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Ecophysiological models: A tool for understanding interactions in freshwater communities?

Ökophysiologische Modelle: Ein Weg zum Verständnis der Interaktionen in aquatischen Lebensgemeinschaften?

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Abstract

The discussion on how aquatic communities are organized is presently dominated by the bottom-up top-down controversy. However, the debate about the relative importance of community control either bottom-up by the availability of resources or top-down by predator effects is useless as organisms on every trophic level must be adapted to respond to selective forces from both directions if they are to persist in a certain community. Ecophysiological models incorporating evolutionary principles which are exclusively based on measurable properties of the organisms can be useful in understanding the interactions in a community. They can be employed to predict the fate of a particular species or guild when the boundary conditions change or to describe the properties of an organism required to exist in a particular set of interactions. This is demonstrated with four different models. The first model considers bottom-up forces. Based on Tilman's competition theory it predicts the result of competition for substitutable resources in rotifers. The second model predicts size selectivity of an invertebrate predator, the midge larva *Chaoborus*, and its impact on the size structure of a zooplankton community. Both directions are considered in a third model. It describes the consequences of different energy allocation patterns to growth and reproduction in *Daphnia* and predicts the optimum life histories for different predation patterns. Finally, a stage structured model is used to study the effects of an ontogenetic shift from one trophic level to the next in *Cyclops*. The model shows that a certain degree of cannibalism has a strongly stabilizing effect on the populations of both predator and prey. These models not only predict what the optimal performance of an organism in the community would be, they can also be used to estimate the necessary degree of phenotypic plasticity in a varying environment.

Introduction

Although climatic and edaphic factors vary in space and time, freshwater communities show a certain degree of structural predictability and of regularity in seasonal succession (Lampert 1987). Concepts of community organization have been particularly well developed for freshwater communities as they are relatively closed systems and their components are small and reasonably easy to sample. Therefore, Halbach (1977) used limnology to demonstrate problems of ecosystem research at the annual meeting of the DZG at Erlangen. His particular concern was modelling of ecosystem processes on different levels of integration. The examples he presented ranged from stochastic models of individual behavior to cybernetic models of community structure. Halbach emphasized the dichotomy between different types of models. Models which incorporate properties of every single species may be very precise but not applicable to different systems. On the other hand, very general models which incorporate only large compartments and concentrate on the key factors do not give precise answers for specific communities. When Halbach gave this lecture, his arguments and the selection of the models was strongly influenced by the concept of the community as a self-regulating system with some homeostasis. Hence, the models presented had cybernetic character.

Experimental manipulations and the discovery of the importance of keystone species (Paine 1980) have changed the view of community ecology in the meantime.

Communities are seen as aggregates of interacting organisms that have been screened; only those species which are adapted to successfully handle direct and indirect interactions with the other species can permanently persist. Understanding the rules of community organization means understanding the selective forces which have shaped coexisting organisms in evolutionary time. The number of different types of interactions is much smaller than the number of species, so that we can construct a template of a community based on interactions and then fill it with guilds or species that fit into the template. The species considered will then specify the interaction quantitatively according to their physiological properties, but will not alter the qualitative system behavior.

Trying to construct such templates has made food web theory very exciting in recent years, but food web models are still qualitative. Due to a static view, they lack components that arise from the dynamics of interactions. Although theory can predict general rules of food web construction, for example, the number of trophic levels in relation to productivity (for a review see Power 1992), it will not be able to predict the fine structure within a trophic level. There may be alternative ways to solve the same problem and each way may represent a species or guild. Considering that every organism in the food web is forced to maximize its fitness, the prediction of the fine structure is the domain of evolutionary physiological ecology (Sibly and Calow 1986). Most interactions in a community are based on the physiological properties of the interacting organism. In ecological time we may, thus, ask if an organism is physiologically flexible enough to respond to changes in the community structure. In evolutionary time the question may be, considering physiological constraints, which solution selection would favor for a particular organism.

Control of community structure

Community ecology has been influenced very much in recent years by the debate on the relative importance of bottom-up and top-down processes (cf. special feature in the June issue of *Ecology* 73, 1992). Although there now is increasing agreement that this dichotomy is artificial (Menge 1992) it has inspired many theoretical and empirical studies and has led to a better understanding of the processes that determine the structure of a community. The two approaches can be illustrated for a freshwater community in Fig. 1. Bottom-up and top-down processes are in some respect fundamentally different. The bottom-up approach considers communities to be controlled from the basis of the food chain i. e., by the availability of resources. The logic is: more nutrients → more algae → more zooplankton → more planktivorous fish → more predacious fish. Note that all the signs in this chain are equal. On the contrary the top-down approach starts with the top carnivores. Each trophic level consists of what has been left over by the next higher level. As a consequence, the following logic emerges: more piscivores → less planktivores → more zooplankton → less algae → more nutrients. In this case signs alternate between trophic levels. There is evidence for both forces acting in a community but they probably do not act at the same time and scale. Large-scale interlake comparisons often demonstrate bottom-up control e. g., a good correlation can be found between lake phytoplankton and phosphorus (Dillon and Rigler 1974). On the other hand, shortterm disturbances (e. g., loss of planktivorous fish) can cascade through the entire community and indicate a very strong top-down force (Carpenter and Kitchell 1988). The importance of both directions may vary during seasonal succession (Sommer et al 1986). Moreover, the relative importance of both forces can vary within a single food chain. McQueen et al (1989) came to the conclusion that both effects are attenuated, so that top-down effects are more important near the top and bottom-up effects near the base of a food chain.

