Comparing energetic and dynamic descriptions of a single food web linkage

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Food webs are a unifying concept that spans population, community, and ecosystem ecology. Yet there is a fundamental dissonance between dynamic food webs, which derive from community ecology and characterize the effect of one species upon another, and energetic-based food webs, which have their roots in ecosystem ecology and characterize the flow of energy and matter among species and trophic levels. Here, we present a framework that explicitly defines food web linkage strength in terms of two key factors: the type of data (energetic vs dynamic), and the trophic perspective (whether the interaction is viewed from the perspective of the consumer or the resource). As a case study, we applied this framework to the well-studied trophic interaction between rainbow smelt *Osmerus mordax* and cisco *Coregonus artedii* in Sparkling Lake, Wisconsin, USA. Energetic and dynamic metrics gave different descriptions of the linkage strength from the perspective of either species. This was particularly true from the cisco perspective: the dynamic metric indicated a strong linkage because smelt extirpated cisco, but the energetic metric indicated a weak linkage because smelt prey on cisco larvae and the flux from cisco to smelt was therefore a small fraction of cisco production. Our approach highlights the need for more careful consideration of how food web linkages and their importance are characterized. Furthermore, it can provide the basis for translating energetic data to an understanding of food web dynamics.

Two distinct approaches for characterizing trophic linkages have dominated food web research since the inception of the field (Paine 1980, Winemiller and Polis 1996). The "energetic" approach is rooted in ecosystem ecology, and describes links as fluxes of matter or energy (Teal 1962). The "dynamic" approach, in contrast, is rooted in community ecology and describes links based on their effects on population growth rates, equilibrium abundances, or similar population-dynamic quantities (Paine 1992). Understanding the dynamic implications of food web linkages is essential for predicting the response of species to harvest, extinctions, invasions, and other environmental perturbations. Yet most empirical descriptions of trophic interactions are based on energetic data. For example, 84% of 107 published marine food webs in a recent survey were energetic webs (Link et al. 2005). Similarly, studies of food web connectance properties are increasingly relying on energetic data as a way to weight the importance of links (Banasek-Richter et al. 2009). Integration of energetic and dynamic perspectives is thus a key frontier for improving our understanding of food webs (de Ruiter et al. 2005).

Unfortunately, the relationship between energetic and dynamic descriptions of food web linkages is poorly understood. Several authors have noted, in the words of G. A. Polis (Polis 1994) that there "is no necessary concordance of dynamics with either dietary or energetic data"; for instance,

the trophic links that are most important for community dynamics may not be the same as those that dominate energetic fluxes through the ecosystem (Raffaelli and Hall 1996). Yet few studies have explicitly compared energetic and dynamic descriptions of the same interaction (Paine 1980, Hall et al. 1990, Raffaelli and Hall 1996). This lack of data, and an associated lack of a clear conceptual framework for making such a comparison, makes it difficult to derive a general understanding of the relationship between energetic and dynamic food webs.

One of the key challenges for comparing energetic and dynamic descriptions of interactions is a difference in perspective rooted in different methodologies (Fig. 1). Energetic webs are constructed from diet data, or from proxies such as isotopic tracers or observations of feeding rates (Polis et al. 2004). Such data describe the flux from the resource to the consumer, and provide a simple estimate of energetic linkage strength from the consumer's perspective. For instance, a resource that comprises a large proportion of a consumer's diet is energetically important to the consumer. It is also possible to describe the energetic linkage strength from the resource's perspective by relating the trophic flux to the production or abundance of the resource, but such estimates are rare due to the difficulty of estimating production. Conversely, empirical estimates of dynamic linkage strengths are almost always from the resource's perspective
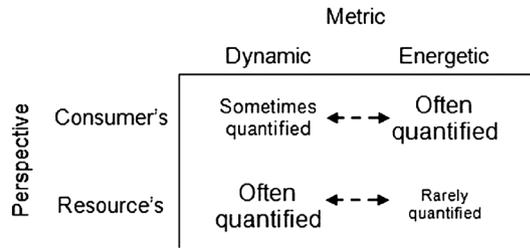
Figure 1. Comparisons (dashed arrows) between energetic and dynamic metrics of food web interactions are difficult because empirical estimates usually describe interactions either in energetic terms from the consumer's perspective or in dynamic terms from the resource's perspective. Quantifying both metrics from each perspective allows better understanding of the relationship between food web energetics and dynamics.

