Experimental measurements of functional response: What is the relevance for food web theory?

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Introduction

The functional response describes how the rate of consumption changes in response to a change in the density of the resource. Since Holling’s (1959) seminal study, ecologists have measured and categorized the functional response for a large number of specific consumer-resource relationships (Jeschke et al. 2002). Functional response curves are ecologically important because they allow inferences about rates of resource depletion, predator preferences for certain prey types, and competitive hierarchies among consumers. Theoretical ecologists, however, have a more general interest in the functional response. They use functional responses as crucial link functions between consumers and their resources in generic multi-species food web models that predict community dynamics over multiple generations. Such models are particularly appropriate for planktonic communities, characterized by short generation times, and make predictions about the stability, biomass distributions, and the importance of indirect effects in these aquatic food webs. The dynamics of such model food webs, however, are extremely sensitive to the type and mathematical formulation of the functional response (Williams & Martinez 2004, Fussmann & Blasius 2005). The cumulative evidence gathered from field observations and experiments can help ecologists choose functional response models representative of natural communities.

I investigated whether the functional response is predator- or prey-dependent (or, more generally, consumer- or resource-dependent) and how this question is best approached in experiments with aquatic microorganisms. Prey-dependence is the traditional assumption in food web models, under which the per-capita resource uptake (g) by the consumer is only a function of the resource concentration (x): \( g = f(x) \). Over the past 2 decades this view has been challenged under the banner of the predator-dependence hypothesis, which claims that per-capita food uptake should depend on both consumer concentration (y) and prey concentration: \( g = f(x, y) \). Ratio-dependence is a special form of predator-dependence; the functional response is a function of the ratio of resource and consumer concentrations: \( g = f(x/y) \). This problem is essentially unresolved, and the arguments that proponents of either view have put forward to strengthen their cases are not discussed here (see Abrams & Ginzburg 2000). However, all debaters agree on 2 points: (1) The question is of great importance for food web theory because models predict dramatically different dynamics depending on whether predator- or prey-dependent functional responses are chosen. (2) Targeted experimentation with real communities can bring us closer to a solution to this debate that has been characterized by an exchange of largely theoretical viewpoints.

In recent years, aquatic and terrestrial ecologists have conducted experiments explicitly designed to distinguish between consumer- and resource-dependence (Skalski & Gilliam 2001, Fussmann et al. 2005, Schenk et al. 2005, Tschanz et al. 2007). Although this trend is generally welcomed, some experiments have also met with criticism (Jensen et al. 2007). It appears that a current point of debate is how such experiments ought to be designed and conducted so they provide discriminatory power and are not biased to back either hypothesis by design (Fussmann et al. 2007, Jensen et al. 2007).

Key words: numerical response, predator-dependence

Methods

I modeled the Rosenzweig-MacArthur consumer (C)-resource (R) system by finite difference approximation (Fig. 1a): \( R_{t+\Delta t} = R_t + \Delta t \times ( r \times R_t (1 - R_t / K) - a \times R_t \times C_t / (1 + b \times R_t + \gamma \times C_t) ) \); \( C_{t+\Delta t} = C_t + \Delta t \times ( a \times R_t \times C_t / (1 + b \times R_t + \gamma \times C_t) - m \times C_t ) \) and parameterized: \( r = 3; K = 1; a = b = 5; \gamma = 0; m = 0.3; \Delta t = 0.01 \) (= continuous time). I then discretized consumer growth with \( \Delta t = 2.0 \). I computed the consumer’s numerical response based on the average of resource concentrations incurred over this time span (i.e., the sum of all consumption contributes to the reproduction at the end of each inter-reproductive consumption interval; Fig. 1b), and compared functional and numerical response by sampling the time series (Fig. 1c). I fitted a Beddington-DeAngelis response (\( \gamma \neq 0 \)) to the numerical response and re-ran the model in continuous time (Fig. 1d).
Which experimental design for which purpose?

Multiple levels of consumer concentrations

An obvious and essential requirement for detecting consumer- versus resource-dependence is that experiments be performed at several consumer densities. Recent studies used 4–5 levels of consumer densities (REEVE 1997, HANSSON et al. 2001, FUSSMANN et al. 2005, SCHENK et al. 2005), but the vast majority of studies reporting functional responses were not designed to test for consumer-dependence and report responses only for a single consumer density. This means that the data base supplied by the existing literature is rather slim and emphasizes the need for new empirical studies.

Allowing for mechanisms

Many biological mechanisms can lead to consumer dependence (Table 1; ARDITI & GINZBURG 1989, ABRAMS & GINZBURG 2000). Not all of them will be relevant for any given organismal system. Hunting in social groups and aggressive or territorial behavior, for instance, will be unusual behavior for plankton communities. For any mechanism to be detected in an experimental setting, the organisms must be able to perform the biological process producing consumer-dependence under as natural conditions as possible. This is typically easier to accomplish for plankton communities, which live in a relatively homogeneous environment, than for other aquatic or terrestrial consumer-resource systems. Nonetheless, some mechanisms that are potentially important in plankton communities can be challenging to test (e.g., vertical migration of the prey, which is induced by a density-dependent stimulus released by the predator; GLIWICZ 1986).

