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Review

New insights into the plasticity of gill structure☆

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ABSTRACT

The ability of some fishes to reversibly remodel their gill morphology has become a focus of research after the discovery of extreme morphological gill plasticity in crucian carp and goldfish—both members of the cyprinid genus *Carassius*. Their lamellae are largely embedded in an interlamellar cell mass (ILCM) during normoxic conditions in cold water. The ILCM regresses in hypoxia, warm water, and during exercise, whereby the respiratory surface area and the capacity for oxygen uptake are greatly increased. There may be several reasons for covering the lamellae when oxygen needs are low. Reducing osmoregulatory costs have been suggested as an advantage of gill remodeling, but this has been difficult to show, putting the importance of the osmo-respiratory compromise into question. Other reasons could be to limit uptake of toxic substances and to reduce the risks for infections. In support for the latter, we present evidence showing that crucian carp infected by gill flukes maintain their ILCM when exposed to hypoxia. So far, gill remodeling in response to oxygen needs has been seen in several cyprinids, killifish and eel. In response to other environmental factors it may also occur in salmonids and anabantoids, revealing a phylogenetically widespread occurrence among teleosts.

1. Introduction

The lamellae of the gills are the primary sites for oxygen uptake in fish, and are in many species of adult fish also largely responsible for active and passive fluxes of ions and water in and out of the animal. These processes are dependent on the functional lamellar surface area, which can be regulated through the extent and rate of blood perfusion of the lamellae. Less than ten years ago it became evident that some species of fish can also drastically alter the lamellar surface area through plastic morphological changes in the gill structure during the course of hours to days (Sollid et al., 2003)—a process subsequently termed gill remodeling (Nilsson, 2007). Since the initial reviews of this phenomenon (Sollid and Nilsson, 2006; Nilsson, 2007), a considerable number of studies have both expanded our knowledge of the function and consequences of gill remodeling and contributed new examples of gill remodeling among fishes, and we feel that there is again a need for summarizing our present knowledge in this area.

In the initial studies, scanning electron micrographs showed that gill filaments of crucian carp (*Carassius carassius*) kept in cold (8 °C) aerated water have a striking, almost sausage-like, appearance, completely lacking protruding lamellae (Fig. 1A and B). After the fish were moved to hypoxic water (C_{O_2} = 6–8% of air saturation; Fig. 1C), a drastic morphological transformation occurred over the course of a few days, resulting in “normal” looking filaments with clearly protruding lamellae and a 7.5-times larger gill surface area. The process was found to be reversible: the gill filaments regained the sausage-like morphology within days after the crucian carp were moved back to cold normoxic water (Sollid et al., 2003). The same type of gill remodeling was soon found to occur in the closely related goldfish (*Carassius auratus*), and not only in response to hypoxia, but also when the fish were moved to warmer water (≥25 °C; Fig. 1D) (Sollid et al., 2005a). Recently, it has been shown that exercise also induces gill remodeling and an increased gill surface area in crucian carp and goldfish (Brauner et al., 2011; Fu et al., 2011; Perry et al., in press). Moreover, it is clear that the increased gill surface area has a functional significance for oxygen uptake, as it reduces the critical oxygen tension ($P_{O_2\ crit}$ = the lowest oxygen partial pressure (P_{O_2}) in water needed for maintaining resting oxygen uptake) to about half that of individuals without protruding lamellae (Sollid et al., 2003; Fu et al., 2011). Indeed, a small ILCM also coincides with a higher maximal rate of oxygen uptake and a higher swimming performance (Fu et al., 2011; Perry et al., in press).

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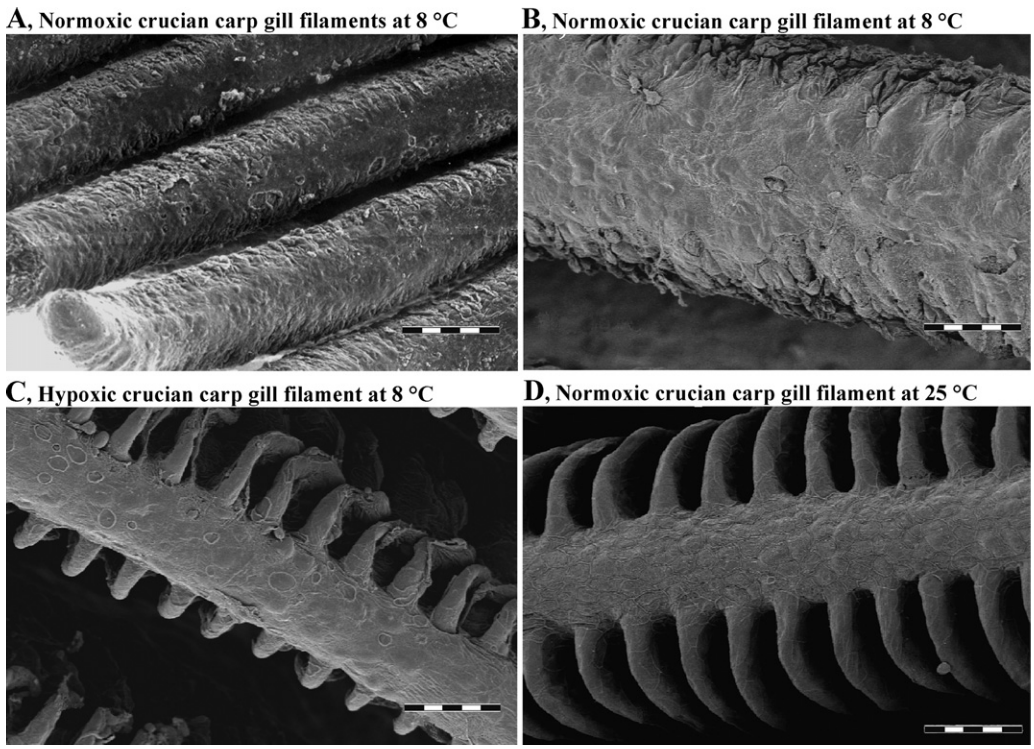

