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Effects of food web complexity on top-down control in tropical lakes

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ABSTRACT

Top-down control in ecosystems is dependent on food web structure. In this study, we developed 126 models describing different trophic link combinations in order to assess the effects of food web structure on the top-down response of shallow tropical lakes. We evaluated the effects of the presence of invertebrate predators, large-bodied herbivorous zooplankton and the degree of omnivory. The results showed that the presence of invertebrate predators and large-bodied herbivorous zooplankton can invert the relation between planktivorous/omnivorous fish and producers (algae). The fact that large herbivores are absent in tropical lakes and invertebrate predators are present in large quantities results in a positive correlation between piscivorous fish and algae biomass, contradicting the classical top-down response described for temperate lakes. We show that omnivory should not be analyzed as a feeding strategy in itself. Omnivory affects many food web processes and its effects are dependent on the trophic level. In our models, omnivory in intermediate trophic levels dampened the top-down control by fish, but omnivory in top trophic levels has an opposite effect increasing the fish carrying capacity and also the strength of the top-down trophic cascade, while simultaneously decreasing the shortest chain length between fish and algae, thus reversing the relation between these two trophic levels.

Epigraph

As stated by Hairston and Hairston (1997) complemented by Polis and Strong (1996): "Any attempt to understand broad ecological patterns will be challenged by the complexity of nature". "Our task as community ecologists is [. . .] to continue to rethink, quantify, model, and test the interplay between complexity and dynamics. Only when we embrace complexity and variability will we truly understand natural systems".

1. Introduction

The indirect effects of top predators on producers' biomass in aquatic environments has been suggested since the 1960s (Hodgson, 2005), but only in the 1980s were experiments performed to prove the existence of top-down trophic cascades in lakes (Carpenter et al., 1985; Carpenter and Kitchell, 1993; Carpenter et al., 1995; Carpenter et al., 2001). These studies led to the trophic cascade hypothesis (TCH), which states that an increase of piscivorous fish biomass reduces the population of planktivorous fish, lowering the consumption of large-bodied herbivorous zooplankton, which increases the grazing under the phytoplankton community, thus decreasing the primary production of the ecosystem. The TCH has received much evidence from enclosure studies (e.g., Brett and Goldman, 1996), whole-lake studies (Meijer et al., 1999) and long-term experiments (e.g., Mittelbach et al., 1995), which showed that biotic interactions within the lake (i.e., differences in food web structure and composition) could explain the deviations from the classical bottom-up relationships between phosphorus and chlorophyll-a or primary production (Vollenweider, 1976; Schindler, 1978; Carpenter et al., 1987).

On the other hand, not all experiments could demonstrate the existence of classical top-down trophic cascades in lakes as described by the TCH. Real food webs are far more complex and other compensatory and antagonistic mechanisms may play a role either buffering or reversing the relation between top predators and producers (DeMelo et al., 1992; Drenner and Hambright, 2002). Among the buffering mechanisms that were already described are stochastic climatic variations (Carpenter et al., 1987), increase in water nutrient concentration by both fish and zooplankton

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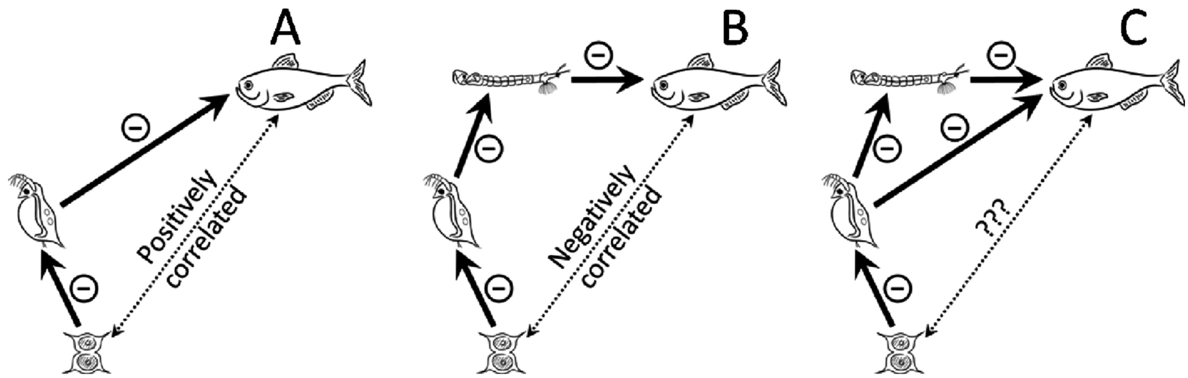

Fig. 1. The influence of chain length on the correlation between the biomasses of planktivorous fish and algae. The circle with minus sign indicates that the biomasses of adjacent trophic levels are negatively correlated due to predation. (A) Three level chain between fish and algae implies in a positive correlation between these two trophic levels. (B) Four level chain between fish and algae implies in a negative correlation between these two trophic levels. (C) The presence of omnivorous fish may create contrasting results.

excretion (Vanni and Findlay, 1990), macrophyte shading, competition and allelopathy (Mcqueen, 1990) and the presence of inedible algae (Meijer et al., 1999).

