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A network-based approach to the analysis of ontogenetic diet shifts: An example with an endangered, small-sized fish

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ABSTRACT

Many organisms exhibit ontogenetic shifts in their diet and habitat use, which often exert a large influence on the structure and expected dynamics of food webs and ecological communities. Nevertheless, reliable methods for detecting these niche shifts from consumption data are limited. In this study we present a new approach for the detection and analysis of ontogenetic diet shifts, based on complex network theory. As a case study, we apply these methods to the endangered, small fish *Aphanius iberus*. The stage-structured consumer population and its set of consumed prey are represented as an unweighted bipartite network. A statistical evaluation of the resulting network structure permits to uncover empirical patterns of ontogenetic diet shifts. We test for changes in niche breadth, as well as nestedness and diet modularity along ontogeny. These tests were carried out on the subnetworks describing consumption, positive electivity, and negative electivity on prey items. The statistical significance was established by means of null model analyses. Our analyses reveal a nested diet, along with a gradual decrease in diet breadth and a modular structure (i.e. abrupt changes) of elected preys along the ontogeny of *A. iberus*. The detection of network structure by means of the use of tools from complex network theory is shown to be a promising method for studying ontogenetic niche shifts.

1. Introduction

Trophic relationships among coexisting species constitute a central theme in ecology, from the individual to the community level. Predator–prey relationships shape the structure of ecological communities, from population dynamics of the species involved (Chen and Cohen, 2001) to the robustness of the community to environmental perturbations (Dunne et al., 2002), and ultimately the persistence of species over time (Melián and Bascompte, 2002).

The architecture and magnitude of trophic interactions among species are, however, not static but highly variable for different causes (Bolker et al., 2003). One such cause is that the set of species a consumer feeds on can depend on consumer's age, size, or developmental stage (Werner and Gilliam, 1984). During the development and growth of organisms, their food requirements often change quantitatively and qualitatively because of the myriad of effects of predator size on metabolic costs, gape limitation, foraging ability and similar variables. In addition, development can be accompanied by shifts in habitat use (Gross et al., 1988), which result in changes of food availability and predation risk (Hjelm et al., 2000), which constrain the ability to exploit different prey types. As a consequence of the adaptation of consumers to changes in food availability, subjected to feeding constraints, many organisms exhibit either abrupt or gradual shifts in feeding habits along their ontogeny. Ontogenetic diet shifts (ODS) generate stage-structure, potentially leading the consumer population to behave as a set of distinctive trophic entities (Polis, 1984), each interacting with different prey assemblages (Werner and Gilliam, 1984). This ontogenetic niche partitioning, accompanied by heterogeneity in prey abundances, may exert a considerable influence on community dynamics (Polis et al., 1996; Takimoto, 2003).

There is an increasing trend in ecology toward the use of tools from complex systems theory, mainly derived from statistical mechanics (Albert and Barabási, 2002; Newman, 2003), for addressing a variety of natural phenomena. These include the analysis of food webs (Pascual and Dunne, 2006), mutualistic

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interactions (Bascompte and Jordano, 2007), and spatial dispersion (Fortuna et al., 2006). The complex network approach has provided a new and simple way for detecting properties of the structure of interactions among biological entities. In this paper, we show how the methods of complex systems theory can offer a new, simple, and robust way of revealing biologically meaningful patterns of ODS from field data. We studied ODS in the endangered fish *Aphanius iberus* by analyzing the network structure of a detailed quantitative record of consumed prey and their availability, previously published elsewhere (Alcaraz and García-Berthou, 2007; Alcaraz et al., 2008). This dataset is well suited for our objectives because of its detailed taxonomic precision, generally to the genus or species level (which is not frequent for fish dietary studies) and the small maximum size of the predator (which makes ODS less strong and apparent than in many other fishes). We analyzed: (i) ontogenetic shifts in diet breadth, (ii) nestedness in prey species composition, and (iii) modularity in prey species composition, for three kinds of diet matrices (consumption, electivity, and avoidance).

2. Methods

2.1. Dataset and adjacency matrices

The Spanish toothcarp (*A. iberus*) is an endangered cyprinodontid fish endemic to the Mediterranean coast of Spain. It is a small fish of total length <5 cm, sexually dimorphic, with longevity up to 2 years, euryhaline and eurythermal (Fernández-Delgado et al., 1988; García-Berthou and Moreno-Amich, 1992; Vargas and de Sostoa, 1997). This fish reproduces from April to October, laying up to 900 eggs in successive spawns, and reaches sexual maturity in a few months at a total length of <2 cm. The Spanish toothcarp is omnivorous, with a diet composed mainly of crustaceans such as harpacticoid copepods and amphipods, but also including plant debris and detritus (Alcaraz and García-Berthou, 2007).

