AVAILABLE POWER AND COMPETITIVE FITNESS IN FISHES

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Natural and human-induced environmental challenges clearly affect fitness in fishes; however, it is often difficult to determine cause-and-effect relationships between specific environmental variables and aspects of fitness. Fitness is normally measured as survival or fecundity following complex interactions between phenotypes and the environment. This complexity makes it difficult to identify and manage extraordinary environmental challenges prior to their effects on fishes. In essence, a decrease in fitness caused by an environmental challenge often cannot be detected until after the challenge has occurred and even then it is difficult to identify the cause.

Available Power

The concept of available power is promising as a potential index of competitive fitness in fishes. Ware (1982) postulated that the basis for natural selection is the availability of energy over time (which has the units of power). This idea is not recent, Lotka (1922) stated the principle that "... in the struggle for existence, the advantage must go to those organisms whose energy-capturing devices are most efficient in directing available energy into channels favorable to the preservation of the species."

Fry's (1947) scope for activity offers a basis for understanding and measuring available power. Respiratory metabolism is normally measured in terms of weight-specific oxygen-consumption rates because oxygen consumption is directly related to energy production which is a measure of power. Therefore, metabolic relations and energetic equations can be described in relation to power as I have done below. Under any set of environmental conditions, a certain amount of power (measured by standard metabolic rate, P_s) is necessary for an organism to maintain itself (consider the decomposition that occurs following death when this maintenance ceases). Under the same set of environmental conditions there is also a limit to the maximum aerobic power that can be generated by an organism (measured by active metabolic rate, P_{max}). The power left after subtracting the power costs for standard metabolic rate from the active metabolic rate is Fry's scope for activity (P_{scope}) and represents the maximum potential aerobic-power available for all functions, including growth, reproduction, survival, and activity under the given environmental conditions:

$$P_{scope} = P_{max} - P_s. \quad (1)$$

Organisms forced by their environment to operate with less power than necessary for standard metabolism, or forced to expend more power than available at the active metabolic rate (by using anaerobic metabolism), will experience a high rate of mortality (Priede, 1977).

The maximum power (maximum P_{scope}) that can be generated by an organism is limited by physical laws and the nature of the organism itself. For example, maximum power is limited by the ability of an organism to assimilate energy and oxygen from the environment under optimal conditions. Available power also becomes reduced from maximum under sub-optimal conditions. Environmental factors that either increase the power required for standard metabolism (e.g., high temperature) or decrease the active metabolic rate (e.g., low temperature, low oxygen availability, and starvation), result in decreased scope for activity and decreased power available for life.

Organisms do not routinely metabolize at maximum levels by expending all of their scope for activity, but metabolize at lower levels leaving unused potential power (P_p) available for environmental challenges. Scope for activity can be subdivided into major power components as follows:

$$P_{scope} = P_a + P_f + P_g + P_p, \qquad (2)$$

where P_{scope} is the maximum metabolic power available under a given set of environmental conditions, P_a is power used by the organism to maintain a given level of activity, P_f is the power required for acquiring energy from food (specific dynamic action; Priede, 1985), and P_g is the power used by the organism to maintain a given level of growth (and reproduction).

Natural Selection for Maximization of Available Power

Natural selection should favor organisms that have greater scope for activity (P_{scope}) than their intraspecific competitors under existing environmental conditions. Priede (1985) described two types of selection that may favor competitors with greater scope for activity (P_{scope}). Type 1 describes how organisms with greater unused available power (P_p) under similar environmental conditions may have a selective advantage. Unused available power would tend to be greater for more efficient phenotypes, or those with greater P_{scope}. Individuals with greater P_p for similar levels of activity would have surplus power that may increase fitness by being channeled into activities such as reproduction. Such surplus power has been hypothesized as a primary focus of natural selection (Ware, 1982) but represents only one of two types of selective advantage described by Priede. Type 1 selection then leads to greater efficiency in use of power and would also favor organisms with greater P_{scope}. Type 2 selection also favors organisms with greater P_{scope} but for a different reason. Priede provides support for the idea that it is not necessary that organisms actually make use of P_{scope} on a regular basis. He argued that it is vital that organisms function within limits of their P_{scope} and that the greater the distance from maximum levels of power expenditure, the lower the probability of mortality. In equation 2, P_p represents this unused available power and can be considered to be a margin of safety. A phenotype with a greater P_p will have a reduced probability of mortality because it is less likely to exceed the limits of P_{scope} when subjected to inevitable environmental challenges. Type 2 selection would also favor more efficient phenotypes and those with greater P_{scope} when faced with similar environmental challenges. Accordingly, these two types of selection should have favored organisms that sought environments that maximized their scope for activity.

Support for the Model

I provide evidence from the literature in support of the concept that available power (scope for activity) is an index of fitness. I also provide support for this concept by testing the hypothesis that fish tend to select temperatures that maximize available power, specifically by testing the prediction that the frequency of time spent at various temperatures is proportional to critical swimming speeds under those same thermal conditions. Results support the idea that at least some fishes seek thermal environments that maximize their available power (Kelsch and Neill, 1990), and frequent sub-optimal temperatures as a function of the amount of available power; however, the exact nature of this relationship remains to be determined. The experimental design did not enable me to study individual variation, population variation, seasonal variation, or variation due to handling stress. Further work is necessary to address these questions.

