

The Influence of Harvesting Pressure on Evolving Food Webs

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Goal

To examine how harvesting pressure influences the evolution of food webs structured by body size.

Background and motivation

Harvesting pressure in fisheries causes drastic ecosystem changes, such as the simplification of trophic structure in food webs (Pauly et al., 1998). While harvesting clearly has ecosystem effects, most fisheries models tend to be single-species models which ignore food web interactions such as predation, competition or indirect effects (Clark, 1990; Hilborn and Walters, 1992). Recently, the importance of understanding harvesting within the context of food web interactions is being recognized (Yodzis, 2001) and incorporated into management models (e.g. EcoSim; Walters et al., 2000). However, the implications of harvesting are not limited to trophic effects, but, when considered over time, can also cause population traits to change and evolve adaptively. Studies have found that harvesting can cause adaptive changes on both short and long time scales. On shorter time scales, changes can occur in species behavior, such as prey preference, foraging time and anti-predator behaviors (e.g. Abrams and Vos, 2003; Matsuda and Abrams, 2004). On longer time scales, changes can occur in life-history traits, such as earlier maturation ages and smaller adult body sizes (Heino, 1998; Heino and Godø, 2002; Gårdmark et al., 2003; Ernande et al., 2004). Yet, while it is known that food web interactions and adaptive responses must be taken into account when considering harvesting pressure (Clark, 1990; Hilborn and Walters, 1992), there have been few studies which take a comprehensive approach incorporating the effects of all three (but see Ernande et al., 2004; Matsuda and Abrams, 2004). Determining how harvesting pressure, multi-trophic interactions and adaptive dynamics interact will thus help in understanding the effects of harvesting pressure on food webs.

For instance, if only food web interactions are considered, increasing harvesting may cause the target species to go extinct (Yodzis, 2001; Matsuda and Abrams, 2005). By contrast, with the inclusion of adaptive dynamics, the target species may not necessarily go extinct; instead, its population traits may change and evolve in response to the fishing pressure. With adaptive dynamics on short time scales, increased harvesting can cause the target species to change its behavior to avoid harvesting or even cause the target species' predator to switch diet (Matsuda and Abrams, 2004). With adaptive dynamics on long time scales, increased harvesting can cause changes in the target species' reaction norms or cause the target species to mature earlier and, consequently, to have smaller adult body sizes (Heino, 1998; Ernande et al., 2004). Hence, the inclusion of adaptive dynamics in food web interactions is critical to understanding the effects of harvesting pressure.

For my proposed project, I intend to study how food webs with adaptive dynamics respond to harvesting pressure. However, as mentioned, adaptive dynamics can occur on short and long time scales. While short and long time scales are equally important, I will focus, for the sake of tractability, only on the inclusion of adaptive dynamics in

the context of long-term evolutionary changes.

Research questions

The main goal of this project is to examine how harvesting pressure influences the evolution of food webs structured by body size. Empirical studies have shown that body size plays an important role in the dynamics and structuring of food webs (e.g. Cohen et al., 1993). Indeed, body size will determine the strength of species interactions through the ratio of predator-prey body sizes or simply through the energetic transfers within the food web. Hence, studying the evolution of body size will help explain how fundamental food web properties can change and respond to disturbances such as harvesting pressure.

In addition, I will investigate how different types of harvesting strategies influence the evolution of food webs. Harvesting typically does not occur at a constant rate, but rather will include some degree of feedback control (Hilborn and Walters, 1992). This can be represented as fixed-quota or fixed-stock strategies. Also, harvesting is not always restricted to a single target species, but can include multiple species at the same or differing trophic levels (Matsuda and Abrams, 2005). Thus, I will study the influence of varying harvesting strategies and of varying the number and type of target species.

Methods and work plan

I intend to study the influence of harvesting pressure on food webs that are assembled based on simple evolutionary and ecological rules, such as foraging optimization (Kondoh, 2003) or trait similarity (Quince et al., 2005). In particular, the food web models I plan on examining use rules based on body size (e.g. Fukami, 2004), adapted from Loeuille and Loreau (2005), with the addition of adaptive dynamics (e.g. Abrams et al., 1993; Dieckmann and Law, 1996).

The basic methodology is to first create food webs that satisfy the following three stability conditions:

1. Demographically stable: Population densities of the species have reached equilibrium.
2. Convergence stable: Absence of directional selection.
3. Locally evolutionary stable: Absence of disruptive selection.

