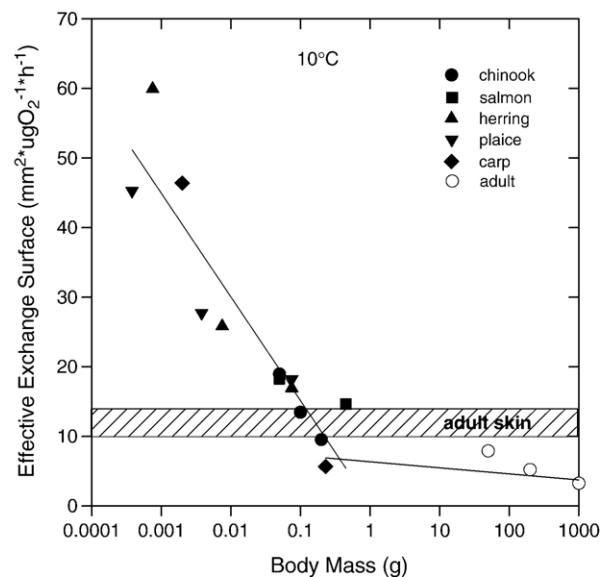

Fig. 1. Effective surface area per unit oxygen uptake for larval and adult fish. The values for the larval fish are for skin only. The values for the adult fish are for gills. The hatched region indicates the range of effective exchange capacities of the skin of adult fish as reported in the literature (data from Rombough and Moroz, 1997).