rather than from the consumer's. The field experiments often used to derive such estimates typically manipulate the presence or abundance of a consumer and measure the effect on the population dynamics of the resource; it is more difficult and less common to manipulate the resource and so estimate the dynamic linkage strength from the consumer's perspective. Thus most empirical studies of food web linkages are either energetic descriptions measured from the consumer's perspective or dynamic descriptions measured from the resource's perspective (Fig. 1).

In this paper, we illustrate these ideas using a case study of a single well-studied consumer-resource interaction between two freshwater fishes. We compare energetic and dynamic estimates of the strength of this interaction from the perspective of the consumer and from the perspective of the resource. Our results highlight one set of conditions in which energetic and dynamic data are likely to provide different descriptions of the strength of trophic interactions. More importantly, they provide a framework that could be applied to other trophic interactions and suggest one avenue for productive synthesis about the relationship between energetic and dynamic descriptions of food web linkages.

Case study

We used field data and a simulation model to quantify energetic and dynamic linkage strengths from both consumer and resource perspectives for the interaction between rainbow smelt *Osmerus mordax* and cisco *Coregonus artedii* in Sparkling Lake, Wisconsin (46°0'N, 89°41'W). Smelt are native to the Atlantic coast of North America, but introductions have extended their range to include many lakes in the interior of the continent. Smelt are primarily zooplanktivorous but also consume larval and juvenile fish. Their introduction often causes drastic declines in the abundance of native fishes (Evans and Loftus 1987, Mercado-Silva et al. 2006).

After smelt invaded Sparkling Lake around 1981, annual monitoring documented a rapid increase in their abundance and a rapid decline in the abundance of native zooplanktivorous cisco (Fig. 2A; McLain and Magnuson 1988). Detailed studies demonstrated that thermal conditions force adult smelt and larval cisco to co-occupy a narrow band of lake habitat for a brief period during the summer, and implicated predation by smelt on larval cisco as the cause of the cisco decline and eventual
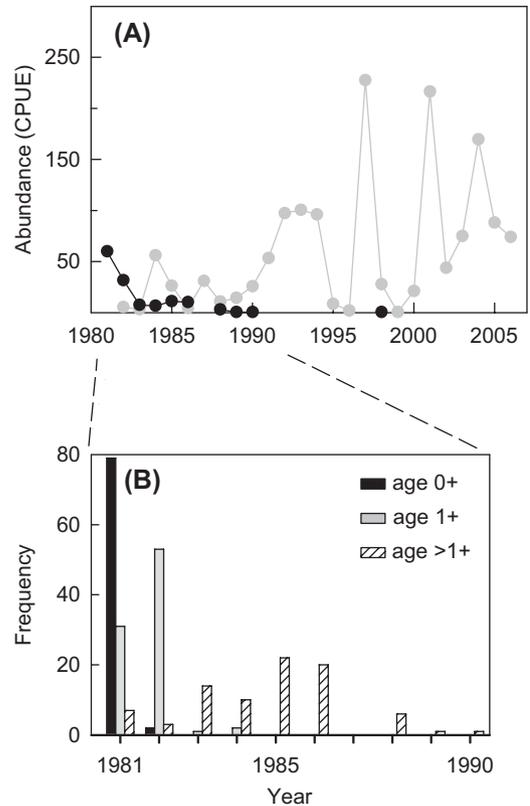

Figure 2. Rainbow smelt invasion caused a rapid decline in the cisco population in Sparkling Lake because smelt preyed on larval (age 0+) cisco. Smelt were first detected in the lake in 1982. (A) Abundance (catch per unit effort) of smelt (grey) and cisco (black) in annual August surveys using vertical gill nets (mesh sizes 19 to 89 mm). (B) Age frequency of cisco in gill net catches from 1981–1990 (data from Hrabik et al. 1998).

extirpation (Hrabik et al. 1998). While spring sampling continued to detect cisco larvae until at least 1988, no larvae survived to be detected in August sampling in any year after 1982 (Fig. 2B; McLain 1991, Hrabik et al. 1998).

