Modelling the food web of a stream in Atlantic Forest

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ABSTRACT: Modelling the food web of a stream in Atlantic forest. Mathematical modelling can be employed in a variety of ways to aid the analysis of ecological communities; here we use it to examine the structure of a lotic food web and make qualitative predictions about the effects of excluding components. We studied a community comprising two species of freshwater shrimp, *Macrobrachium* sp. and *Potimirim* sp., a dominant ephemeropteran, other macroinvertebrates, periphyton and detritus. Previous experiments showed that when shrimps were excluded, periphyton and sediments decreased and when shrimps and Ephemeroptera were excluded, periphyton and sediments increased. We interpreted this as a trophic cascade in which shrimps repress ephemeropterans which are the principal herbivore-detritivores. The result is interesting in the light of (i) other Neotropical stream research with similar fauna which did not show trophic cascade and (ii) food web theory which predicts that a dominant omnivore should not produce a trophic cascade. We modelled the system using modified Lotka-Volterra equations and the program Model Maker. The model reproduced the results of excluding shrimps and shrimp + ephemeropterans. It also predicted the outcome of manipulating other components. The model was sensitive to the strength of the herbivory of *Macrobrachium* on periphyton, which we interpreted as important for the stability of the trophic cascade.

Key words: ecological modelling, food webs, trophic cascade, exclusion experiment, press perturbation

RESUMO: Modelando a rede trófica de um córrego de Mata Atlântica da Ilha Grande, Rio de Janeiro. A modelagem matemática pode ser empregada de diversas maneiras para auxiliar a análise de comunidades ecológicas. Neste trabalho, nós a usamos para examinar a estrutura lótica de redes tróficas e fazer previsões qualitativas sobre o efeito da exclusão de outros componentes. Estudamos uma comunidade composta por dois tipos de camarões, *Macrobrachium* sp. e *Potimirim* sp., efemeropteras, outros macroinvertebrados, perifíton e sedimentos. Experimentos anteriores mostram que a exclusão de camarões reduzem a quantidade de algas e sedimentos e a exclusão de camarões e efemeropteras aumenta a quantidade de algas e sedimento. Interpretamos isso como uma cascata trófica na qual os camarões reprimem a atividade dos efemeropteras, que seriam os principais herbívoros-detritívoros. O resultado é interessante pois (i) pesquisas em outros rios Neotropicais com fauna similar não tem cascatas tróficas e (ii) teorias de redes tróficas prevêem que não existem cascatas tróficas onde existe um onívoro dominante. Modelamos o sistema usando equações derivadas das equações Lotka-Volterra no programa Model Maker. O modelo reproduz os resultados da exclusão de camarões e da exclusão de camarões e efemeropteras. Também prevê os resultados de manipulações de outros componentes. O sistema foi sensível à pressão de herbivoria de *Macrobrachium* no perifíton, que interpretamos como importante para a estabilidade da comunidade.

Palavras chave: modelagem, redes tróficas, cascatas tróficas, exclusão

Introduction

The analysis of food webs is basic to community and ecosystem ecology. Quantitative studies of material flow between components of an ecosystem normally implies the combining of similar taxa into functional groups, as in the classic work of Lindeman (1942). On the other hand, qualitative descriptions of the trophic relationships between the species of communities aim to be as specific and comprehensive as possible. Many food webs have been described and a data base of them continues to expand (Cohen, 1978). These descriptions have provided the basis for the analysis of general properties of food webs (Cohen, 1978; Cohen et al., 1993) and the reality with which theoretical analysis can be judged (Pimm, 1982). Goldwasser & Roughgarden (1997) provide a warning about the uncritical use of this database, claiming that incomplete food webs can give incorrect interpretations of patterns of connectance.

The dynamics and stability of food webs can be studied also as a matrix of influences between the components, as opposed to a quantitative or qualitative description of the transfer of material between the components (Pimm, 1982). This approach has yielded a large body of theory (May, 1973; May, 1976; Yodzis, 1988) which examines the stability, resilience and structure of food webs. Real-world testing this theory has been divided into "press" and "pulse" experiments, (as well as the observational evidence cited above). Press experiments maintain one or more of the components in an altered state, for example, excluding a species or maintaining a species at a higher level using a cage. Pulse experiments cause an alteration to the community and observe the result, usually in terms of time-course to recovery.

