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Energy homeostasis as an integrative tool for assessing limits of environmental stress tolerance in aquatic invertebrates

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ABSTRACT

Energy balance is a fundamental requirement of stress adaptation and tolerance. We explore the links between metabolism, energy balance and stress tolerance using aquatic invertebrates as an example and demonstrate that using key parameters of energy balance (aerobic scope for growth, reproduction and activity; tissue energy status; metabolic rate depression; and compensatory onset of anaerobiosis) can assist in integrating the effects of multiple stressors and their interactions and in predicting the whole-organism and population-level consequences of environmental stress. We argue that limitations of both the amount of available energy and the rates of its acquisition and metabolic conversions result in trade-offs between basal maintenance of a stressed organism and energy costs of fitness-related functions such as reproduction, development and growth and can set limit to the tolerance of a broad range of environmental stressors. The degree of stress-induced disturbance of energy balance delineates transition from moderate stress compatible with population persistence (pejus range) to extreme stress where only time-limited existence is possible (pessimum range). It also determines the predominant adaptive strategy of metabolic responses (energy compensation vs. conservation) that allows an organism to survive the disturbance. We propose that energy-related biomarkers can be used to determine the conditions when these metabolic transitions occur and thus predict ecological consequences of stress exposures. Bioenergetic considerations can also provide common denominator for integrating stress responses and predicting tolerance limits under the environmentally realistic scenarios when multiple and often variable stressors act simultaneously on an organism. Determination of bioenergetic sustainability at the organism's level (or lack thereof) has practical implications. It can help identify the habitats and/or conditions where a population can survive (even if at the cost of reduced reproduction and growth) and those that are incapable of supporting viable populations. Such an approach will assist in explaining and predicting the species' distribution limits in the face of the environmental change and informing the conservation efforts and resource management practices.

1. Introduction

Energy metabolism plays a central role in organism's survival and function, as well as in stress adaptation and tolerance. The amount of available energy, the rate at which it can be gained and metabolically transformed as well as the capacity to store it are inevitably limited in any organism. Therefore, regulation of energy expenditure and its allocation to different functions are fundamental to the organism's fitness. Environmental stress can strongly affect the energy balance of an organism due to the additional energy needed to recover and maintain homeostasis that can put strains on the systems involved in energy acquisition, conversion and conservation. The potential energy cost of stress response and homeostatic regulation against the environmental disturbances have been discussed in several excellent reviews (Calow, 1983, 1989; 1991; Calow and Forbes, 1998; Van Straalen and Hoffmann, 2000). However, up until recently, few experimental studies have explicitly tested the energy cost of stress response and its role in stress tolerance to validate the theoretical framework proposed in these reviews. The past few decades saw a steady growth in the number of studies focusing on metabolic responses to stress. An important common theme emerging from these studies points

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towards energy balance as a key factor that determines stress tolerance limits of an organism and can directly translate into population- and ecosystem-level consequences. Recently, quantitative bioenergetic models [such as the family of the dynamic energy budget (DEB) models proposed by Kooijman (Kooijman, 2010)] have been used to link whole-organism bioenergetics to population growth in a variety of organisms and to incorporate environmental forcing variables such as toxins, food availability and temperature stress (van Haren et al., 1994; Pouvreau et al., 2006; Kooijman et al., 2009; Einarsson et al., 2011). These models are extremely useful in predicting the ecological and population-level consequences of bioenergetic shifts. However, they require extensive parameterization that is time- and effort-consuming and feasible only for a few well-studied species (Van Haren and Kooijman, 1993; van Haren et al., 1994; Bacher and Gangnery, 2006; Kooijman et al., 2009; Sarà et al., 2012). Given enhanced anthropogenic pressure on wild populations, it becomes increasingly important to identify approaches to rapidly assess the degree of stress experienced by the population, to integrate the effects of multiple stressors and predict its likely outcome for the population persistence. In this review, we propose incorporating the physiological models of oxygen- and capacity-limited thermal tolerance (OCLTT) (Pörtner, 2002, 2010) with the fundamental tenets of energy allocation and trade-offs developed in the DEB models (Kooijman, 2010) in a conceptual framework that can be used to integrate the physiological effects of multiple stressors at the organism level and link them to the long-term, population-level consequences. We also argue that the bioenergetic framework provides a common ground for comparison of physiological responses to different stressors regardless of their nature and helps distinguishing between the moderate environmental stress compatible with the long-term population persistence and the extreme stress that can lead to population decline and extinction. Using case studies of aquatic invertebrates, we aim to demonstrate the utility of the proposed bioenergetic framework for determining the limits of stress tolerance and understanding the mechanisms setting these limits, to identify metabolic biomarkers that mark ecologically important physiological transitions during stress exposure and point to the gaps in our knowledge in the hope to stimulate further research on bioenergetic underpinnings of stress physiology and ecology of aquatic ectotherms.