These results demonstrated that the linkage strength from the cisco perspective measured in terms of dynamics ($LS_{cs, D}$) was very strong: it extirpated cisco from the lake within about a generation of smelt establishment. However, field data collected at the time were not sufficient to estimate $LS_{cs, E}$, $LS_{sc, D}$, or $LS_{sc, E}$ (where s and c denote smelt and cisco, and E and D denote energetic and dynamic metrics of linkage strength; Fig. 1). In order to compare energetic and dynamics measures of linkage strength from the cisco perspective and also from the smelt perspective, we used a model of the Sparkling Lake food web that integrates our knowledge about this well-studied lake. Below we give an overview of the essential features of this model, which is described in full elsewhere (Roth et al. 2010); we then describe our linkage strength metrics.

Simulation model

We modeled the biomass dynamics (kg ha^{-1}) of smelt and cisco at a weekly time step for 30 years using a delay-difference model coupled to bioenergetic models of growth

and consumption (Kitchell et al. 1977, Hanson et al. 1997, Quinn and Deriso 1999). The model tracked young-of-year (YOY, age class 0+), yearling (age 1+), and adult (age 2+ through 5+) stages of smelt and cisco (Carlander 1969). Walleye *Sander vitreum*, a predator of smelt and cisco, are also included in the simulation model; a number of research and management questions focus on interactions among these three species (Roth et al. 2010), but the specifics of the interactions with walleye are unimportant for understanding the smelt-cisco interaction and we do not describe this aspect of the model in detail here. Three parameters for which empirical constraints were lacking (describing walleye harvest mortality and smelt cannibalism) were calibrated so that model output qualitatively matched observed fish abundance trends in Sparkling Lake. All other parameter values were derived from empirical Sparkling Lake data or from the literature. Sensitivity analyses demonstrated that cisco collapsed and smelt persisted as long as adult smelt consumed YOY cisco and YOY smelt competed with YOY walleye, and that varying parameter values by ± 10% had little qualitative effect on model outcomes (Roth et al. 2010).

A small population of age 1+ smelt was introduced to the system in year 1. Both smelt and cisco consume zooplankton in the model, though they do not compete because of different prey size selectivity (Hrabik et al. 1998, Beisner et al. 2003). Adult smelt may additionally consume YOY cisco or their own YOY. Specifically, YOY cisco comprise up to 18% of smelt diets during an eight-week period when they occupy the same thermal habitat as adult smelt and are small enough to be consumed by them, and YOY smelt are consumed in proportion to their biomass when temperatures are below 10°C (Selgeby et al. 1978, 1994, Hrabik et al. 1998, Parker-Stetter et al. 2007).

Reproduction and density-independent mortality occurred at the end of each model year. We modeled reproductive output (biomass of new YOY) as a constant proportion (smelt: 0.10; cisco: 0.115) of the biomass of individuals age 2+ or older for smelt or age 1+ or older for cisco (Carlander 1969, Rudstam 1984, Rose et al. 1999, Lantry and Stewart 2000, McDermot and Rose 2000). Similarly, density-independent mortality occurred as an instantaneous loss of a proportion of the biomass in each stage; this proportion was set at 1 for individuals in the oldest age class, and derived from literature for other age classes (Rudstam 1984, Lantry and Stewart 1993, McDermot and Rose 2000).

Within years, the weekly biomass of each stage was modeled as:

$$B_{t+1} = B_t - M_t + B_t \times G_t \qquad (1)$$

where B_{t+1} is the biomass of the stage at time $t+1$, M is mortality of the stage due to predation, and G is the growth of the stage. The growth term in Eq. 1 is given by a modified bioenergetics model (Kitchell et al. 1977, Hanson et al. 1997). Growth is summed across all the ages i to k in the stage, and modified by a density dependent term d that allows growth to resemble empirical estimates when densities are low, but forces growth towards zero as the density of the stage approaches an estimated carrying capacity (Carlander 1969). The bioenergetic approach allows us to identify the contribution of each prey species to the growth of the predator.