In particular, tropical and subtropical lakes have some buffering mechanisms that may suppress the occurrence of top-down trophic cascades (Drenner and Hambright, 2002; Jeppesen et al., 2005). For instance, the top-down control on primary producers may be less pronounced in the tropics because large-bodied herbivorous cladocerans are considered a key factor for the control of algae biomass (Dawidowicz, 1990), and tropical zooplankton species are generally smaller than the temperate ones (Gillooly and Dodson, 2000). Moreover, juvenile fish and invertebrate predators, like *Chaoborus* larvae, are dominant and reproduce throughout the year, resulting in a high predation pressure on zooplankton, particularly the more vulnerable ones like cladocerans (Van Leeuwen et al., 2007).

The presence of intermediate predators, like *Chaoborus* larvae, also implies shifting from the classical three-level chain (i.e., Fish–cladocera–algae) to a four-level chain (i.e., Fish–*Chaoborus*–cladocera–algae), thus increasing the chain length and reversing the correlation sign between fish and algae, because decreasing the planktivorous fish density would release *Chaoborus* larvae from predation, which suppresses cladocera populations, leading to higher algae density (Fig. 1). This inverted top-down response due to the presence of intermediate predators was already described from both modeling (Hart, 2002) and field studies (Pinto-Coelho et al., 2008) and has important implications for the use of biomanipulation in the tropics.

Omnivory is another process that influences the top-down response in food webs, however its effects are still not conclusive. Omnivorous tropical fish, specially the juveniles ones, can also feed on zooplankton and algae (Lazzaro, 1997), introducing an intraguild predation structure in the food web, making the top-down response less predictable (Fig. 1). Modeling studies are now discussing the importance of self-limitation (i.e., density-dependent regulation) as a key component that determines both the direction and strength of the top-down response (Hart, 2002; Heath et al., 2014), however these studies have focused on few food web structures, thus limiting the conclusions to temperate environments.

Our aim in this study is to analyze the role of food web structure on top-down effects of fish on producers (strength and direction of the relation, whether it is positive or negative), evaluating all possible realistic combinations of interactions and functional groups that may be present in a simple food web of a shallow lake, also including food web structures that are specific for the tropics. In these model variants three characteristics of food web structure were evaluated: the presence of omnivory, the presence of intermediate predators like *Chaoborus* larvae and the presence of large-bodied cladocera species.

2. Materials and methods

2.1. Model design

Our most complex model was based on the conceptual one described by Carpenter et al. (1985) with a few modifications. We considered the following state variables: planktivorous fish (F), *Chaoborus* larvae (C), small-bodied cladocera (D_1), large-bodied cladocera (D_2), nannoplankton (A_1) and edible phytoplankton (A_2). Piscivorous fish were considered to be constant and were included as a mortality term of planktivorous fish (m_F). We first developed a full model including all biologically meaningful interactions among all these species (Fig. 2). From the full model we derived 125 simpler models by systematically leaving out all possible combinations of interactions and state variables (i.e., species) except planktivorous fish, small cladocera and nannoplankton which were always present (Table A.1—Appendix). The resulting food web structures included all combination of invertebrate predators (e.g., *Chaoborus* larvae), large-bodied cladocera and edible algae and varying omnivory degree in each consumer trophic level.

We assumed interactions of the Lotka–Volterra type among the state variables and included a density-dependent stabilizing

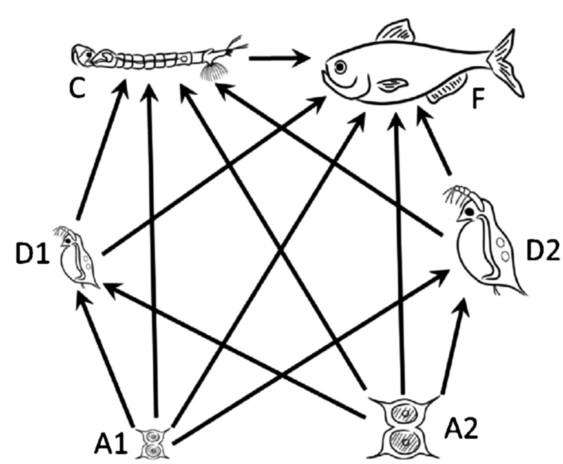

Fig. 2. The conceptual scheme of the full model, showing the state variables: planktivorous fish (F), *Chaoborus* larvae (C) small-bodied cladocera (D_1), large-bodied cladocera (D_2), nannoplankton (A_1) and edible phytoplankton (A_2).