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Predator bioenergetics and the prey size spectrum: Do foraging costs determine fish production?

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HIGHLIGHTS

- Two hypotheses on how prey availability affects predator production are contrasted.
- Constant activity versus constant satiation form a continuum of foraging strategies.
- A model of fish production dependent on prey size spectrum is used to compare them.
- Satiation is the most likely if fish optimizes both production and life history.
- It suggests that variation in activity can be a major driver of predator–prey dynamics.

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ABSTRACT

Most models of fish growth and predation dynamics assume that food ingestion rate is the major component of the energy budget affected by prey availability, while active metabolism is invariant (here called constant activity hypothesis). However, increasing empirical evidence supports an opposing view: fish tend to adjust their foraging activity to maintain reasonably constant ingestion levels in the face of varying prey density and/or quality (the constant satiation hypothesis). In this paper, we use a simple but flexible model of fish bioenergetics to show that constant satiation is likely to occur in fish that optimize both net production rate and life history. The model includes swimming speed as an explicit measure of foraging activity leading to both energy gains (through prey ingestion) and losses (through active metabolism). The fish is assumed to be a particulate feeder that has to swim between consecutive individual prey captures, and that shifts its diet ontogenetically from smaller to larger prey. The prey community is represented by a negative power-law size spectrum. From these rules, we derive the net production of fish as a function of the size spectrum, and this in turn establishes a formal link between the optimal life history (i.e. maximum body size) and prey community structure. In most cases with realistic parameter values, optimization of life history ensures that: (i) a constantly satiated fish preying on a steep size spectrum will stop growing and invest all its surplus energy in reproduction before satiation becomes too costly; (ii) conversely, a fish preying on a shallow size spectrum will grow large enough for satiation to be present throughout most of its ontogeny. These results provide a mechanistic basis for previous empirical findings, and call for the inclusion of active metabolism as a major factor limiting growth potential and the numerical response of predators in theoretical studies of food webs.

1. Introduction

Predation is one of the most important factors structuring ecological communities (McCann, 2011). Knowing how predators limit, and are limited by prey is then crucial for predicting the dynamics of natural populations and the consequences of human disturbances, such as fisheries or species introductions, and their mitigation by conservation programs. Our current understanding of predator–prey interactions has been developed mostly from simple models, such as the Lotka–Volterra and the Rosenzweig–MacArthur consumer–resource models (Rosenzweig and MacArthur, 1963; Verhoef and Morin, 2010), which form the building blocks for more recent models of community and ecosystem dynamics that seek to include a realistic — yet simple — representation of individual physiology or bioenergetics (e.g., Yodzis and Innes, 1992; Persson et al., 1998; Brose et al., 2005; Weitz and Levin, 2006; Law et al., 2009; Hartvig et al., 2011; Giacomini et al., 2013). These models have benefited from the consistent allometric relationships between several bioenergetic rates

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and body size, that have emerged from empirical studies (Peters, 1983; Brown et al., 2004; Brose, 2010), and from the prevalence of body size as the main trait defining ecological interactions in food webs (Jennings et al., 2001; Woodward et al., 2005; Eklöf et al., 2013). However, scaling up from individuals to communities requires knowledge of how these basic bioenergetic processes respond to variation in prey availability. Among the most important of these processes are ingestion rate and active metabolism. Ingestion is expected to be limited by prey when encounter rates between predator and prey decrease with decreasing prey density (Gerritsen, 1984). This limitation can be counterbalanced by increasing foraging activity (Munk, 1995), but at the cost of increasing energy loss through active metabolism. Population and community models so far have put an enormous emphasis on the ingestion component (Holt et al., 1994; Hastings, 1997; Verhoef and Morin, 2010; McCann, 2011; Sibly et al., 2013), probably due to the influential concept of the functional response (Holling, 1959; Oaten and Murdoch, 1975; Abrams and Ginzburg, 2000), whilst activity is usually ignored or assumed constant (adaptive foraging models are notable exceptions, e.g. Abrams, 1984, 1991; Valdovinos et al., 2010; although they usually assume a different type of cost associated with foraging, such as increasing mortality from upper trophic levels).