Thus the production of smelt that is attributable to consumption of cisco is directly extractable from the model, as is the amount of cisco production lost to smelt predation.

Calculating linkage strengths

We calculated energetic LS for each species by relating the trophic flux between the species to the production of the focal species. Specifically, we measured energetic linkage strength as:

$$LS_E = P_I / P_T \qquad (2)$$

where P_I is the production that the focal species derived from (or lost to) the other species, and P_T is the total production of the focal species. LS_E therefore ranges between 0 and 1, and, because both P_I and P_T have units of kg ha^{-1} y^{-1}, LS_E is unitless. From the smelt perspective, LS_E is the proportion of annual smelt production that is attributable to consumption of cisco. From the cisco perspective, LS_E is the proportion of annual cisco production that is lost to smelt.

To calculate dynamic linkage strength, we used the model to conduct an exclusion experiment. Field estimates of dynamic linkage strength often compare the abundance of a focal species between control plots and plots where a particular predation interaction has been selectively prevented. In the same manner, we ran a model scenario in which we disallowed smelt predation on cisco (i.e. set C_a for smelt on cisco to 0), and compared smelt and cisco abundances in this scenario to their abundances in the nominal scenario. Specifically, we calculated dynamic LS for each species as:

$$LS_D = \frac{(N_{i,t\,j>0} - N_{i,t\,j=0}) / (N_{i,0} \times N_{j,0})}{x / (N_{i,0} \times N_{j,0})} \qquad (3)$$

The numerator of Eq. 3 is Paine's index (Paine 1992, Berlow et al. 1999), where $N_{i,t\,j>0}$ is the abundance of the focal species at time t when the interacting species j is present, $N_{i,t\,j=0}$ is the abundance of the focal species at time t when the interaction is experimentally prevented, and $N_{i,0}$ and $N_{j,0}$ are the initial densities of species i and j. The denominator of Eq. 3 gives the most extreme value that Paine's index could take given the initial abundances of species i and j. When i is the prey species, the most extreme value occurs when $N_{i,t\,j>0} = 0$ (that is, when the prey cannot persist until time t in the presence of the predator), and we set $x = -N_{i,0\,j=0}$. When i is the predator species, the most extreme value occurs when $N_{i,t\,j=0} = 0$ (that is, when the predator cannot persist until time t without the prey present), and we set $x = N_{i,0\,j>0}$. This rescaling forces LS_D to be between 0 and 1, facilitating comparison with our energetic metric.

Results

Results from the simulation model support the hypothesis that smelt predation on larval cisco rapidly extirpated cisco from the lake. Smelt abundance (kg ha^{-1}) increased rapidly after establishment in year 1, and then exhibited high-magnitude cycles as a result of cannibalism (Fig. 3A). Declines in cisco abundance began soon after smelt establishment, and
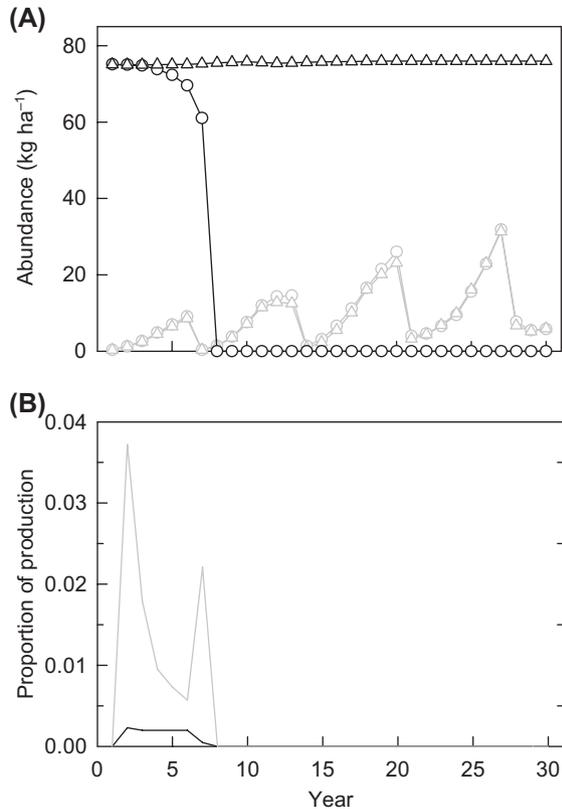
(A)