Food webs are evolved from an initial set of “founding” species which are distributed in trait space, in this case body size. The initial species are then allowed to interact according to their population and adaptive dynamics, from which a community that is demographically, convergence and evolutionarily stable should emerge. On this basis, I will examine the influence of harvesting pressure on the resulting food webs. In the first stage, I will examine harvesting pressure on food webs without adaptive responses to harvesting, while in the second stage I will examine webs with adaptive responses to harvesting.

a. Demographic dynamics

The basic population dynamics can be described using a simple equation with linear functional responses,

$$\frac{dN_i}{dt} = N_i \left(\sum_{j=1}^n e_{ij} \gamma_{ij} N_j - m_i - \sum_{j=1}^n \alpha_{ij} N_j - \sum_{j=1}^n \gamma_{ji} N_j \right), \quad (1)$$

where e_{ij} is the conversion efficiency of N_i on N_j ; m_i is the intrinsic mortality rate of N_i ; γ_{ij} and α_{ij} are functions which, respectively, represent the consumption rate and interference competition of species N_i on N_j .

The function describing the consumption rate is based on empirical studies that observed that consumers have the highest consumption rates on prey that satisfy an ideal predator-prey body size ratio (r_o), while deviations away from it have lower consumption rates. A Gaussian function with standard deviation δ_c can describe the consumption rate of a predator with body size B_i on prey with body size B_j ,

$$\gamma_{ij} = \frac{\gamma_o}{\delta_c \sqrt{2\pi}} \exp\left(-\frac{1}{2\delta_c^2} \left(\log_{10}(B_i/B_j) - \log_{10}(r_o)\right)^2\right), \quad (2)$$

where γ_o is a scalar scaling the maximum consumption rate.

Similarly, the function describing the amount of interference competition is based on empirical observations that species with similar body sizes tend to have more interference competition. Again, a Gaussian function with standard deviation δ_I can describe the amount of interference competition from species N_j on species N_i ,

$$\alpha_{ij} = \frac{\alpha_o}{\delta_I \sqrt{2\pi}} \exp\left(-\frac{1}{2\delta_I^2} \left(\log_{10}(B_i/B_j)\right)^2\right), \quad (3)$$

where α_o is a scalar scaling the maximum amount of interference competition.

b. Adaptive dynamics

Adaptive dynamics are incorporated into the food web model using the canonical equation as described by Dieckmann and Law (1996). In this case, the trait which is allowed to evolve is body size,

$$\frac{dB_i}{dt} = k(B_i) \left. \frac{\partial W_i(B'_i, B_i)}{\partial B'_i} \right|_{B'_i=B_i}, \quad (4)$$

where $W_i(B'_i, B)$ is the invasion fitness of the individuals with body size B_i in the environment determined by the resident trait values B , and $k(B_i)$ scales the rate of change of the trait B_i . I will use two alternative forms for $k(B_i)$ to compare the assumptions of adaptive dynamics (AD) and the assumptions of quantitative genetics (QG). To examine the assumptions of AD, I will use a form for $k(B_i)$ that is proportional to the population densities N_i . To examine the assumptions of QG, I will use a form for $k(B_i)$ that is independent of population densities.

c. Harvesting

Following the creation of stable food webs, I intend to study the effects of harvesting pressure. I will examine three types of harvesting strategies (Hilborn and Walters, 1992): constant rate, fixed-stock, and fixed-quota strategies. For a constant rate strategy, the harvested population of species N_i can be expressed as

$$H_i = \mu_c N_i, \quad (5)$$

where H_i is the amount harvested from population N_i and μ_c is a scalar scaling the harvesting rate. For a fixed-stock strategy, the harvested population of species N_i can be expressed as

$$H_i = N_i - \mu_s, \quad (6)$$

where μ_s represents the minimum population density to be maintained. Finally, for a fixed-quota strategy, the harvested population of species N_i can be expressed simply as

$$H_i = \mu_q, \quad (7)$$

where μ_q represents the maximum quota that can be harvested in a population.

d. Measuring the effects of harvesting

To measure the effects of harvesting, I will compare the changes in population density in all species, keeping track especially of instances when species go extinct. Taking the perspective of fisheries, I will also study the changes in the average yield from the harvested species (Y_i), which can be calculated as

$$Y_i = \frac{1}{T} \int_0^T H_i dt, \quad (8)$$

where T is the time interval for which the average yield is calculated.

In order to gain some understanding of the influence of harvesting on population dynamics, I will examine changes in stability in terms of persistence (minimum persistence of the species) and variability (global stability as characterized by the dominant Lyapunov exponent).

Relevance and link to ADN's research plan

This project fits into to ADN's research focus on Fisheries-Induced Adaptive Change. It will also contribute to ADN's new theme on Evolving Biodiversity.

Expected output and publications

This work will be included as a chapter in my PhD thesis. I also intend to publish this work as a co-authored research article.

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