The concept is not as straightforward as Fig. 1 may suggest. Many animals are omnivores and may exploit more than one trophic level, even the same animal can change its trophic role

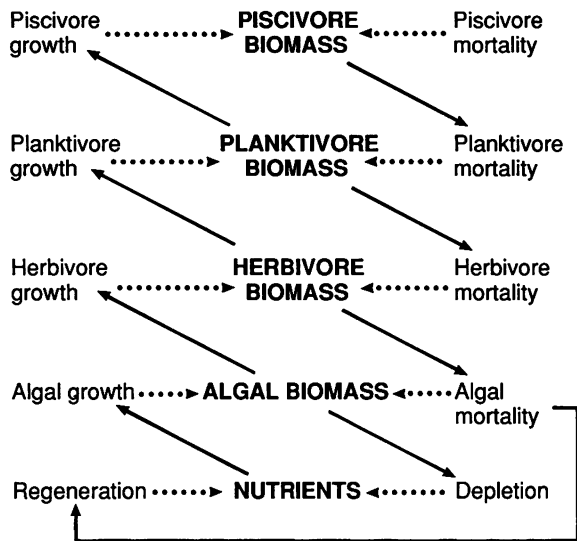


Fig. 1: Schematic representation of the interactions in a pelagic freshwater food chain. Bottom-up forces are depicted on the left side of the graph while top-down forces are shown on the right side. The biomass on each trophic level is the result of growth processes (bottom-up control) and loss processes (top-down control). The separation of planktivores into fish and invertebrate predators and the microbial loop have been omitted to simplify the graph.

during ontogeny. There are also feedbacks as indicated at the bottom of Fig. 1. Moderate grazing may stimulate algal growth via regeneration of nutrients (Sterner 1986).

Organisms can only coexist in a community if they are adapted to the interactions with other organisms of the same or adjacent trophic levels. Such interactions may be exploitative or interference competition and predator-prey relationships. Bottom-up and top down forces imply the evolution of fundamentally different mechanisms of adaptations in order to increase fitness. When bottom-up forces are important i. e., resources are limiting, the evolutionary response must be a higher efficiency of uptake and use of resources. Bottom-up forces will mainly select for fitness components that increase the rate of reproduction. However, energy flow and resource uptake have serious thermodynamic and physiological constraints that cannot be overcome so that the possibilities for adaptation are limited. The mechanism of top-down forces is mortality, hence, the evolutionary response must be defence. Although defences are costly, there is no *a priori* reason for a limitation of the adaptation. A prey can become perfectly protected if the predator is unable to coevolve because of other constraints.

In order to illustrate the differences between adaptations to bottom-up and top-down forces we have selected model examples for both theories. However, it will become evident that each model must contain elements of both to give reasonable results.

Competition models

The structuring force in bottom-up control is competition for limiting resources. Resources must be understood as any factor that is consumed like inorganic nutrients, food, light (in a vertically structured plant community), and space. The underlying assumption is that, as long as a resource is limiting, a higher availability leads to a higher reproductive success.

The classical Lotka-Volterra competition models are not physiological but phenomenological models. The competition coefficients can only be determined *a posteriori* from the result of a competition experiment. They cannot be estimated directly from physiological properties

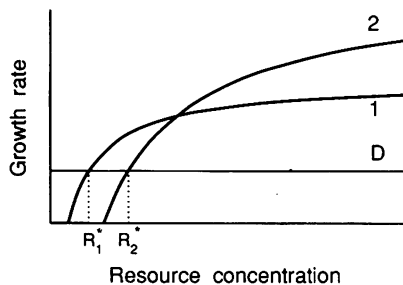


Fig. 2: Growth curves in response to resource concentration of two species (1 and 2) which differ with respect to maximum growth rate, half-saturation constant and threshold concentration. Thick lines indicate gross growth rates. Net growth rates are represented by the difference between gross growth rates and the loss rate (D). R^* is the zero net growth concentration for the respective species (after Tilman 1982).

of the competitors or from a measure of «niche overlap» (Giller 1984). Hence these models have low predictive power.

On the contrary, the models of resource competition developed by Tilman (1982) are mechanistic models that allow a *priori* predictions of the outcome of competition before any experiment has been done. They are exclusively based on the physiological properties of the organisms i. e., on their resource limited growth kinetics and loss rates. The basic assumption is the growth equation of Monod (1950). In zoological terminology it may be written with a threshold:

$$r = r_{\max} \frac{S - S_0}{S - S_0 + k_s}$$

r : intrinsic growth rate (d^{-1})

r_{\max} : maximum (unlimited) growth rate (d^{-1});

k_s : half-saturation constant;

S : concentration of the limiting resource;

S_0 : minimum resource concentration for growth.

Fig. 2 presents Monod curves for two species with differing r_{\max} , k_s and S_0 . They represent the gross growth rates for the two species which are dependent on a single resource. The loss rate (mortality) is assumed to be equal for both species. As the net growth rate is the difference between gross growth rate and loss rate, the intersections mark the resource concentrations required to balance growth and losses (R^*) i. e., the zero net growth concentration. If the two species compete for the limiting resource they will reduce its concentration until the zero net growth concentration of species 2 (R_2^*) is reached. At this point species 2 can no longer grow but species 1 can, although at a reduced rate. Hence the species with the lower R^* will win the competition. Note that R^* is also affected by the loss rate. The order of R^* s can be reversed in our example when the two species have differing loss rates or when the common loss rate is increased above the intersection of the two Monod curves.

This model can be expanded for multiple limiting resources. Fig. 3 shows resource planes for two resources. Each axis represents the availability of one resource. Instead of one point (R^*), we now have a «zero net growth isoline» (ZNGI) that connects all possible combinations of the two resources where growth is zero. Growth is negative at all resource combinations closer to the origin than the ZNGI. As long as both resource concentrations are higher than the ZNGI, growth is permitted.

It is now important to discriminate between non-substitutable and substitutable resources. In particular plants take up elements that cannot be substituted for one another e. g., even large amounts of nitrogen cannot replace limiting phosphorus. On the other hand, animals get their food in packages that contain many different nutrients. Different types of food may be of different quality, but it might be possible that more of the less valuable food can have the same effect as less of the more valuable one. Hence, these resources are, at least partly, substitutable.