Rarely have real-world experiments quantified the matrix of interactions; Schmitz, (1997) provides a notable exception. On the other hand, there is a large literature of experimental manipulations of communities and a corresponding body of generalizations. The pioneering work of Paine (1966) and many subsequent press experiments in the rocky intertidal have revealed the importance of top predators in mediating competitive interactions of lower trophic levels. The phenomenon has come to be known as the key-stone predator concept and its importance in understanding and conserving ecosystems has been emphasised by Power et al. (1996). Hurlbert (1997) provides a salutary criticism of the concept.

Pertinent to our research are experiments that demonstrate the strong interaction of certain fauna on the benthos of Neotropical rivers and streams: Flecker (1996) studied benthic-feeding fish in a Venezuelan piedmont river and characterized their action ("environmental engineering") in sediment removal and the effect on benthic organisms, (see also Power, 1997). In Puerto Rico and Costa Rica, various publications have found strong effects of atyid and palaemonid shrimp (Crowl et al., 1996; Pringle, 1996; Pringle et al., 1993; Pringle & Blake, 1994) and fish (Pringle & Hamazaki, 1998). In all of these cases, the dominant organisms (shrimp and fish) are much larger than their prey (macroinvertebrates, algae, detritus) and are omnivorous. They apparently do not produce a "trophic cascade" in which their predation on intermediate herbivores would have a positive effect on the growth of algae. Trophic cascades are commonly seen in aquatic systems (Vanni et al., 1997; Strong, 1992), and Pringle & Hamazaki (1998) attribute their absence in this case to the omnivorous relationships of the top consumers. This is also predicted from theoretical considerations of a food web with a dominant omnivore.

Our work is part of a study of the food web and community dynamics of a Neotropical stream which has similar organisms to those of the above mentioned studies in Puerto Rico and Costa Rica: atyid and palaemonid shrimp, macroinvertebrates, benthic algae and sediments. We use mathematical modelling to

analyse the dynamics of the food web using the known feeding relationships and results of press perturbations (exclusion experiments). The output of the model can indicate if our understanding of the system is correct, at least in terms of the structure of the trophic relationships and interactions. It can also predict the consequences of exclusions other than those for which we have experimental observations. We did not have measurements of the real parameters for growth rate, carrying capacity or interspecific interaction coefficients. However this was not an impediment to the modelling exercise since we were interested in the qualitative behaviour of food webs with various structures. Therefore we experimented with different values for the parameters and adjusted the model to simulate the behaviour observed in the field.

The food web of Mãe D'água and experimental exclusions

Our experimental area is at a site know locally as "Mãe D'água" in a third-order stream, Rio Andorinha, close to the research facility CEADS of Universidade do Estado de Rio de Janeiro at Vila Dois Rios, Ilha Grande, Rio de Janeiro, (23° 11'S, 44° 12'W). At this site the substrate is a continuous granite slab, with a pool area upstream, a relatively shallow area (4 to 30 cm deep) in which we worked and an inclined rock face and waterfall downstream (Moulton & Souza, 1998). The biotic community has a reduced diversity of species probably because of the low structural heterogeneity. The principal organisms are: the palaemonid shrimp *Macrobrachium olfersi* (Wiegmann, 1836), the atyid shrimp *Potimirim glabra* (Kingsley, 1878), larval baetid ephemeropterans (four morphospecies), larval chironomid dipterans (four morphospecies) and periphytic algae. Trichopterans and plecopterans are rare within the study area, although common on the rockface.

We categorized the community using the functional feeding groups of Cummins & Klug (1979). *Macrobrachium* was considered mainly as a shredder of organic matter, but could also act as a predator, *Potimirim* as a scraper of algae and detritus, Ephemeroptera as a grazer and Chironomidae as a collector. For the purposes of the model, we did not separate the algae, but note that they comprise a mucilaginous epilithon of cyanophytes, diatoms and chlorophytes, with associated fungi, bacteria and detritus. Filamentous green algae (*Spirogyra* spp. and others) occur sporadically.

