

## Dissolved oxygen and fish behavior

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### Synopsis

This essay reviews the behavioral responses of fish to reduced levels of dissolved oxygen from the perspective of optimization theory as used in contemporary behavioral ecology. A consideration of oxygen as a resource suggests that net oxygen gain per unit of energy expenditure will be the most useful currency for ecological models of breathing. In the process of oxygen uptake, fish always expend energy on perfusion, usually on ventilation and often on locomotion. These costs, and the risk of predation, will vary with oxygen availability and the type of behavioral response shown. The principal categories of behavioral response to reduced external availability of dissolved oxygen are (1) changes in activity, (2) increased use of air breathing, (3) increased use of aquatic surface respiration, and (4) vertical or horizontal habitat changes. Fish should choose whichever combination of responses minimizes the costs of meeting their oxygen demands. A small number of studies provides qualitative support for this prediction.

### Introduction

The Krebs Cycle and the electron transport chain are the main energy-producing pathways of most organisms, including fishes (Driedzic & Hochachka 1978). Oxygen, the final electron acceptor of this pathway, is therefore potentially as important as organic substrates derived from food in determining the energy budget. For organisms that live in air, the relatively high concentration of oxygen means that oxygen limitation is likely only during periods of intense demand; in general, activity is more likely to be limited by food than by oxygen supply. However, oxygen is much more likely to be limiting for aquatic organisms than for terrestrial ones. In part, this is due to the lower availability of oxygen in water and in part to the high density and viscosity of water which increase the costs of ex-

traction (Kramer 1983a).

When oxygen supply is insufficient to meet the minimal energy demands of essential functions, suffocation occurs. This may happen in nature when fish which normally live in well-oxygenated water are confronted with oxygen-deficient water from which they cannot escape. However, suffocation is rare where oxygen deficiency occurs naturally. Fish from such habitats are remarkably effective at oxygen extraction, frequently possess alternative modes of oxygen uptake and sometimes have more oxygenated alternative habitats available. A few species can also meet minimal energy needs through anaerobic pathways (Hochachka 1982). In contrast to survival, a wide range of dissolved oxygen levels affect the maximal rate of oxygen uptake (Fry 1971). Therefore, dissolved oxygen availability may affect the ecology of fishes

more through the availability of energy for locomotion, growth and reproduction than through its direct effects on survival.

Recognition of the importance of the non-lethal consequences of reduced oxygen availability has generated numerous studies relating physiology and behavior to dissolved oxygen levels. However, the relevance of such studies to predicting the effects of reduced oxygen levels on fishes in nature is limited. Habitat shifts and the use of alternative breathing modes, such as air breathing or aquatic surface respiration, not only alter oxygen availability, but can also change other crucial ecological parameters such as predation risk and food availability. For example, suppose that one wished to predict how eutrophication of a small river would affect a recreational fishery. Eutrophication is expected to reduce nocturnal dissolved oxygen levels. Laboratory studies show that the expected minimal levels are not lethal but that growth rates may be reduced. However, the fish may not simply remain in the oxygen-deficient water. They may rise to the surface to breathe the oxygenated surface layers, reducing the growth effect but increasing the risk of predation by herons and kingfishers. On the other hand, they may move upstream of the pollution source, to sites where they would experience severe food competition and become more vulnerable to fishermen. The impact of eutrophication may depend critically on which of the available alternatives is taken. In general, laboratory and field studies have not attempted to determine which of several responses will be used. Rather, they emphasize the physiological or behavioral effects of low oxygen within the framework of a particular response type. The field of behavioral ecology has begun to develop a methodology for predicting the use of alternative responses in organisms faced with environmental variation. I believe that this approach can be usefully applied to respiration and the consequences of reduced oxygen availability.

Behavioral ecology uses optimality theory to predict the use of alternative responses or 'tactics' of resource gain. A resource is 'any substance or factor which can lead to increased growth rates as its availability in the environment is increased, and

which is consumed by an organism' (Tilman 1982, p. 11). Optimality theory assumes that animals will maximize the net rate of resource uptake or minimize the cost of obtaining some required amount. Simple mathematical models that attempt to incorporate the main cost parameters are used to predict the optimal strategy under specified conditions. The effects of modifying factors such as need of other resources, predation risk or limited information may be incorporated. Finally, the possibility of frequency-dependent processes of competition or cooperation may be taken into account (see Maynard Smith 1978 for a general discussion). Despite objections to both its theoretical structure and its application in practice (e.g. Gould & Lewontin 1979), this approach had had considerable qualitative and some quantitative success in producing *a priori* predictions of feeding strategies (e.g. Krebs et al. 1983, Pyke 1984). In aquatic systems, at least, oxygen fits the definition of a resource. Thus, the optimality approach is as relevant to predicting breathing modes and habitat shifts as it is to diet and foraging site decisions.

In the present paper I briefly review the factors which influence the availability of dissolved oxygen. I then elaborate upon the concept of oxygen as a resource. This provides a framework to review what is presently known about alternative behavioral responses to oxygen availability and their potential costs. Finally, I summarize the limited evidence that the behavioral ecological approach can actually predict the alternative responses of fishes to reduced oxygen availability. In a related essay, I analyzed the potential costs of breathing in more detail, and used this analysis to discuss the evolution and maintenance of different breathing modes (Kramer 1983a). Several other reviews have considered the ecological implications of low oxygen for fish and other aquatic organisms (Doudoroff & Shumway 1970, Davis 1975, Holeyton 1980). However, these have been largely physiological rather than behavioral in viewpoint and have not attempted to apply optimality theory to the problem.