In this paper, we analyze data previously reported elsewhere (Alcaraz and García-Berthou, 2007; Alcaraz et al., 2008) and we refer to those publications for full details on the field and laboratory procedures. Sampling of the toothcarp and its preys was carried out in Fra Ramon, a small coastal lagoon located at NE Spain, at 42°1′49″ N, 3°11′29″ E and 1.75 m below the sea level. The lagoon was sampled on the mornings of 21–22 November 2002. Prey organisms in the water column were sampled with a 1 m long transect of 50 μm mesh dip net (volume sampled = 0.038 m^3). Benthic organisms were sampled with a 225 cm^2 benthic grab. Details on the post-sampling procedures can be found elsewhere (Alcaraz and García-Berthou, 2007; Alcaraz et al., 2008). Fish were sampled with a throw trap consisting of a 1 m high cylinder of 90 cm in diameter. From the samples taken at 38 sites, we analyzed the entire gut content of fishes and determined the relative density of each prey item in the environment (water column and benthos). In the laboratory, all fish individuals were measured and weighed to the nearest 0.1 mg, after being eviscerated. Prey organisms were identified with the highest possible taxonomic precision, usually to the genus or species level. The total number of fish and prey in the gut that were analyzed was 62 and 10,839, respectively, with prey belonging to 20 taxonomic groups.

Although gut contents give information about realized trophic interactions within food webs, the assessment of feeding preferences must consider the abundance of prey types in the environment. The use of food types in relation to their availability in the environment is often analyzed by means of electivity indices (see e.g. Alcaraz and García-Berthou, 2007; Mas-Martí et al., 2010). These indices allow detecting over- or under-representation of prey items in the diets compared to the resource availability. In this work, electivity on prey types by consumers was measured through the relativized electivity index e of Vanderploeg and Scavia (1979), an index strongly supported by comparative evaluations (Lechowicz, 1982):

$$e = \frac{w_i - n^{-1}}{w_i + n^{-1}}, \quad \text{with} \quad w_i = \frac{r_i}{p_i}\left(\sum_{k=1}^{n}\frac{r_k}{p_k}\right)^{-1},$$

where r_i is the relative abundance of prey i in the diet, p_i is the relative abundance of prey i in the environment, and n is the number of prey types. This index ranges from +1 (positive selection) to -1 (negative selection or avoidance). If prey were consumed according to their availability in the environment, then $e = 0$. Therefore we need to set a critical point above and below which observed values of e would be considered different from zero. We defined a threshold electivity value $u = 0.17$, which was the 5th percentile of the absolute values of the calculated e for each individual consumer on each prey type. Values of $|e| < 0.17$ were considered not significantly different from zero. Moderate variations in the value of u did not alter the outcome of our analyses.

The interaction system formed by the consumer's ontogenetic stages and their prey can be visualized as a bipartite network (Fig. 1), in which nodes represent consumers and prey. The links represent realized consumption interactions that can be classified into three types, i.e. whether a prey is being positively ($e > u$), negatively ($e < -u$) or neutrally ($-u < e < u$) selected by the consumer. Accordingly, the network is represented as a set of adjacency matrices (Fig. 1). The consumption matrix **C** contains information about the prey items recorded in the diet of each stage. In this matrix the element $c_{ij} = 1$ indicates that prey i is consumed by stage j, and $c_{ij} = 0$ otherwise. The electivity matrix **E** shows the prey items positively selected by each ontogenetic stage. In this matrix, elements $e_{ij} = 1$ indicate that prey item i displays a value of $e > u$ for stage j. Finally, avoidance matrix **A** contains elements

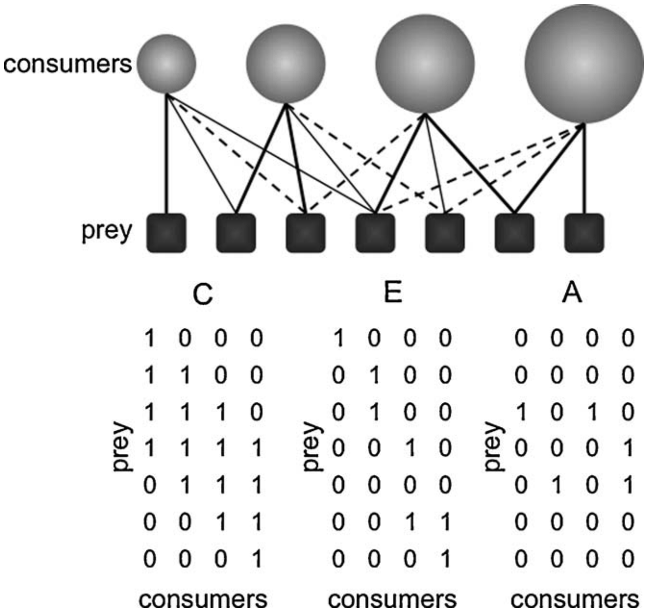

Fig. 1. Network (top) and matrix (bottom) representation of the interactions between a multi-stage consumer population and its prey resources, for the study of ontogenetic diet shifts. This figure does not represent real data. Spheres represent ontogenetic stages of the consumer species, squares represent prey items, and links represent realized prey–consumer interactions. Thick links indicate positive electivity of the prey, dashed links represent negative electivity (i.e. avoidance), and continuous thin links show null electivities. In the matrices, consumer stages and prey items are represented in columns and rows, respectively. In the consumption matrix **C**, ones indicate realized consumption interactions, and zeroes indicate unobserved consumption of item i by consumer stage j. Positive and negative electivities are represented in matrices **E** and **A**, respectively.