Our interpretation of the trophic relationships comes from a series of experiments. We manipulated this community using exclusion by cages and electric fences (Table I). When shrimps were excluded by cages, algal biomass decreased (Siviero & Moulton, 1998). We interpreted this result as indicating a trophic cascade in which shrimp were

Table I: Principal results of previous field experiments.

Experiment	Type of exclusion	Results	Reference
Exclusion by cages	Shrimps of both families	Algae (chlorophyll) decreased in absence of shrimps	Siviero & Moulton, 1998
Exclusion using weak electric current	Shrimps of both families	Algae decreased in area of exclusion	Moulton et al., 1999
Exclusion using strong electric current	Shrimps of both families and Ephemeroptera	Algae, sediments and chironomids increased in area of exclusion	Moulton et al., 1999; Siviero, 1998

inhibiting an important herbivore, and it appeared that common baetid ephemeropterans were likely to be exerting this function. The result was apparently repeated using an electric fence which excluded shrimps but not ephemeropterans (unpublished data, quoted in Moulton et al., 1999). The experimental method was then enhanced by electric fence capable of excluding the larger ephemeropterans and observed a dramatic increase in periphytic algae, sediments and chironomids

(Moulton et al., 1999; Siviero, 1999). With these results we confirm that the shrimp fauna are "strong interactors" as in streams of Puerto Rico and Costa Rica, but that the dynamics appear to be different, and, at least in the area studied, there appears to be a trophic cascade.

We stress that these results are preliminary, and we do not extract quantitative parameters from the data, the phenomena and trophic relationships upon which the model is based are merely the best information that we have at this stage of our investigations. The model hopefully indicates to us how well we understand the system and what further observations and experiments are necessary for a fuller understanding.

Materials and methods

The model was based on a modification of Lotka-Volterra equations developed by Berryman et al. (1995):

$$\frac{1}{X_i} \cdot \frac{dX_i}{dt} \equiv R_i = a_i - b_i X_i - \frac{X_i}{c_i X_{i-1}} - \frac{d_i X_{i+1}}{X_i}$$

where R_i is the specific rate of growth attained by population X_i, a_i is the maximum rate of growth per capita, b_i is the impact of an individual on the per capita growth rate of its own species, X_i is the number of individuals of species i in the population, c_i is the coefficient of interaction between the species in question and the species it consumes, X_{i-1} is the number of individuals in the consumed species, d_i is the coefficient of interaction between the species in question and the species that consumes it, and X_{i+1} is the number of individuals in the predator species.

The model was developed in the program Model Maker (1994), with compartments representing each component of the food web and connections ("influences") between each compartment conforming to the above equation. The parameters we used to build the model were calculated via Model Maker modelling software and common sense. We tried several parameter combinations until we found one able to reproduce the qualitative behaviour of our field experiments. Subsequently, we tested various manipulations of the model (exclusion of species) in order to investigate its properties and relate the outcomes to the observed experimental results. We also carried out manipulations that were not observed in the field.

The matrix of components and interactions included detritus, which, although not an organism, had a rate of accumulation and consumption that could be modelled by the same equation. The abundances of the components correspond to those of an area of 16 m² except for the two species of shrimp which have a higher mobility and derive from an area of 324 m². We assume that the populations are at equilibrium before provoking perturbations. As can be seen, there are interactions between almost all of the components of the model, but some are stronger than others (Table II). The principal interactions of the model are: Principal predator - *Macrobrachium*, principal detritivore - *Potimirim*, principal herbivore - Ephemeroptera.