The best experimental design is not necessarily the one that allows for all mechanisms to be operating in a single experimental trial. If consumer-dependence is detected, it will be difficult to identify the responsible biological mechanism(s). An all-encompassing design will also compromise the probability of observing any particular mechanism; for instance, using large volumes to allow for vertical migration might make it impossible to produce the high densities of predators necessary to detect the threshold for physical interference. It is therefore preferable to perform multiple trials allowing for different likely mechanism or, if that is impossible, to restrict the interpretation of results to mechanisms detectable under the current design.
How long should experiments last when they are concerned with detecting effects of consumer-dependence? Currently, this is probably the most contentious issue with regard to proper experimental design (Fussmann et al. 2007, Jensen et al. 2007). The root of the problem is that many of the processes potentially producing consumer-dependence operate on longer time scales than the process of resource uptake (Table 1). A planktonic filter feeder will have consumed a lot of its resource before a transgenerational-induced morphological change in the resource becomes effective; therefore, experiments targeted at detecting any of the “slow” mechanisms (Table 1) must be performed at the long time scale needed for these mechanism to take effect.

Long-term measurements of functional response entail depletion of resources over the duration of the experiment. In many experimental settings it is impractical to replace the consumed resources. In my opinion, resource depletion during the experiment is an undesirable complication that leads to inaccurate measurements of the functional response. Long-term experiments with substantial resource depletion will also produce biased results because, at higher consumer concentrations, resources are depleted more quickly, and consumers spend on average more time at low resources, which reduces their per-capita consumption (Fussmann et al. 2007). Because such long-term experiments will always produce consumer-dependence, I recommend avoiding depletion and running experiments over the shortest time interval that will allow the experimenter to detect the targeted mechanism of consumer-dependence.

This approach attempts to measure the functional response on the short time span during which it operates in standard food web models based on ordinary differential equations. A group of theoretical ecologists have labeled this approach the “fallacy of instantism” (Ginzburg & Colyvan 2004, Jensen & Ginzburg 2005) and criticize it because it favors a resource-dependent view of community dynamics. They argue that biological processes are never truly instantaneous, and that the longer time scale of the consumer’s reproductive cycle (the scale of the numerical response) should have priority in a dynamic community context. In particular, mathematical food web models and experiments should both integrate over this longer time interval and explicitly allow for the resource depletion. Because resource depletion is more severe at high consumer densities, consumer-dependence may occur under this scenario. A model simulation (Fig. 1) shows that the functional response (Fig. 1c) obtained from a discrete-time approach (Fig. 1b) may indeed be slightly reduced compared to the instantaneous approach (Fig. 1a) due to consumer-dependence. However, introducing a consumer-dependent functional response into the continuous-time system (Fig. 1d) does not explain the dynamics of the discretized system. It appears that the dynamic consequences of the discretization are

Table 1. Biological mechanisms that potentially produce predator-dependence in ecological communities.

<table>
<thead>
<tr>
<th>Mechanism</th>
<th>fast/slow*</th>
<th>Description‡</th>
<th>Plankton example</th>
</tr>
</thead>
<tbody>
<tr>
<td>Physical interference</td>
<td>fast</td>
<td>Physical contact</td>
<td>(Hansson et al. 2001)</td>
</tr>
<tr>
<td>Sensory interference</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>visual</td>
<td>fast</td>
<td>Sight of other predators</td>
<td>–</td>
</tr>
<tr>
<td>acoustic</td>
<td>fast</td>
<td>Noise/voice of other predators</td>
<td>–</td>
</tr>
<tr>
<td>olfactory</td>
<td>fast to slow</td>
<td>Smell indicating predator crowding</td>
<td>(Lürling et al. 2003)</td>
</tr>
<tr>
<td>Induced, plastic responses of the prey</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>morphological / life history</td>
<td>slow</td>
<td>Anti-predator traits induced by predator-released chemicals</td>
<td>(Lass &amp; Spaak 2003)</td>
</tr>
<tr>
<td>behavioral</td>
<td>fast to slow</td>
<td>Predator avoidance induced by predator</td>
<td>(Bollens et al. 1994)</td>
</tr>
<tr>
<td>Group effects</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>heterogeneous distributions</td>
<td>fast to slow</td>
<td>Patchy predator or prey occurrence (e.g. swarming)</td>
<td>(Amblar 2002)</td>
</tr>
<tr>
<td>social effects</td>
<td>fast to slow</td>
<td>Group hunting; social interaction, aggression</td>
<td>–</td>
</tr>
<tr>
<td>Resource depletion</td>
<td>slow</td>
<td>Prey becomes scarce before predator reproduces</td>
<td>(Kreutzer &amp; Lampert 1999)</td>
</tr>
</tbody>
</table>

* Time scale on which the mechanism typically operates, i.e. on the scale of a single predation event (fast) or on longer time scales (slow).
‡ Process generating reduced per capita prey uptake with increasing predator density (except for “group hunting” which has a positive effect on predation).
much more severe than the effects of consumer-dependence. Allowing for mechanisms different than consumer-dependence in continuous time (e.g., time delays) would probably be a more suitable method to account for the disparate time-scales of resource uptake and consumer reproduction.

Conclusions

Experiments measuring the functional response should be designed to allow for the specific mechanisms producing consumer-dependence. The right duration of experiments is a contentious issue. Short-term experiments may miss slow mechanisms that can lead to consumer-dependence. Long-term experiments have to deal with the problem of resource depletion. Introducing consumer-dependent functional responses into continuous-time food web models is probably not the best way to reconcile the different time scales of functional and numerical responses.

References


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