Resource planes for non-substitutable and substitutable resources look different (Fig. 3). The ZNGIs for non-substitutable resources form a rectangular line. Growth ends abruptly

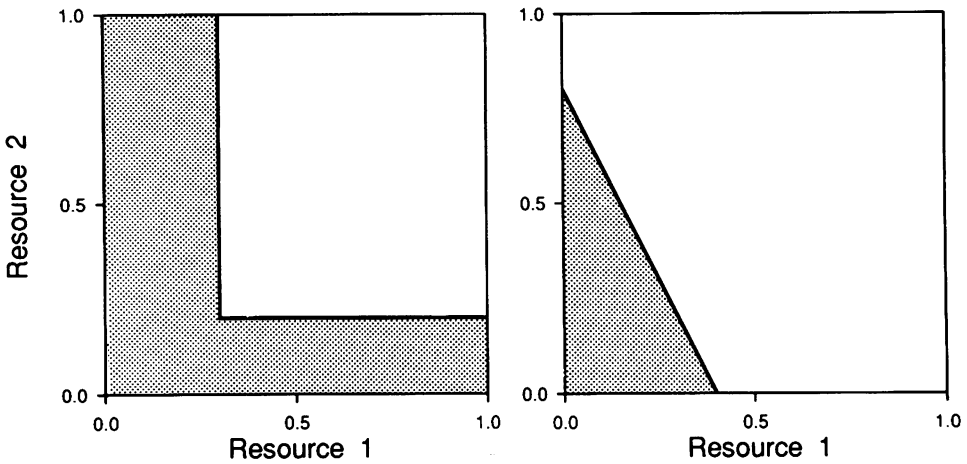


Fig. 3: Resource planes for two non-substitutable resources (left) or two perfectly substitutable resources (right). Any combination of the two resources supplied to the organisms is represented as a supply point on this plane. The zero net growth isocline (ZNGI) separates the white area where a consumer can grow from the shaded area, where no population growth is possible. (after Tilman 1982)

when either of the two resources falls below a certain concentration. A straight line connects the R^* s for the single resources if they are perfectly substitutable. The ZNGI then connects the R^* s for all possible combinations of the two resources. Models for non-substitutable resources have been very successful in predicting the results of competition between plants. In particular, it is possible to predict the dominance of certain guilds or species in phytoplankton from the ratio of the available nutrients (Sommer 1983). Although they are equilibrium models by definition, they can be used for fluctuating resource concentrations (Sommer 1985).

The theory for substitutable resources is not yet as advanced as for non-substitutable ones, but it is of special importance for animal competitors (Rothhaupt 1990a). Only one experiment has been reported so far that demonstrated the applicability of Tilman's models to animals. It has been conducted on rotifers which have a very simple life cycle and can be cultured in chemostat like devices (Rothhaupt 1988). Experimental animals were the pelagic rotifers *Brachionus calyciflorus* and *B. rubens* which have earlier been used in competition experiments by Halbach (1969). The resources were two algae, the small *Monoraphidium minutum* (equivalent spherical diameter 3.5 μm) and the larger *Chlamydomonas sphaeroides* (ESD 12 μm). Preliminary experiments had shown that these resources were in fact substitutable. Growth rates of each rotifer species were identical when they ingested the same amount of carbon regardless of the algal species. However, they did not ingest the same amount when the two species were offered at identical concentrations. *B. calyciflorus* needed a higher concentration of *Monoraphidium* than of *Chlamydomonas* in order to reach the same ingestion rate, but the situation was reversed for *B. rubens*. This difference is caused by the different size selectivities of the two rotifer species (Fig. 4). Offered particles of varying size, *B. rubens* has a maximum of food collection at about 5 μm while *B. calyciflorus* prefers about 10 μm . Hence the efficiency of food collection is higher for *Monoraphidium* in *B. rubens* but higher for *Chlamydomonas* in *B. calyciflorus*.

The ZNGIs for the two rotifer species in the *Monoraphidium/Chlamydomonas* resource plane, thus, have different slopes and intersect (Fig. 5). They delineate four regions. None of the species can grow below both ZNGIs (region A). In region B only *B. calyciflorus* can exist while in region C only *B. rubens* can exist. Stable coexistence is possible at the point of intersection. Region D provides a different situation. When resources are constantly supplied in any combination in region D the populations will grow and, thus, consume more and more

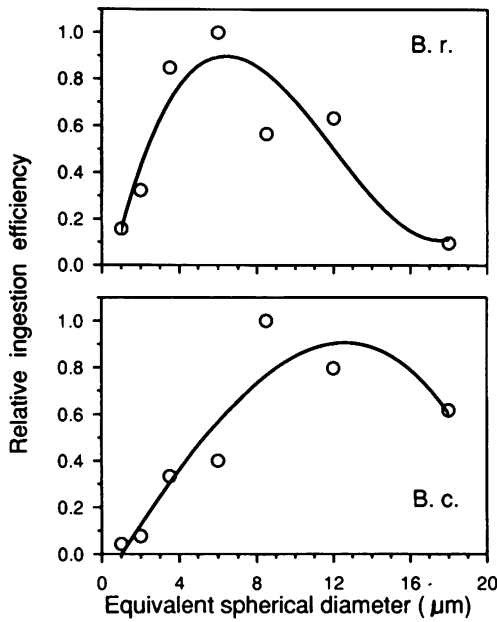


Fig. 4: Particle size selection of two rotifer species feeding on algae of different size. B. r.: *Brachionus rubens*; B. c.: *B. calyciflorus* (after Rothhaupt 1990b).