Results

We carried out a simulation of the two experiments of exclusion by electrification, in which first the two shrimp species were excluded, then shrimps plus Ephemeroptera (Fig. 1, Table I). The dynamics of the components followed qualitatively the results of the experiments (Table I): the algae diminished when the shrimps were excluded and increased when the Ephemeroptera were also excluded (Fig. 2).
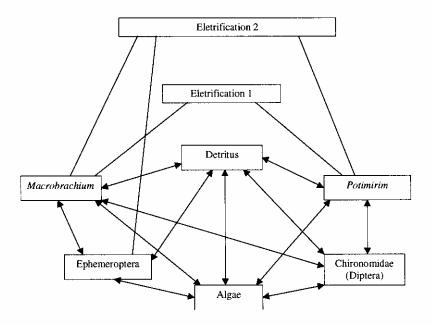
Figure 1: The food web with experimental exclusion by electricity. The two experimental exclusions were not executed simultaneously and are represented by "Electrification 1" and "Electrification 2".
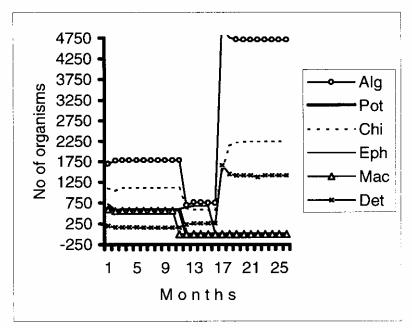

Figure 2: Dynamics of the food web including effects of the two electrical exclusions. The food web remained without impacts until the 11th month when the two shrimp species were excluded (simulating low-intensity electrification, Electrification 1). At the 15th month, Ephemeroptera were excluded in addition to shrimps (simulating Electrification 2). "Alg" = algae, "Mac"= *Macrobrachium*, "Ch" = Chironomidae, "Eph" = Ephemeroptera, "Pot" = *Potimirim* and "Det" = detritus.

We also ran simulations of exclusions other than those for which we had experimental observations (Table III). All were carried out with the same interaction coefficients as in the previous model (Table II), excepting for the last in which the

Table II: Parameters used in the model*.

Relation	Parameters
Algae effect on *Potimirim*	+1
Algae effect on Chironomidae	+4
Algae effect on *Macrobrachium*	+1
Algae effect on detritus	+0.2
Potimirim effect on detritus	-0.002
Potimirim effect on algae	-0.00002
Potimirim effect on Chironomidae	-0.000005
Chironomidae effect on algae	-0.00008
Chironomidae effect on *Potimirim*	+2
Chironomidae effect on *Macrobrachium*	+3
Chironomidae effect on detritus	-0.0002
Ephemeroptera effect on *Macrobrachium*	+5
Ephemeroptera effect on detritus	-0.00025
Algae effect on Ephemeroptera	+3
Ephemeroptera effect on algae	-0.001
Macrobrachium effect on algae	-0.0000002
Macrobrachium effect on Chironomidae	-0.0001
Macrobrachium effect on Ephemeroptera	-0.15
Macrobrachium effect on detritus	-0.00002
Detritus effect on algae	-0.5
Detritus effect on *Potimirim*	+4
Detritus effect on Chironomidae	+1
Detritus effect on Ephemeroptera	+2.5
Detritus effect on *Macrobrachium*	+3
Algae growth rate	1
Potimirim growth rate	0.3
Ephemeroptera growth rate	0.35
Chironomidae growth rate	0.2
Macrobrachium growth rate	0.15
Detritus growth rate	1
Algae Carrying Capacity	6000
Potimirim Carrying Capacity	1000
Ephemeroptera Carrying Capacity	2000
Chironomidae Carrying Capacity	5000
Macrobrachium Carrying Capacity	1000
Detritus Carrying Capacity	50000
Increased *Macrobrachium* effect on algae	-2.2
Increased Algae effect on *Macrobrachium*	+0.0004

Table III: Principal results of the model. Population Increase ⬆. Population decrease ⬇. No change in population numbers O.

