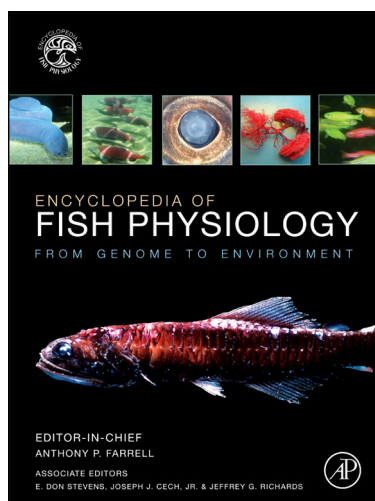


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ENERGETICS

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Physiological Functions that Scale to Body Mass in Fish

Energetics: An Introduction

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Energy Use by Fish

Glossary

Entropy A thermodynamic property measuring the amount of disorder in the system. Greater disorder is energetically favorable; thus, entropy favors unfolding of proteins.

Specific dynamic action (SDA) The additional amount of oxygen or energy consumed above SMR as a result of feeding, measured during the period after feeding until metabolic rate returns to SMR; SDA represents the

energetic cost of digestion, assimilation, and protein turnover.

Standard metabolic rate (SMR) The minimum metabolic rate of survival. Typically, SMR is measured on resting, unstressed adult animals in the post-absorptive state under normothermic conditions. For fish, normothermic is defined as a temperature well within the species tolerance limits for which the animals have had ample time to acclimate.

Energy Use by Fish

Metabolism is the word used to describe the totality of energy-consuming, manipulative, and storage chemical reactions undertaken by organisms. The second law of thermodynamics demands that all processes increase the amount of entropy (disorder) in the universe. Thus, a highly ordered entity like a fish requires a constant input of energy to remain ordered, even in the absence of growing. In the process of obtaining and assimilating that energy, the fish randomizes the rest of the universe more than the ordering of the fish itself. This results in a net increase in the disorder of the universe and the possibility of fish life, but only with this constant energy input. Therefore, a primary goal of fish existence is to obtain sufficient energy to offset this universal randomization process. This energy needs to be of two types, chemical bond energy and high-energy electrons (reducing power) which, along with some minerals and macromolecules that fish are unable to synthesize themselves, constitutes the daily dietary requirement for that fish

species (see also **Food Acquisition and Digestion: Digestive Efficiency**). A subsequent, but equally essential goal of fish life is to obtain these components in sufficient excess to fuel growth and reproduction, leading to eventual evolutionary success. This excess fuel can also support locomotion or other work done on the environment. A bioenergetics flow chart, such as **Figure 1**, summarizes the energy inputs and outputs of a fish.

Of the energy consumed in food (C), only a certain fraction is actually absorbed across the intestinal epithelium into the fish (A), with the remainder being lost as feces (along with a small, not depicted, fraction of energy lost from the sloughing of gastrointestinal cells into the eventual feces). Fish tend to be very efficient at retaining the energy contained in their food. Of the absorbed energy (A), nitrogen in excess of the animal's requirements for protein and nucleic acid growth or turnover is not available to the organism and is excreted. The energy contained in this lost nitrogen as well as any energy lost in processing it, for