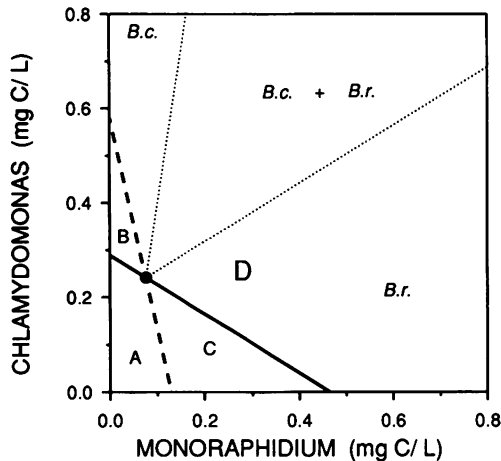


Fig. 5: Resource plane for two rotifer species (cf. Fig. 4) supplied with two differently-sized algal species. The thick lines are the ZNGIs for *Brachionus rubens* (broken) and *B. calyciflorus* (solid). Letters A–D denote differing areas of the resource plane (see text). Area D is separated by the consumption vectors (dotted lines) into three sectors where either only one species (indicated by abbreviated name) can exist or coexistence is possible. The graphical model predicts the result of competition of the two rotifers when food algae are supplied in varying proportions (after Rothhaupt 1988).

of the resources. Consumption and supply will balance each other at the equilibrium point. We can now construct consumption vectors that pass the equilibrium point according to the relative consumption of the two resources by the two rotifer species. These consumption vectors divide region D into three areas. In the area between the consumption vectors, the joint effect of resource supply and consumption moves resource densities towards the point of

equilibrium. Hence, coexistence is possible whenever resources are supplied in a combination as bounded by the slopes of the consumption vectors. Outside this area either *B. calyciflorus* or *B. rubens* wins competition. The model predicts that the result of competition for two resources is only dependent on the supply ratio of the two resources.

This model is based exclusively on physiological properties of the organisms (food selectivity, food conversion to growth, mortality rate). It was tested in competition experiments with varying ratios of the two algae at two loss rates (Rothhaupt 1988). Fig. 6 presents the results which show concordance between model predictions and experimental observations. In eleven out of twelve cases, theory accurately predicted the result of competition which is survival of only one species or coexistence. There was only one case when coexistence was predicted, but *B. rubens* won.

It is interesting to compare the competition experiments of Halbach (1969) and the results of Rothhaupt (1988); both of them used the same rotifer species. Halbach studied the population dynamics of the competing species. He was only able to make an *a posteriori* statement. In the absence of a predator, *B. rubens* always won the competition. This result could have been predicted *a priori* by Rothhaupt's physiological model. Halbach provided *Monoraphidium* as the only food species. In that case the model clearly predicts the exclusion of *B. calyciflorus* (cf. Fig 5). This comparison nicely illustrates the different approaches.

Size selective predators

Two types of predators are important in freshwater planktonic communities: fish (sometimes salamander larvae) and invertebrates. They differ radically in their prey selection and impact on the community. With few exceptions, planktivorous fish are visual hunters. Their feeding success depends mainly on the detection of prey. Larger and more conspicuous prey can be seen from a longer distance and are thus more likely to be eaten. As a consequence fish select for large prey items. Although fish are usually much larger than their prey, so that handling is of minor importance, the evasiveness of the prey must be considered. Among freshwater plankton, copepods usually have stronger escape responses than cladocerans, with the exception of *Diaphanosoma*. Fish not only passively select cladocerans over copepods as they are easier to catch; they even learn that hunting for cladoceran prey is more profitable (Brooks 1968). Persson (1987) showed that the net energy input of planktivorous fish is high-

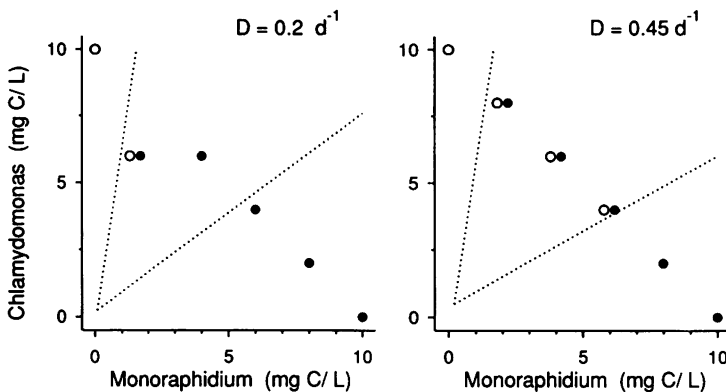


Fig. 6: Experimental test of the predictions generated by the model depicted in Fig. 5. The two algal species were supplied to the two rotifers in different proportions indicated by the circles. The symbols represent the results of the competition experiments (open circle: *B. calyciflorus* wins; closed circle: *B. rubens* wins; both symbols: coexistence). Dotted lines are consumption vectors that separate the areas of exclusion or coexistence as in Fig. 5. Note that Fig. 5 is an enlarged picture of the area close to the origin (see axes). Experiments were run at two death rates (D) (after Rothhaupt 1988).

est when they spend their time searching for large *Daphnia* even if alternative prey is more abundant.

The most important invertebrate predators in temperate plankton communities are *Chaoborus* larvae, carnivorous and omnivorous copepods, and carnivorous cladocerans (e.g., *Lepidodora*, *Bythotrephes*). They do not use optical cues but detect their prey by mechanoreceptors. Although they are usually larger than their prey, they are themselves small and subject to intense fish predation. Contrary to the vertebrates, handling of the prey is the limiting step in the prey cycle of invertebrate predators. Hence they select for small prey items.

Prey selection has been subject to a large variety of ecophysiological models both from the perspectives of the prey and of the predator. Models of optimal prey choice and of constraints to prey selection can be used to generate estimates for the probability of differential mortality of prey types. Therefore they can predict changes in a community under the influence of certain predators. For example, such models have been used to predict the reactive distance of fish to different prey types i. e., the maximum distance where a prey can be attacked (O'Brien 1987). We illustrate this type of model with a typical example for an invertebrate predator.