Treatment	Effect					
	Algae	"Mac"	"Pot"	"Eph"	"Chi"	"Det"
Exclusion of Ephemeroptera and *Potimirim*	⬆	⬆	—	—	⬆	⬆
Exclusion of *Macrobrachium* shrimps	⬇	—	⬇	O	⬇	⬇
Exclusion of Ephemeroptera and Chironomidae	⬆	O	O	—	—	⬆
Exclusion of Ephemeroptera	⬆	O	⬆	—	⬆	⬇
Exclusion of Chironomidae	⬇	⬇	⬇	⬇	—	⬆
Exclusion of Ephemeroptera and *Macrobrachium*	⬆	—	⬆	—	⬆	⬇
Exclusion of *Potimirim*	⬇	⬇	—	O	⬇	⬆
Increased effect of *Macrobrachium* on algae	⬆	O	O	Extinction	⬆	O

effect of *Macrobrachium* on algae was intensified. Some of these exclusions would be difficult, if not impossible, to carry out in practice. Some of the results are quite counter-intuitive, as is often the case in trophic web models (Pimm, 1982). For instance, when *Macrobrachium* was excluded, Chironomidae, decreased and Ephemeroptera did not change, apparently due to feedback loops in other parts of the model.

Discussion

The results of the simulations of exclusion by electricity showed that the absence of both species of shrimp reduces the amount of algae and Chironomidae, and when Ephemeroptera were also excluded the algae, Chironomidae and organic matter increased (Fig. 2). These outputs mimic the results of the actual experiments and suggest that our understanding of the system is correct. We cannot, of course, distinguish a Type II error of obtaining the correct result but through erroneous logic, but we are heartened by the fact that the model responds correctly to more than one manipulation.

The biological result is the opposite to that seen by Pringle & Hamazaki (1998) and appears also to conflict with food web theory (Pimm, 1982) in that an omnivore should not cause a trophic cascade if it acts on the same primary food source as its prey. It seems, however, that in our case where the omnivores are feeding on herbivores and substantially on detritus (organic matter), their absence can provoke a trophic cascade in which the release of the prey herbivore reduces the primary level (algae). In this situation, the omnivore is not seriously competing for the same food source (algae) as its prey, and thus coexistence is maintained. Support for this hypothesis comes from the manipulation in which we increased the pressure of herbivory by *Macrobrachium* and observed the extinction of Ephemeroptera (Table III, last line).

The equation developed by Berryman et al. (1995) appeared to function well for the simulation of interspecific interactions that we wanted to model. The separation of the organisms into functional groups made the modelling more simple than trying to incorporate all of the different species (even taking into account the naturally depauperate status of the study area). For the purposes of the modelling exercise, the imprecision thus generated did not apparently diminish the result, bearing in mind that we wished to obtain a general picture of the community dynamics. We can easily imagine improvements to the details and realism of the model: the algal component, for example, could profitably be separated into functional types of erect and prostrate, and general taxonomy (blue-green, diatom and green), which could be modelled as having different rates of herbivory of the different herbivores.

The model made predictions about the effects of excluding components other than those for which we had experimental results (Table III). This could be very useful for designing new experiments and eventually for making predictions about real-world events, such as anthropogenic impacts and natural perturbations. Despite the fact that the model was not based on measured parameters, it was able to describe the behaviour of the natural system and could possibly provide a starting point for rational diagnosis and planning. The fidelity that the model has for natural processes will, of course, depend on the correctness of its structure (trophic relationships) and precision of its interaction coefficients. As these improve, we will be able to make more realistic and precise predictions. An obvious extension of the work is to experimentally determine the interaction coefficients and incorporate them into the model (cf. Schmitz, 1997). A cautionary note to the general applicability of perturbation experiments was given by Yodzis (1988), but it is not obvious that subsequent work over the last 10 years has born out his pessimism (Pimm, pers. comm.).

Overall, the modelling exercise presented here demonstrates the potential critical importance of analysing the community as a whole. Many of the interactions of Table III

are quite counter-intuitive and a single factor analysis would arrive at erroneous conclusions or at least a conundrum. For instance, the intensification of herbivory of *Macrobrachium* on algae resulted in a higher standing crop of algae. A simplistic interpretation of this might postulate a stimulation of algal growth caused by grazing activity, whereas in the model the effect was caused by interaction with Ephemeroptera. Of course we must not credit the model with a complete explication of reality and it is imperative to test any of the model's predictions before accepting them as reality. Likewise the application of these results to other areas needs to be made with caution, but the potential of insight is great.

Acknowledgements

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