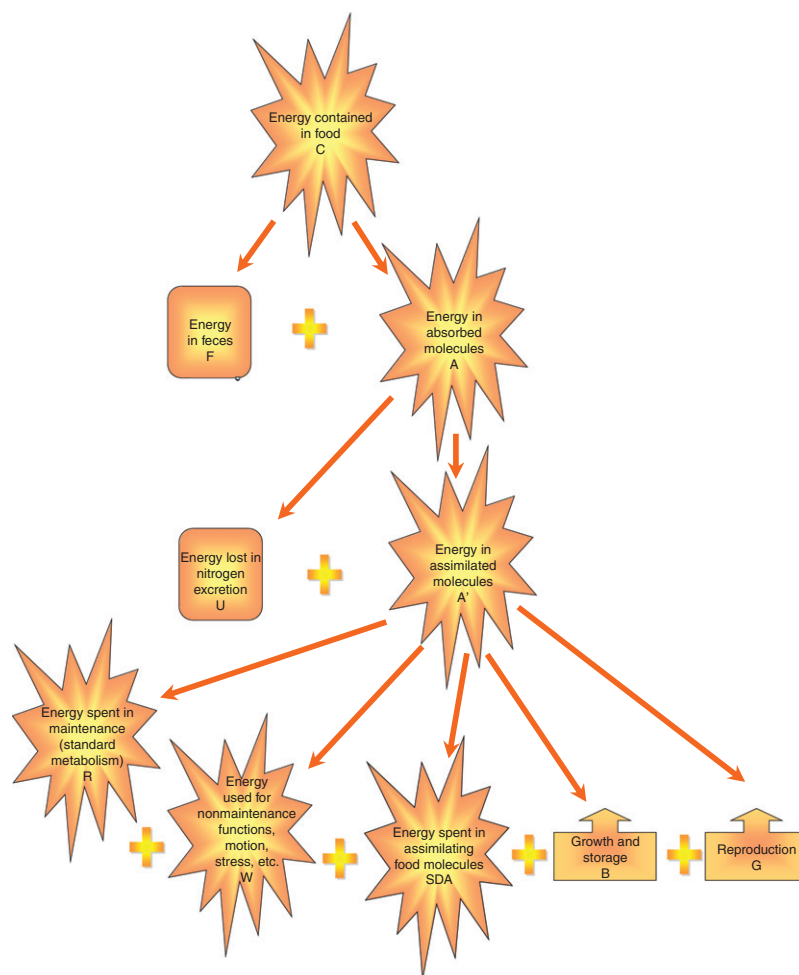


Figure 1 A bioenergetics flowchart for fish. Squares depict energy losses, stars potential or used energy, and rectangles energy storage. Details are contained in the text.

example, to urea, $\text{CN}_2\text{H}_4\text{O}$, is represented by the term U and is not available to the animal (see also **Nitrogenous-Waste Balance**: Excretion of Ammonia and Ureotelism). The remaining energy (A') is available to the organism and can be used to support either maintenance functions (R), nonmaintenance activities (W), or the work of assimilating more food molecules (SDA) (see also **Food Acquisition and Digestion**: Cost of Digestion and Assimilation). Excess energy is then available for storage or to support organismal growth (B) and gonad maturation (G) so that the animal can be successful from an evolutionary perspective and reproduce. This flow chart is often expressed in the form of an energy budget equation such as eqn (1) for modeling fish energy requirements:

$$C = (F + U) + (R + W + SDA) + (B + G) \quad (1)$$

where, F is the fraction of ingested energy lost in the feces. This section of the encyclopedia focuses on this flow of energy through a fish. The section is divided into three

main subsections: (1) energy acquisition, the energy cost to the fish to find, internalize, and extract the energy and other key molecules found in their food and how extrinsic and intrinsic factors influence that cost; (2) energy utilization, a detailed examination of the different ways that fish allocate the energy they procure from the environment and the effects of the variable aquatic environment on that allocation process; and (3) models and applications, where we explore how knowledge of the energy flow through fishes has led to advances in the management of exploited fish stocks and improvements in the aquaculture industry.

Energy acquisition encompasses the cost to the fish of finding food, successfully subduing it, manipulating it to the point that it can be swallowed, and then the cost of mechanically and chemically breaking down the macromolecules in food to a size that can be absorbed across the intestinal epithelium (digestion). Also included in this cost are the biochemical costs of manipulating the absorbed molecules into the proper forms to become self or storage compounds.

Lara Ferry-Graham opens this section with a consideration of how fish morphology matches up with the prey they consume, presumably minimizing energy acquisition costs, and how past evolutionary events may or may not have shaped these relationships. Shaun Killen continues with a discussion of the energetic costs of prey handling and ingestion, and how those costs may influence which prey items a fish actually attempts to consume. Donovan German then details what happens to the energy in food after it is ingested, that is, what factors determine the amount of energy extracted by a given fish on a given diet. Finally, Stephen Secor wraps up the 'energy acquisition' subsection with a detailed examination of the energetic costs associated with processing a meal.

The 'energy utilization' subsection deals with the main ways that fish can expend the energy they acquire with the exception of reproduction, which is dealt with in other areas of the encyclopedia (see also **Hormonal Control of Reproduction and Growth**: Endocrine Regulation of Fish Reproduction). The chapter by Jay A. Nelson and Denis Chabot focuses on just the standard metabolism (SMR) term R of eqn (1). This is the energy required by the organism just to stave off the forces of entropy and includes both extrinsic and intrinsic determinants of SMR. Resolving the terms of eqn (1) is essential if we are to predict growth and thus production in any fish species, which is the subject of Bob Wootton's first chapter. He then goes on to explore how environmental factors can change energy allocation to growth in a second contribution. Environmental effects on fish

energy allocation are also the subject of Hans-Otto Pörtner's chapter, but his focus is on how the environment influences energy consumption or metabolic rate. Finally, David McKenzie details the energy cost of exercise in fish and how that integrates with the other parts of the bioenergetic budget because, of course, most fish need to move to procure food in the first place, or to avoid becoming food themselves!

The last subsection of the bioenergetics section, 'models and applications' deals with how this bioenergetic information is put to work solving real-world problems of fisheries management and aquaculture. Equation (1) needs to be resolved on an ecosystem level if we are to understand how changes in a species' numbers will influence energy flow in their ecosystem. Chuck Madenjian details the history of bioenergetics use in fisheries management and presents several case studies where bioenergetics models have been essential in making good fisheries-management decisions. Finally, Malcolm Jobling presents a cogent argument for why all food production is basically an exercise in bioenergetics and how the aquaculture industry is steadily improving the bioenergetic basis of how it operates.

See also: **Food Acquisition and Digestion:** Cost of Digestion and Assimilation; Digestive Efficiency.

Hormonal Control of Reproduction and Growth: Endocrine Regulation of Fish Reproduction.

Nitrogenous-Waste Balance: Excretion of Ammonia; Ureotelism.