Fig. 1. Scanning electron micrographs showing gill filaments from crucian carp kept in 8 °C normoxic water (A and B), in 8 °C hypoxic water (C), or in 25 °C normoxic water (D). Scale bars are 150 μm in A and 50 μm in B–D.
From Sollid et al. (2003, 2005a).

As we shall see, gill remodeling in response to a change in oxygen needs (i.e. during hypoxia, high temperature or exercise) is presently known to occur in several cyprinid fishes and eel. A morphologically similar gill remodeling also occurs in salmonids and anabantoids during exposure to aluminum and/or acid water. Moreover, a species of killifish has been found to remodel its gills after emergence from water to land. Certainly, more examples of gill remodeling in fish wait to be discovered.

2. Mechanisms of gill remodeling

Light micrographs of sectioned crucian carp gills reveal that gill remodeling involves the expansion or reduction of a cell mass between the lamellae of the gills (Fig. 2). Sollid et al. (2003) termed this an interlamellar cell mass (ILCM), a term generally used in subsequent studies. When it comes to the mechanisms responsible for increasing or reducing the ILCM, most of what we know comes from studies on crucian carp and goldfish, which both reduce their ILCM in response to an increased demand on oxygen uptake, either due to falling water oxygen levels, or due to increased oxygen consumption caused by a rise in water temperature or exercise. Thus, it appears that it is the oxygen need, rather than the water oxygen level in itself, that triggers gill remodeling in these species. Unfortunately, we still know very little about the signaling pathways linking oxygen demand with the change in ILCM size. However, we do know quite a bit about what is happening to the ILCM when it expands or regresses.

2.1. Cell removal and redistribution during gill remodeling

In normoxic crucian carp kept at 8 °C the ILCM often completely fills up the space between the lamellae (Fig. 2A), virtually hiding them, which explains their sausage-like appearance on scanning electron micrographs (Fig. 1A and B). As the fish is exposed to

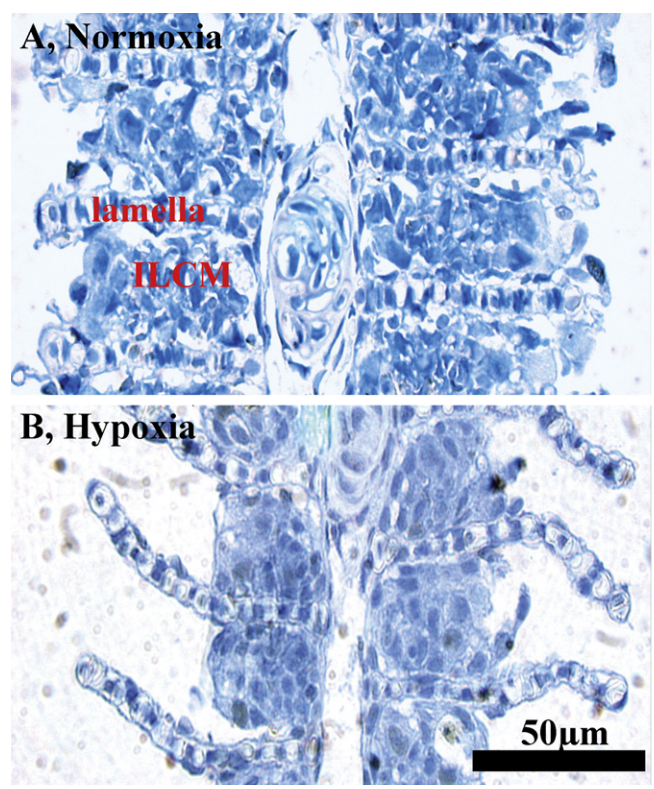

Fig. 2. Light micrographs showing gills from crucian carp kept in normoxic (A) or hypoxic (B) water at 8 °C. Note that the lamellae are present in both conditions but that hypoxia leads to a regression of the interlamellar cell mass (ILCM), making the lamellae protrude.
From Sollid et al. (2003).