Stress Response as a Mechanism for Avoiding Dangerous Stimuli

What implications does maximization of available power in the laboratory have for fishes living in real environments? I predict that they would tend to maximize available power within two primary constraints. First, since environments do not often have clear gradients of abiotic factors, organisms can only be expected to tend toward environments that offer local maxima of available power. Once there, they are expected to form some distribution about the local maximum that is a function of available power. The second constraint is the effect of biotic factors such as predators or competitors. Competitors may alter the environment by reducing oxygen concentrations or food supply, but how would territorial displays or the presence of a predator affect maximization of available power? The stress response (Wedemeyer et al., 1990) may enable biotic interactions to have an effect on available power.

One difficulty with the concept that organisms maximize available power is the time frame in which this maximization is done. Consider a small fish swimming toward a better environment (one that offered greater available power) that was occupied by a predator (or a dominant competitor). An alert fish would certainly attempt to avoid the predator at the cost of reduced available power, for the potential to maximize available power in the future. What is the time frame for maximizing available power? Perhaps all organisms tend to maximize available power over the short-term (minutes; see Priede, 1985), and organisms with a neuro-endocrine system avoid risk of mortality or high power expenditure due to their stress response.

The stress response of animals may be an adaptive mechanism that internally increases power costs (perhaps by channeling power to emergency systems) thereby reducing available power in the vicinity of the stressor (Figure 1). This may result in relatively greater available power in nearby non-stressful environments, which would tend to direct movement away from the stressor while maximizing available power. Studies have shown that stress decreases scope for activity, probably by increasing standard metabolism (p_S in equation 2), and reduces performance (Schreck, 1990; Wedemeyer et al., 1990) by using power that is then unavailable for other functions. An advantage of such a system is that because it is neuro-

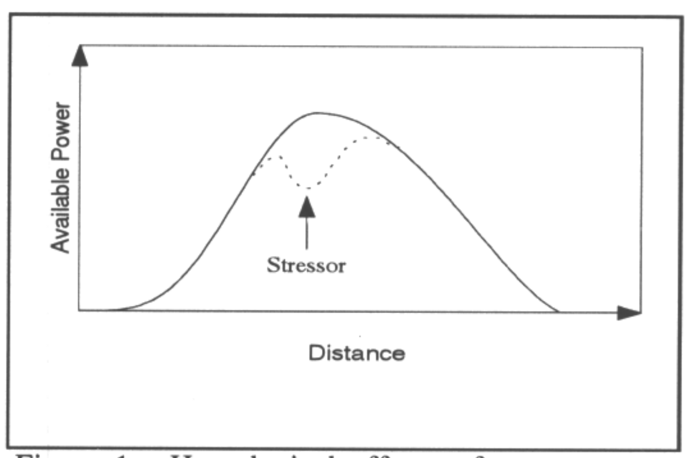

Figure 1. Hypothetical effects of a stressor on available power. The stress response is predicted to reduce available power near a stressor (dashed line).

endocrine, the stress response could be modified by learning. Animals could avoid unknown dangerous stimuli while learning not to have a severe stress response to new, non-dangerous stimuli. They could also avoid intraspecific competition and associated energy expenditures. Such a scenario makes sense of some of the seemingly mal-adaptive characteristics of the stress response including reduced disease resistance, reduced growth, and reduced survival (Stickney and Kohler, 1990; Wedemeyer et al., 1990). The occur because the adaptive response of avoiding stressors is hindered in captivity.

Implications

Available power is a useful property in that it may offer a method to assess the combined effects of phenotypic and environmental factors on organisms. It is essentially impossible to assess the relative advantages of existing phenotypic differences and the effects of these and their interactions in available environments. It is, however, possible to measure the amount of power available to these individuals under a given set of environmental conditions, for example, by comparing critical swimming speeds. Although only temperature varied in this study, it is likely that the effects of other important environmental variables would have an integrated effect on available power. Any multidimensional environment should yield a single amount of available power to which an organism can respond.

In addition, this work provides, at best, highly limited support for the concept for that fishes tend to select temperatures (or other environments) on the basis available power. Much more work is necessary to support the concept that natural selection favors organisms with adaptations and behaviors that maximize their available power (scope for activity). Priede (1977, 1985) provided a basis for understanding how natural selection may favor competitors with more available power either by greater energetic investment in activities such as reproduction or by reduced mortality resulting from greater available power which functions as a safety reserve for environmental challenges. This concept has been developed for fishes but may also apply to other organisms.

References

Fry, F. E. J. 1947. Effects of the environment on animal activity. University of Toronto Studies, Biological Series 55. (Publications of the Ontario Fisheries Research Laboratory 68:1-62.)

Kelsch, S. W., and W. H. Neill. 1990. Temperature preference versus acclimation in fishes: selection for changing metabolic optima. Transactions of the American Fisheries Society 119:601-610.

Lotka, A. J. 1922. Contribution to the energetics of evolution. Proceedings of the National Academy of Sciences 8:147-151.

Priede, I. G. 1977. Natural selection for energetic efficiency and the relationship between activity level and mortality. Nature 267:610-611.

Priede, I. G. 1985. Metabolic scope in fishes. Pages 33-64 in P. Tytler, and P. Calow, editors. Fish energetics: new perspectives. Johns Hopkins University Press, Baltimore, Maryland. U. S. A. 349 p.

Schreck, C. B. 1990. Physiological, behavioral, and performance indicators of stress. American Fisheries Society Symposium 8:145-166.

Stickney, R. R., and C. C. Kohler. 1990. Maintaining fishes for research and teaching. Pages 633-663 in C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland. U. S. A. 684 p.

Ware, D. M. 1982. Power and evolutionary fitness of teleosts. Canadian Journal of Fisheries and Aquatic Sciences 39:3-13.

Wedemeyer, G. A., B. A. Barton, and D. J. McLeay. 1990. Stress and acclimation. Pages 451-489 in C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland. U. S. A. 684 p.