Pastorok (1981) developed a model for prey size selection of fourth instar larvae of the predacious midge *Chaoborus*. By two pairs of tracheal gas bladders, these larvae can regulate their

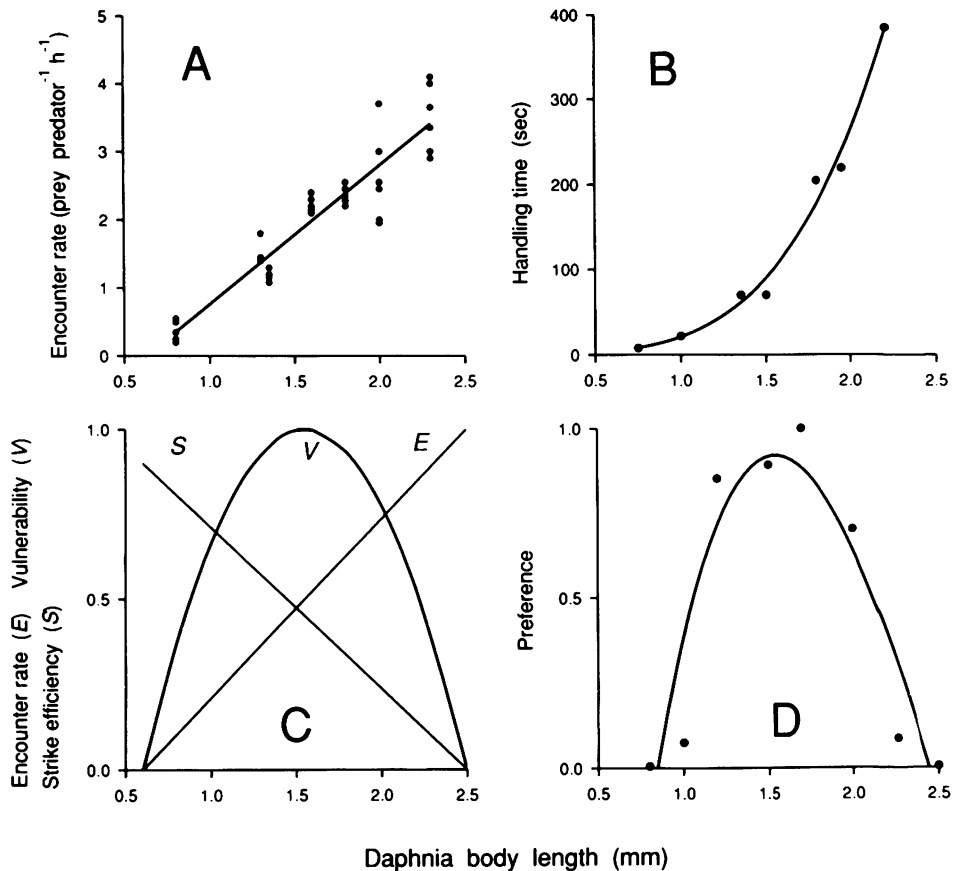


Fig. 7: Model of the impact of fourth instar larvae of *Chaoborus* on *Daphnia* of varying size (after Pastorok 1981). A: Encounter rate increases with prey size. B: Handling time increases with prey size. C: The product of the increasing encounter rate (E) and the decreasing strike efficiency (S) yields the vulnerability (V) of different prey sizes. D: Experimental test of the model. *Chaoborus* larvae select for the predicted size class of daphnids.

buoyancy, so that they act as sit-and-wait predators. They feed on small zooplankton which they recognize by mechanosensors. Important components of the prey cycle are: encounter, strike, handling and ingestion. The model (Fig. 7) describes this sequence in dependence on the size of the prey (*Daphnia*). Large daphnids swim faster than small ones. As the predator waits motionless, the encounter probability increases with the prey size (A). The time needed to handle and ingest a prey increases exponentially with the prey size (B). When the handling time is long, daphnids have a better chance to escape. This affects the strike efficiency (the percentage of strikes to a prey which ends with ingestion), so that it decreases exponentially as handling time increases. As a result, strike efficiency decreases linearly with prey size. Assuming that a hungry predator strikes at every prey, the model (C) now combines the two functions. The product of encounter probability (P) and strike efficiency (E) represents the vulnerability of the prey (V). The model predicts that the predator selects for an intermediately sized prey, not for the smallest. This prediction is confirmed by selection experiments (D).

This model is based on easily measurable behavioral and physiological properties of the predator but its predictions have serious consequences for the structure of a community. Daphnids of the appropriate size will be excluded from the community under pressure of *Chaoborus*. However, we can also conclude from these results that only those *Daphnia* species which have evolved defense structures in the critical size class can coexist with *Chaoborus*. In fact, recent studies have shown that daphnids coexisting with chaoborids are able to respond to the

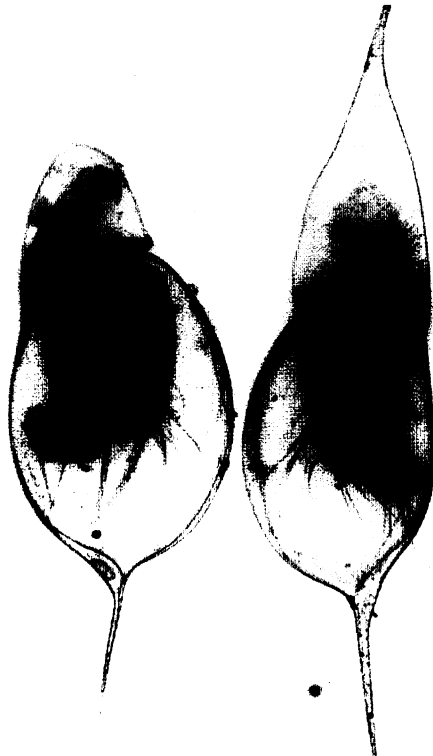


Fig. 8: Phenotypic plasticity of *Daphnia cucullata*. The development of a helmet is induced by a chemical cue released by *Chaoborus* larvae. Body size of *Daphnia* (excluding helmet and spine) 1.2 mm. (Photo: R. Tollrian).

presence of these predators with morphological and life-history changes. The changes are triggered by a chemical cue, a kairomone produced by the predator. The relatively large *Daphnia pulex* which is invulnerable as an adult produces protective «neck teeth» in the juvenile instars (Krueger and Dodson 1981). The smaller *D. cucullata* (Trollrian 1990) and *D. ambigua* (Hanzato 1990) produce bizarre helmets as adults (Fig. 8).

