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Review

Estimates of metabolic rate and major constituents of metabolic demand in fishes under field conditions: Methods, proxies, and new perspectives

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A B S T R A C T

Metabolic costs are central to individual energy budgets, making estimates of metabolic rate vital to understanding how an organism interacts with its environment as well as the role of species in their ecosystem. Despite the ecological and commercial importance of fishes, there are currently no widely adopted means of measuring field metabolic rate in fishes. The lack of recognized methods is in part due to the logistical difficulties of measuring metabolic rates in free swimming fishes. However, further development and refinement of techniques applicable for field-based studies on free swimming animals would greatly enhance the capacity to study fish under environmentally relevant conditions. In an effort to foster discussion in this area, from field ecologists to biochemists alike, we review aspects of energy metabolism and give details on approaches that have been used to estimate energetic parameters in fishes. In some cases, the techniques have been applied to field conditions; while in others, the methods have been primarily used on laboratory held fishes but should be applicable, with validation, to fishes in their natural environment. Limitations, experimental considerations and caveats of these measurements and the study of metabolism in wild fishes in general are also discussed. Potential novel approaches to FMR estimates are also presented for consideration. The innovation of methods for measuring field metabolic rate in free-ranging wild fish would revolutionize the study of physiological ecology.

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1. Introduction

An organism's energy metabolism can be subdivided into supply ($Energy_{in}$), transformation or use ($Energy_{out}$) and accretion of tissue mass for growth or storage ($Energy_{retained}$) and reproductive effort which may be in the form of gonadal investment ($Energy_{retained}$) or may be $Energy_{out}$ with the release of gametes (Fig. 1). However, the interactions between the environment and an individual's energetic costs are complex and vary according to species, developmental stage, season and even subpopulation/geographic region. This complexity may confound direct extension of laboratory-derived estimates of energetic parameters to field-relevant questions. As such, robust means of estimating metabolic rate that can be extended for field use are critical to understanding the energy balance in individuals. Knowledge at the individual or population level can then be applied to study how variation in energetics may influence the species' role in the ecosystem. The interdisciplinary extension of laboratory-level techniques to field level questions represents an opportunity for significant advancement, as long as the assumptions and limitations of these approaches are recognized.

In many, if not most, aquatic ecosystem fishes are critically important consumers. Fishes are often high level predators and, within the same ecosystem, smaller forage species may be key energy conduits between trophic levels. Moreover, fishes are well recognized for their susceptibility to environmental disturbances, including anthropogenic alterations, and are of worldwide economic and cultural importance. However, despite such ecological and sociological significance of fishes, there is a dearth of direct information for metabolic rate (MR) in free swimming fishes under field conditions. The limited information on MR for fish under truly natural conditions leaves an important information gap in the ability to relate fish energy demands with, for instance, environmental change or anthropogenic challenges. The aim of this article is to synthesize many of the strategies that can be applied to estimate MR (e.g. energy expenditure) or alternatively, that can provide proxy measures of major components of energy balance in fishes. Our goal is to cover several levels of investigation from the currently available approaches that predominate in this area of research, telemetry and respirometry, to longer term or integrative methods as well as more indirect proxies at the organ and tissue levels. Each of these levels of investigation could warrant a review unto themselves but our task is to consolidate options in one place to encourage further discussion, development and inquiry.

It is also worth adding that while we refine our focus to specifically consider fishes, the majority of the following may be applicable to other organisms, including aquatic and non-aquatic species. We also emphasize that while it is simpler to complete metabolic studies under controlled laboratory conditions, and much excellent work has done so, it is difficult, if not impossible, to fully replicate truly environmental conditions and stochasticity in a controlled setting. As such, we focus here on approaches with potential for extension to field conditions or wild sampled fishes. We will first address some key definitions and broad scale aspects important to all metabolic work on fishes, including some specific areas of relevance. This is followed by a brief review of several approaches to measuring MR, or major components that contribute to metabolic demands.

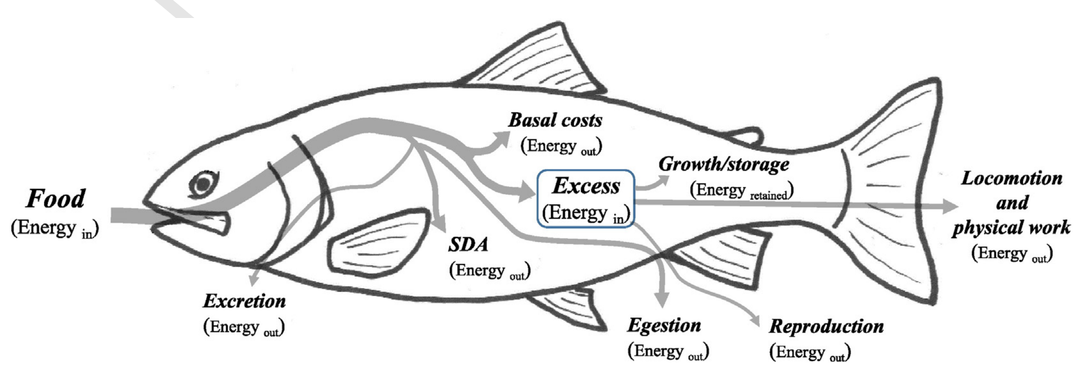

Fig. 1. *Illustration of the energy budget in a fish.* Energy intake as *Food* requires energetic costs as specific dynamic action (*SDA*) and some energy will be lost from the animal as *Egestion* (indigestible material and carbon not assimilated) or as nitrogenous *Excretion*. The remaining energy will be used to meet the costs of life (*Basal costs* such as maintenance of ion gradients, protein and DNA repair) with the energy in *Excess* of basal requirements being allocated to *Growth/storage*, *Locomotion and physical work* or *Reproduction* which can be either output as gametes or retained as gondal investment (which can also be viewed as *Growth/storage*). The $Energy_{in}$, $Energy_{out}$ and $Energy_{retained}$ nomenclature are described in the text.

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