2. Basics of energy balance in animals

Living objects can be defined as non-equilibrium, thermodynamically open systems relying on the external energy sources and constant energy flow. In its simplest form, the net energy exchange in an organism can be described by a balance Eq. (1) (Winberg, 1960):

$$C = P + R + U + F \qquad (1)$$

where C is consumption (energy acquired through food ingestion); P (production) is the energy incorporated into e.g. somatic and gonad tissue growth, storage tissues, gamete production, and exoskeleton and mucus deposition; R (respiration) is the basal maintenance cost including metabolic costs of growth, development and reproduction and is equivalent to total metabolic heat losses; U is energy excreted with the products of protein metabolism (ammonium, urea, etc.); F is part of the energy of ingested food which is not assimilated and excreted with feces. Importantly, the net energy exchange and energy balance of an organism depends not only on the amount of the available food, but also on the rates of its incorporation and metabolic conversion that channel the energy flux to different processes. Thus, all terms in the Eq. (1) include a time component (i.e. are calculated per unit time). The DEB models (Kooijman, 2010) represent further development of these ideas and can be broadly applied to assess the bioenergetic consequences of homeostasis and stress response [e.g. (Hall et al., 2007; Jager et al., 2010) and references therein]. The standard DEB model assumes that energy and matter assimilated from food is first directed into the reserve pool and distributed throughout the organism (Kooijman, 2010). The utilization of this energy occurs through its allocation into two main sinks - building and maintenance of somatic structures (including somatic maintenance and growth, as well as activity) and reproduction (metabolic needs for development, maturation and production of gametes). The fixed fraction of energy/matter (κ) is allocated in somatic needs, while the rest of the flux is directed to reproduction (so-called κ-rule).

In order to survive and to maximize Darwinian fitness, the organism must be able to balance its energy gains from the environment against its metabolic losses and to ensure an optimal allocation of surplus energy to somatic growth and to reproduction (Kozłowski, 1992; Perrin and Sibly, 1993). Importantly for our subsequent discussion, the components of an organism's energy budget are functionally linked together, so that changes in any of the processes have consequences for one or more of the others. This functional linkage is provided by two major constraints that require allocation of available energy (in terms of calories) and metabolic power: 1) the limitation in energy input including the overall amount of available food and the rate of its assimilation (Barnes, 1974; Barnes and de Villiers, 2000; Beukema and Cadeé, 2001); 2) limitation of the maximum metabolic capacity (e.g. in oxygen supply capacities or mitochondrial efficiency) for conversion of the food and channeling it toward different physiological processes (Guderley and Pörtner, 2010).

3. Metabolic principles of stress response and the role of energy balance in setting stress tolerance limits

Energy balance plays a critical role in environmental stress tolerance and in setting limits for the survival of organisms and their populations under stressful conditions. Metabolic adaptations to environmental stress can involve flexible allocation of energy resources and/or metabolic power as well as a switch between different metabolic processes responsible for energy acquisition and conversion. In the DEB model (Kooijman, 2010), the energy assimilated by an organism is incorporated in a common pool from which it is used for maintenance, activity, growth/development and reproduction (Fig. 1). A certain amount of assimilated energy is incorporated into the energy reserve in the form of lipids, carbohydrates, and/or proteins thus providing for the storage of surplus energy. Although deposition of energy reserves falls under the overall umbrella of growth, the distinction is important in the context of the metabolic responses to environmental stress, because energy reserves play an important role in the rapid provision for elevated energy demands during stress exposure. This involvement of energy reserves in metabolic stress responses may compete with other functions such as provision for high energy flux during reproduction (gametogenesis and spawning) or buffering of the fluctuations in food availability to ensure continuous supply of metabolic energy.

The maintenance costs encompass the energy demand for basal cellular and organismal maintenance to fuel key cellular processes (e.g. ion and acid–base regulation, protein turnover, anabolism) and essential systemic activities such as ventilation, circulation and excretion (Figs. 1 and 3). Somatic maintenance is the major component of the energy budget and unlike activity, growth and reproduction cannot be reduced below a certain limit. These maintenance costs can be measured as standard or basal metabolic