Ecophysiological models of predator-prey interactions have helped increase our understanding of the components of the size-efficiency hypothesis (Hrbáček 1962, Brooks and Dodson 1965) which is probably the most successful concept predicting size and species structure of freshwater zooplankton communities. It has become a paradigm that zooplankton communities consist of small species when planktivorous fish are abundant but of large species in the absence of planktivores.

Optimum life histories

In the center of planktonic food webs zooplankton is faced with changing predation pressure as well as with limited food resources. A species will only be able to persist in a given community if it has adapted to optimize the use of the limiting resources. Energy allocation to growth and reproduction is an important physiological parameter underlying an animal's life history. The differing patterns of energy allocation in different species may, therefore, be used to predict their success in a certain community.

Cladocerans can grow all their life. However, when they reproduce they must invest a large proportion of the available energy into eggs, so that their somatic growth slows down. Given sufficient food, larger cladocerans will have more eggs than smaller ones. This results in the following tradeoff: If the animals mature at a small size and continue to put most of their energy into reproduction they will remain small. Hence they will produce offspring early and have more clutches, but each clutch size will be small. If they delay maturation they will become larger. In that case they will have fewer clutches but more eggs per clutch. We would expect evolution to have favored different life history patterns for communities with differing predation regimes.

The physiology of the cladoceran *Daphnia* is well known and models have been used to describe the energy balance under differing environmental conditions (McCauley et al. 1990). Gabriel and Taylor (1991) and Taylor and Gabriel (1992) used a growth model for *Daphnia pulex* and devoted varying proportions of the total production to egg production. The size specific production rates used in the model have been determined experimentally (Taylor 1985). Fecundities for different stages could then be calculated from the total mass allocated to reproduction and the weight of one egg. Different functions of size specific mortality were constructed to mimic invertebrate, vertebrate and non-selective predation. Energy allocation to reproduction was varied in order to maximize the population growth rate (r). With overlapping generations, r can be used as a measure of fitness (Maynard Smith 1989). It was calculated by numerical solving of the Euler equation (c. f. Fig. 9).

Fig. 9 demonstrates clearly how bottom-up and top-down processes affect the components of the Euler equation and thus r . Food conditions affect the size specific fecundity (m_x) while predation affects size specific mortality i. e., the probability of survival to a certain size (l_x). All the components of the model can be measured as basic physiological functions.

The optimal life history varies substantially for different predation regimes (Fig. 10). Age at maturity is delayed for invertebrate predation and the proportion allocated to reproduction increases through several instars until it reaches the maximum. Daphnids grow fast and obtain a large final size. On the contrary, under fish predation, daphnids mature quickly and allocate nearly all the net production into reproduction already in the last pre-reproductive instar. As a consequence, they remain small. Nonselective predation results in an intermediate life history.

Two important results of the model must be noted: (1) All predation regimes result in a gradual increase of the proportion of net production allocated to reproduction. We do not see

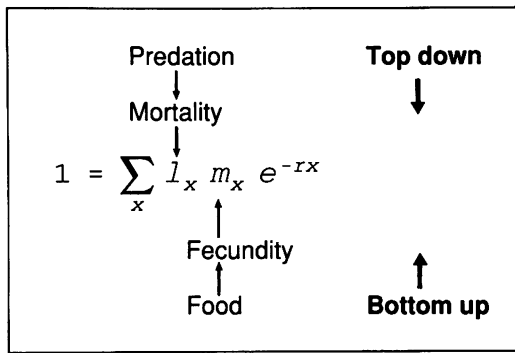


Fig. 9: The Euler equation as the core of a model of optimal life history of *Daphnia*. The model optimizes the rate of population growth (r) by varying the proportion of energy allocated to reproduction under different combinations of bottom-up and top-down forces. Food affects the energy input and, thus, the age specific fecundity (m_x). Size specific predation affects the probability of survival to a certain age (l_x).