In this paper, we will argue that there is a continuum of possible bioenergetic relationships that may govern the predator–prey dynamics of natural systems. At one end of this continuum stands the commonly assumed hypothesis that ingestion is driven by prey dynamics and that the activity costs associated with predation remain constant. We will refer to this as the **constant activity hypothesis** (Fig. 1a). At the other end of this continuum stands the hypothesis that it is activity costs that are driven by prey dynamics while ingestion remains constant. If ingestion is at the maximum physiological level, we can refer to this as the **constant satiation hypothesis** (Fig. 1b). These two hypotheses differ fundamentally in how the predator and prey populations affect each other. If satiation is the rule rather than the exception, we should expect a shift in emphasis within ecological models towards less variable prey capture rates and more variable trophic transfer efficiencies. The consequences of this shift are not yet obvious; for instance, the stability of predator–prey dynamics may either decrease with satiation, as it corresponds to a strongly saturated functional response (Oaten and Murdoch, 1975), or increase due to the intensified outflow of predator energy caused by increasing active metabolic rate (McCann, 2011), especially at low prey densities. The implications are potentially serious, depending on the magnitude of these changes, as many conclusions from traditional models of community or ecosystem dynamics may need to be reassessed if the constant activity hypothesis is not as general as usually assumed.

Empirically, the constant satiation hypothesis has received strong support from studies in aquatic ecosystems over the last two decades. Variation in active metabolism has been shown to be responsible for much of the variation in fish growth patterns in nature (Boisclair and Leggett, 1989a; Aubin-Horth et al., 1999; Rennie et al., 2005). Conversely, several estimates of functional response in the field lead to ingestion rates approaching maximum levels throughout the relevant variation in prey density (Mackenzie et al., 1990; Eby et al., 1995; Jeschke, 2007). It is not only prey density that defines growth potential — prey quality may be even more important. A widely recognized pattern is the increase in growth rate and efficiency caused by increases in prey size (Paloheimo and Dickie, 1966; Kerr and Ryder, 1977; Werner and Gilliam, 1984; Forseth et al., 1994; Saint-Jacques et al., 2000; Juncos et al., 2011), which may explain the ontogenetic diet shifts observed in many species (Mittelbach and Persson, 1998; Sherwood et al., 2002b). In several studied fish species, the bioenergetic modifications resulting from variation in prey size or density are predominantly driven by foraging activity: where prey is large and/or more abundant, predators tend to be less active (Trudel et al., 2001; Pazzia et al., 2002; Sherwood et al., 2002b; Iles and Rasmussen, 2005; Kaufman et al., 2006). On the other hand, ingestion rate seems to play a minor role, not varying as substantially as activity with changes in prey quality or availability (Boisclair and Leggett, 1989b, 1989c, 1989d; Trudel et al., 2000; Pazzia et al., 2002; Sherwood et al., 2002b; Henderson et al., 2004; Rennie et al., 2005).

Despite empirical evidence and the potential implications for our understanding of ecosystem dynamics, there is still no comprehensive theory providing a mechanistic support for constant satiation or showing that activity could be a limiting factor for predator populations. Here we propose such a theory for aquatic systems: we assess the benefits to fish of adopting a constant satiation strategy and we identify those situations where this strategy is likely to predominate. We analyze the case of a focal fish that optimizes both foraging activity and life history, preying upon a size spectrum that provides the opportunity to undertake ontogenetic diet shifts. This is representative of aquatic systems in general, whose trophic interactions are constrained by size relationships between predator and prey organisms (Jennings

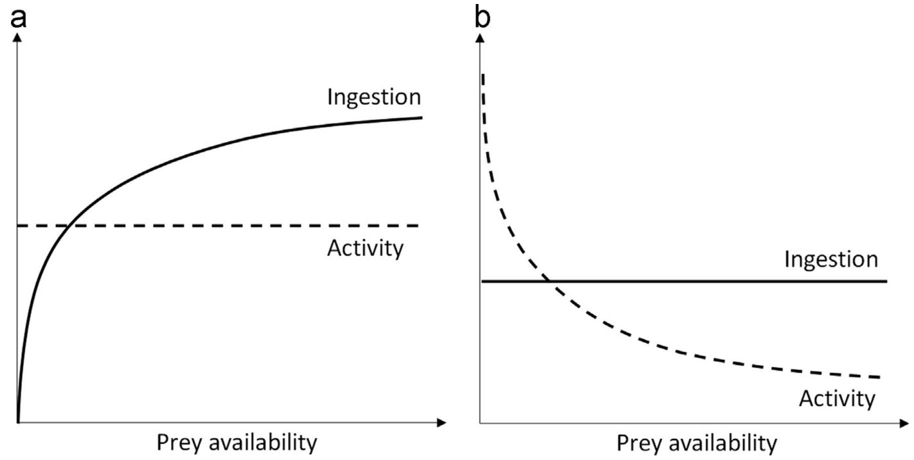

Fig. 1. Two alternative hypotheses on how ingestion and activity rates vary as a function of prey availability. (a) most commonly assumed in ecological studies, the constant activity hypothesis states that ingestion rate is the energy budget component varying with prey availability, generally through a predator's functional response (here represented by a type II); (b) in the constant satiation hypothesis, ingestion does not vary along the relevant range of prey availability (but it will if availability tends to zero), and activity is the major component responding to prey availability, usually through adjustments in foraging effort.