(B)

Figure 3. Simulation model results show the effect on population dynamics, and the energetic importance, of the interaction between smelt (grey lines) and cisco (black lines). (A) Year-end abundance (kg ha^{-1}) of smelt and cisco following establishment of smelt in year 1. Circles: nominal scenario, in which larval cisco comprise up to 18% of smelt diet during a brief period in early summer. Triangles: scenario in which smelt do not consume cisco. (B) Energetic importance to each species in the nominal scenario. Grey line: proportion of annual smelt production derived from consuming cisco. Black line: proportion of annual cisco production lost to predation by smelt.

were appreciable by the time smelt abundance exceeded 3 kg ha^{-1} in year 4. In the nominal scenario, in which cisco larvae constituted up to 18% of smelt diets during the brief predation window, no larval cisco survived their first summer in years 2–6 nor in any year after year 8. Consequently, cisco abundance declined precipitously to zero in year 9, as the remaining adult cisco senesced or were consumed by predators. Similar patterns in smelt and cisco abundance (as catch per unit effort, not kg ha^{-1}) were observed in the empirical Sparkling Lake data (Fig. 2A).

Disallowing smelt predation on larval cisco produced very similar smelt dynamics, but very different cisco dynamics (Fig. 3A). As in the nominal scenario, smelt abundance in this no-predation scenario increased rapidly after establishment, then exhibited high-magnitude cycles. The small effect of cisco on smelt dynamics was apparent in slight differences (positive and negative) in smelt abundance in a given year between the two scenarios (Fig. 3A). In contrast, disallowing smelt predation on cisco drastically altered cisco dynamics; instead of crashing within the first nine years, the cisco population in the no-predation scenario remained nearly constant for the entire 30-year period.
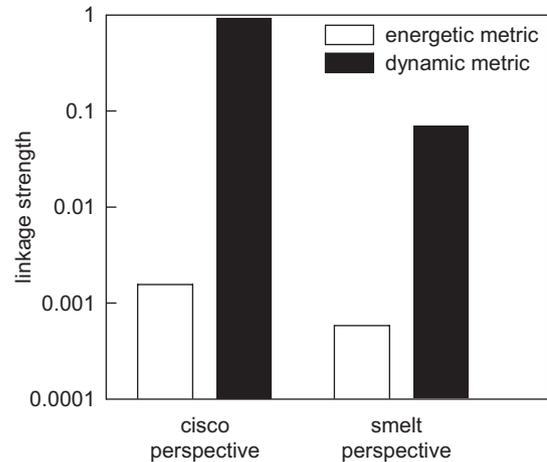

Figure 4. Comparison of energetic and dynamic metrics of linkage strength from the smelt (consumer) and cisco (resource) perspective. Note log scale on y-axis.

The energetic flux between cisco and smelt was small from the perspective of either species (Fig. 3B). Only larval cisco are vulnerable to smelt predation, but most of cisco production is due to growth of adults. Consequently, the proportion of annual cisco production that was lost to smelt never exceeded 0.0023. The proportion of smelt production that was derived from consuming cisco was considerably higher but still quite small, never exceeding 0.0372 in any year.

The energetic metric indicated weaker interactions than the dynamic metric, particularly from the cisco perspective (Fig. 4). We chose to present linkage strength estimates based on the first nine years of the time series. This time span provides the most meaningful estimates of LS_E; for instance, estimates of $LS_{sc, E}$ calculated after year 9 misrepresent the energetic importance of cisco to smelt because they include in the denominator of Eq. 2 smelt production that could not possibly be fueled by consumption of cisco. Furthermore, the entire dynamic effect of the interaction is apparent by year 9, such that there is little change in estimates of LS_D after this point. From the smelt perspective the interaction was quite weak in terms of energetics; the proportion of total smelt production that derived from consuming cisco (i.e. $LS_{sc, E}$) was only 0.00058. This effect was larger when measured in terms of dynamics, but still relatively weak ($LS_{sc, D} = 0.07$), in keeping with the minor impact of cisco on smelt dynamics (Fig. 3A). In contrast, energetic and dynamic metrics gave qualitatively different impressions of the interaction from the cisco perspective (Fig. 4). For cisco, an interaction that could not have been any stronger in terms of dynamics ($LS_{cs, D} = 1$) appeared to be three orders of magnitude weaker in terms of energetics ($LS_{cs, E} = 0.0016$).