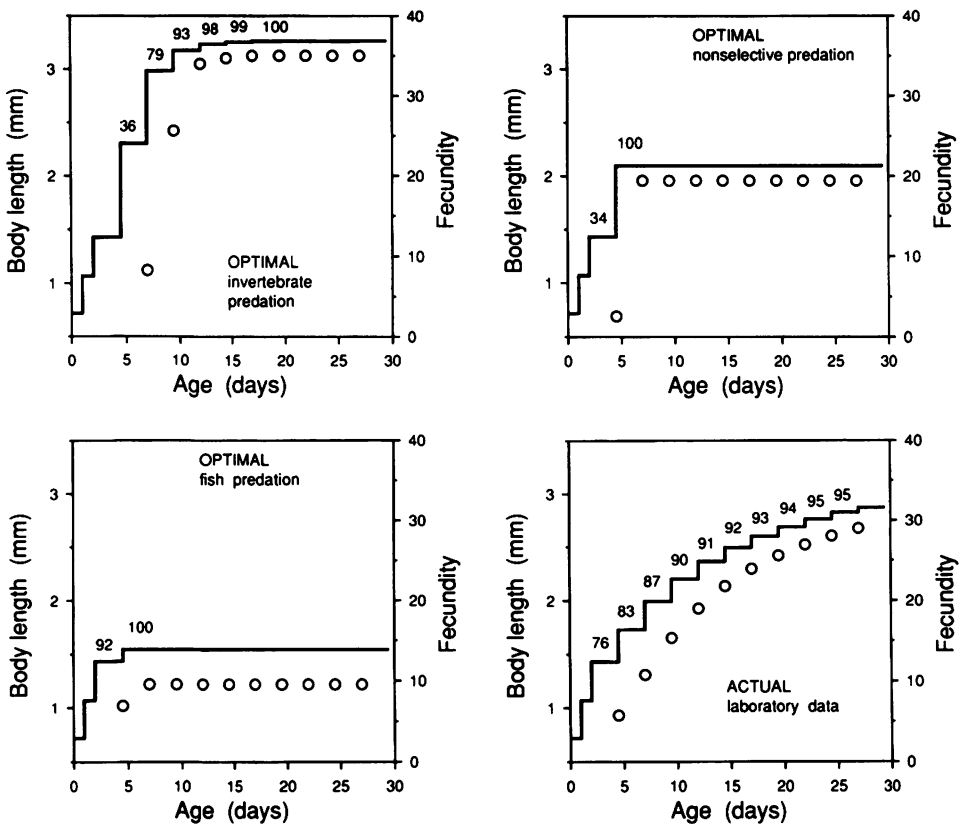


Fig. 10: Optimal life histories of *Daphnia* at high food levels as predicted by the model depicted in Fig. 9 for different predation regimes. The solid line indicates body growth. Each step represents one instar. Open circles denote fecundities (eggs/female). Numbers above the line indicate the proportion of the total assimilated energy allocated to reproduction at the respective instar. The box at the bottom right shows life history data measured in the laboratory for *Daphnia pulex*. (after Taylor and Gabriel 1992).

a perfect «on-off» strategy (i. e., grow first then allocate all energy to reproduction) as has been proposed theoretically (Perrin et al. 1987), although the optimal life history under fish predation comes closest to this pattern. (2) None of the optimal life histories mimics the pattern found for *Daphnia pulicaria* in the laboratory (Fig. 10D). Energy allocation to reproduction increases much more gradually than predicted by the model. This may be a compromise as *D. pulicaria* lives under moderate fish and invertebrate predation. An alternative explanation might be that the laboratory pattern has been obtained in a predator-free environment. The model does not explore in detail the consequences of temporal variation in predation pressure and predation regime for the optimal life history. In a variable environment, the genetically determined life history may just be a template that is phenotypically modified according to the predators present. In fact, it has been shown that *Daphnia* can react to the presence of predators by changing their life history. There is recent experimental evidence that chemical cues from either *Chaoborus* larvae or fish shift the energy allocation pattern in *Daphnia* to the respective direction predicted by the model (Dodson 1989, Stibor 1991, Macháček 1991).

This model describes life history adaptations in a constant environment. Phenotypic reactions or clonal successions may be a response to short term variations of interactions in a community. Restriction to basic physiological properties of the animals is the advantage of the model; it will predict the optimal physiological response regardless of how this response is achieved. We now can define the requirement in terms of life history that a species must fulfill in order to exist in a certain community.

Stage-structured population models

Food web analysis is often hindered as certain species cannot be appointed to a certain category, e. g. they may perform an ontogenetic shift of their feeding habits. Models describing the physiology of such species are more complicated than the ones treated so far, as the impact of environmental factors (e. g. food limitation and predation) can be very different for the different stages of the life cycle. New techniques of stage-structured population modelling (Nisbet and Gurney 1986) help to overcome this problem.

Cyclopoid copepods are an important component of freshwater communities with physiologically distinct age classes. Nauplii and small copepodites are herbivorous while CV cope-

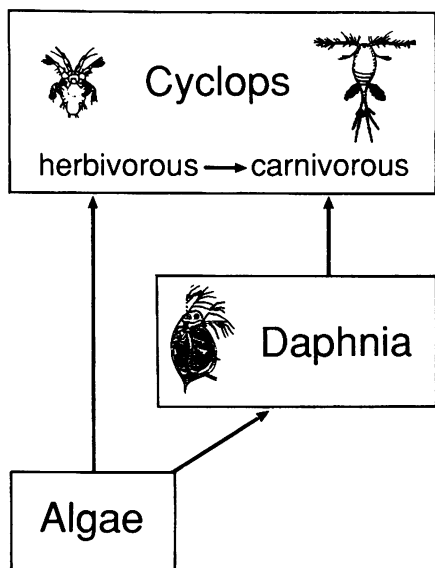


Fig. 11: Changing interactions due to an ontogenetic shift of cyclopoid copepods. Nauplii and small copepodites compete with *Daphnia* for algal food. Adult *Cyclops* prey on neonate *Daphnia* but at the same time on their own larval stages.

podites and adults are carnivorous. Intermediate copepodite stages gradually take more animal prey. This leads to changing interactions in a plankton community (Fig. 11). Herbivorous cyclopid stages compete with *Daphnia* for common resources (algae). Carnivorous stages, however, prey on small daphnids and may be able to control a *Daphnia* population. Moreover, carnivorous stages can prey on their own nauplii i.e., they are cannibalistic. A stage-structured physiological model has been constructed to study the boundary conditions of this system and in particular the impact of cannibalism (van den Bosch and Gabriel 1991, Gabriel and van den Bosch 1991).

This model can be visualized as a conveyor belt system (Fig. 12). Each stage is represented by its own belt. The copepod model discriminates between five stages after the nauplius has hatched from the egg. Nauplii and CI/CII copepodites and CIII/CIV are considered herbivorous. CV copepodites are partially predacious and adults are obligate carnivores. When an individual ages within its stage it moves on the conveyor belt to the right until it falls onto the next belt i.e., enters the next stage. During their movement on the belt individuals gain weight, but some of them die. A series of differential equations describes input and losses from the single stages. The length of the conveyor belt represents the duration of this stage. It enters the equations as a time lag. In contrast to compartment models, the dynamics of the age structure in each stage is fully covered by the model equations.

