

Optimal lamellar arrangement in fish gills

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Fish respire through gills, which have evolved to extract aqueous oxygen. Fish gills consist of filaments with well-ordered lamellar structures, which play a role in maximizing oxygen diffusion. It is interesting that when we anatomically observe the gills of various fish species, gill interlamellar distances (d) vary little among them, despite large variations in body mass (M_b). Noting that the small channels formed by densely packed lamellae cause significant viscous resistance to water flow, we construct and test a model of oxygen transfer rate as a function of the lamellar dimensions and pumping pressure, which allows us to predict the optimal interlamellar distance that maximizes the oxygen transfer rate in the gill. Comparing our theory with biological data supports the hypothesis that fish gills have evolved to form the optimal interlamellar distances for maximizing oxygen transfer. This explains the weak scaling dependence of d on M_b : $d \sim M_b^{1/6}$.

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Fish gills have evolved exclusively in aquatic creatures to extract aqueous oxygen. Because oxygen has considerably low solubility and diffusivity in water, the efficiency of respiration is critical (1). Gills consist of plate-like structures called filaments that are covered by an array of lamellae enclosing a capillary blood network, as shown in Fig. 1 (1, 2). Oxygen-rich water passes through the narrow channels formed by the lamellar layers, where oxygen diffuses into the capillaries. The densely packed lamellar structure is advantageous because it provides a large surface area for oxygen transfer; however, it also generates considerable viscous resistance. This resistance is overcome by pumping. Fish typically adopt one of the following two pumping mechanisms: branchial pumping and ram ventilation. Most teleost fish, members of the diverse group of ray-finned fish, use branchial pumping, and muscular compression in the pharynx enables water flow through the gills. In ram ventilation, which is used by many pelagic fish, the dynamic pressure generated by their swimming drives water flow into the gills (3).

Most previous studies on the structure of fish gills have focused on the dependence of the total surface area of the gill upon the body size and species of fish (1, 4, 5). We consider the convective oxygen transfer that occurs in fish gills. As water passes through the narrow lamellar channels, increased viscous resistance impedes water flow at a given pumping pressure, which is limited by muscle power or swimming speeds; this leads to a lowering of the oxygen transfer rate. Hence, the flow rate within the gaps of the lamellae and the extended surface area play important roles in determining the oxygen transfer rate. The number of lamellae per unit length of gill filament determines both the surface area for diffusion and the size of the water channels. Therefore, we investigate the relationship between lamellar distance and oxygen transfer rate, an aspect that previously has seldom been explored.

Results

Theoretical Analysis. We compiled interlamellar distances in a broad range of fish species, as shown in Fig. 2. It is remarkable that whereas the body mass of these species varies over six orders of magnitude from 0.1 g to 100 kg, the interlamellar distances vary within a very small range, ~ 20 – $100 \mu\text{m}$ (6, 7). To explain the

relatively uniform interlamellar distances, we mathematically modeled the oxygen transfer rate in fish gills, which is driven by the gradient of oxygen partial pressure. For an infinitesimal control volume shown in Fig. 1F, the conservation of oxygen can be written as $dQ_o/dx = -h\beta s(P_w - P_b)$, where Q_o is the oxygen flow rate, h the convective mass transfer coefficient, β the oxygen solubility coefficient of water, s the wetted perimeter of the control volume, P_w the average oxygen partial pressure in water, and P_b the oxygen partial pressure on the lamellar surface. The oxygen flow rate can be expressed in terms of the water flow rate through the channel Q_w as $Q_o = Q_w\beta P_w$. Because the lamellar height $H \sim 400 \mu\text{m}$ is typically much greater than the interlamellar distance $d \sim 40 \mu\text{m}$, as shown in Fig. 2 (2, 8–11), $s \sim 2H$, which allows us to write

$$Q_w dP_w/dx + 2hH(P_w - P_b) = 0. \quad [1]$$

For the characteristic flow speed through interlamellar channels $u \sim 0.01 \text{ m/s}$ (2, 11), water density $\rho \sim 1,000 \text{ kg/m}^3$, viscosity $\mu \sim 0.001 \text{ Pa}\cdot\text{s}$, interlamellar distance $d \sim 10 \mu\text{m}$, and lamellar length $l \sim 1 \text{ mm}$, the ratio of inertial to viscous effects, prescribed by the Reynolds number $Re = \rho u d^2 / (\mu l) \sim 10^{-3}$, implies that the flow within the interlamellar channel is laminar with negligible entrance effects. Accordingly, h is given by $h = ShD_w/2d$, where Sh is the Sherwood number, the ratio of convective to diffusive mass transfer (12), which is estimated as 7.5, and D_w , the oxygen diffusion coefficient in water (13), is $2 \times 10^{-9} \text{ m}^2/\text{s}$.

To solve Eq. 1 for P_w as a function of x , we first consider the x dependency of P_b . One expects that P_b approximates the partial pressure of oxygen in the capillaries due to negligible diffusive resistance between the lamellar surface and the capillaries (1). Hemoglobin in the capillaries rapidly combines with oxygen molecules, thus stabilizing the partial pressure of oxygen at a relatively low value (14–17). Hence, the relative variation in partial pressure in capillaries to that in water $\Delta P_b / \Delta P_w \ll 1$,

Significance

It is generally assumed that shapes encountered in nature have evolved in a way as to maximize the robustness of a species. Nevertheless, given nature's notoriously complex designs, it is often unclear what is being optimized. The lamellar pattern of fish gills is one of the few cases in which optimization in nature can be well defined. We demonstrate that the lamellar pattern of fish gills has been optimized, such that fish display interlamellar spaces of similar dimension regardless of body mass or species, thereby revealing the primary evolutionary pressure on fish gills. This natural optimization strategy demonstrates how control of the channel arrangement in microfluidic devices enhances heat and mass transfer.

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(22) and laboratory-on-a-chip systems for drug delivery (23) and biochemical analysis (24).

Materials and Methods

Mass-Transfer Experiments Using an Engineered Gill. We fabricated an engineered gill system consisting of PDMS microchannels, where gas transfer occurs across the membranes separating the channels. The PDMS structure was constructed using a 10:1 mixture of Sylgard-184 (Dow Corning) cured by baking for 30 min at 80 °C in a vacuum oven. We coated the inner wall of the upper and lower layers with 0.6 wt% Teflon-AF (DuPont 601S2 and 3M Fluorinert Electronic Liquid FC40) to prevent oxygen diffusion out of the channels. All three channels had identical widths of 2 mm and lengths of 70 mm. The membrane thickness was 20 μm . We changed the height of the central channel from 70 to 190 μm , and the heights of the other channels were fixed at 200 μm . Sodium sulfite was used to control the concentration of dissolved oxygen in water. Channel flow was achieved using

a syringe pump (Harvard PHD 22/2000). Reynolds numbers range from 0.002 to 0.3, and the flow is laminar. An oxygen microsensor (Unisense OX-100) was used to measure the partial pressure of oxygen at the outlet of the central channel.

Scanning Electron Microscopy. The gill of a rockfish, *Sebastes schlegelii*, was fixed in Karnovsky fixative solution and then postfixed with 1% osmium tetroxide in a 0.05 M cacodylate buffer. The specimen was dried in a drying device (Baltzer CPD030) after partial dehydration using a graded ethanol series. The dried specimen was coated with a thin layer of platinum in a sputter coater (Bal-Tec SCD005) and examined using a field-emission scanning electron microscope (Carl Zeiss SUPRA 55VP).

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