Discussion

The dynamics of populations are intrinsically linked to their energetics; organisms cannot grow or reproduce without taking in energy, and losses to predation are losses of accumulated energy as well as of individuals. Nonetheless, many authors have observed that energetic fluxes need not and do not necessarily translate to an understanding or prediction of

a species' dynamics (Paine 1980, Polis 1994). In a marine intertidal food web, for instance, the flux to a fish from its amphipod prey was large relative to the fluxes from its other prey, and relative to other fluxes in the food web. Yet experimentally preventing consumption of the amphipod by the fish did not significantly increase amphipod density (Raffaelli and Hall 1996). This example and others like it compare an energetic measure from the consumer's perspective to a dynamic measure from the resource's perspective. Such comparisons emphasize the distinctions between the largely bottom–up food web paradigm of ecosystem ecology and the largely top–down food web paradigm of community ecology, and demonstrate the importance of explicitly defining concepts of linkage strength.

In this paper we have compared energetic and dynamic descriptions of a single interaction while holding the trophic perspective (consumer's or resource's) constant (Fig. 1). This approach aims to isolate the difference between energetic and dynamic metrics from the difference between bottom–up and top–down paradigms. It may therefore provide a useful step towards a more synthetic understanding of the relationship between energetic and dynamic descriptions of trophic linkages, and ultimately food web interactions. For example, size-structured predation interactions played a role in the mismatch between energetic and dynamic linkage strength from the cisco perspective in our case study; smelt prey voraciously upon only very small juvenile cisco, so that from the perspective of the cisco population the magnitude of the energy flux to smelt is much smaller than the effect of the interaction on population dynamics. This result suggests the hypothesis that similar mismatches might be common in other size-structured trophic interactions. Regardless of whether this simplistic hypothesis is correct, a framework that allows meaningful consideration of these sorts of questions could provide a springboard for improving our understanding of energetic-dynamic relationships, and perhaps even for developing some ability to translate from widely-available energetic data to much-needed dynamic predictions.

At least two important challenges will face efforts to test these sorts of hypotheses. First, multiple research approaches will be required in order to generate energetic and dynamic measures of the strength of a single interaction. For instance, in this study we synthesized long-term data on population abundance, short-term data on diets, and the results of a natural experiment, using a simulation model that allowed us to calculate linkage strength estimates that we could validate against field patterns. The limited number of previous studies that have brought together energetic and dynamic food web perspectives have similarly employed a suite of observational, experimental, and modeling approaches (de Ruiter et al. 1995, Raffaelli and Hall 1996). The need for multiple field and modeling approaches is driven by the diverse types of data necessary for estimating LS_E and LS_D, and by the limited feasibility of some potentially informative field experiments (e.g. predator and prey exclusions). Second, our quantitative estimates of linkage strength should be viewed with caution. A different choice of LS_D from among the many available (Berlow et al. 2004), or a different calibration of the simulation model, might change our quantitative estimates to some degree. Future work to develop better quantitative frameworks for comparing

energetic and dynamic descriptions of linkage strengths would greatly improve our ability to understand the kinds of data that we have presented here.

For many years, energetics and dynamics were the separate domains of two distinct approaches for the study of food webs, and were motivated by largely separate research questions (Paine 1980, Winemiller and Polis 1996). Yet researchers are increasingly gleaning new insights by blurring the lines between these paradigms (de Ruiter et al. 1995, Teng and McCann 2004, Williams et al. 2004). We hope that in this study we have suggested a productive avenue for further synthesis, by explicitly defining a framework for comparing energetic and dynamic metrics of trophic linkage strengths.

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