Mortality of cycloids in each stage consists of two components, a stage-specific natural mortality and a mortality imposed by predators (carnivorous stages). The difference between the rate of recruitment into a stage (from the upper belt) and the transfer rate (to the following belt) describes the dynamics of a stage of the *Cyclops* population. The number of eggs recruited into the first stage is calculated from the total food uptake of the adults. Food uptake consists of alternative prey and of young cycloids. Alternative prey populations (other than *Cyclops*) are assumed to follow a logistic growth curve. The predators' food uptake follows a Holling type II functional response, which depends on prey densities (alternative prey plus cannibalized stages). Hence cannibalism is a function of total prey abundance and the proportion of alternative prey. All parameters needed for the model (e.g., functional response, food conversion, stage durations) can be measured in physiological experiments. The model is quite

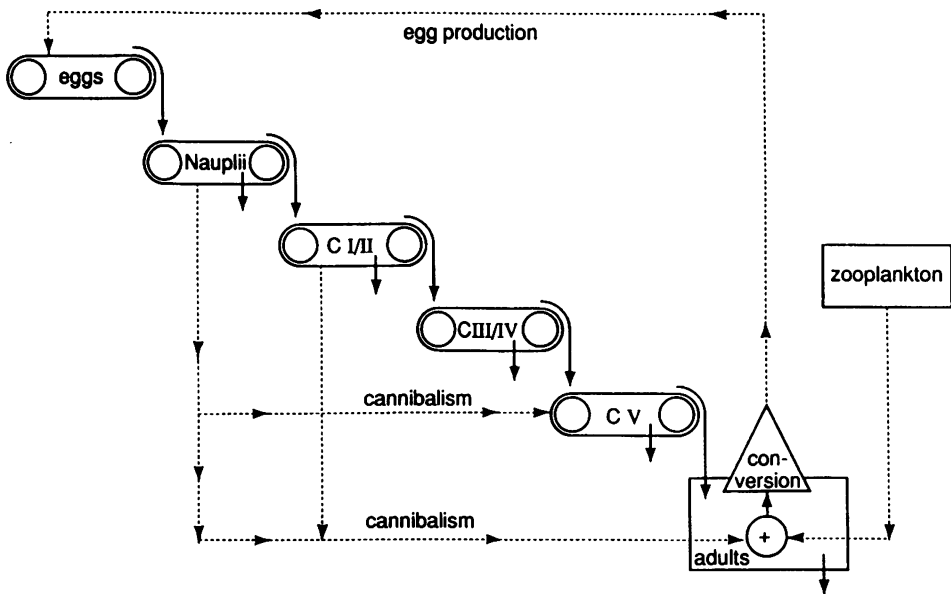


Fig. 12: Stage structured model of the *Cyclops* population visualized as a series of conveyor belts (after Gabriel and van den Bosch 1992).

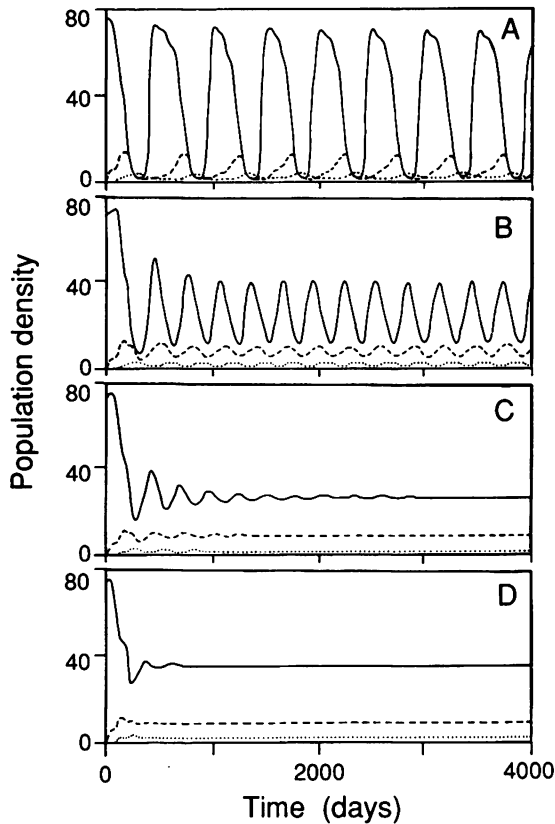


Fig. 13: Time course of predator and prey populations predicted by the stage structured population model for various degrees of cannibalism. Solid line: prey (zooplankton); broken line: *Cyclops* nauplii; dotted line: adult predators. A: no cannibalism; D: model uses attack rates on nauplii as measured in the laboratory; B: attack rates 40% of laboratory measured values; C: attack rates 60% of laboratory measured values (after Gabriel and van den Bosch 1991).

complex as it consists of 29 differential equations, most of them with time delays, but appropriate software for integration on personal computers is available.

We can ask this model several questions. For example, it can be hypothesized that a cyclopoid population can live without alternative prey only by cannibalism. The young stages may gain energy from primary producers, then the adults can consume this energy by preying on the young. Model calculations (Gabriel and Lampert 1985), however, show that this is only possible if adults suffer a size specific mortality.

Fig. 13 presents another interesting result of the stage-structured model. It shows the time course of predator and prey populations under varying degrees of cannibalism. Predator prey cycles with very high amplitudes are observed in the absence of cannibalism. Such large oscillations bear the risk of extinction by random fluctuation. Increasing cannibalism reduces the fluctuations and finally leads to dampened oscillations. When attack rates on nauplii as measured in the laboratory are entered, the model predicts a rapid transition from fluctuations to a stable equilibrium (D). Cannibalism has a strong stabilizing effect on the population (see also Gabriel 1985), although even in the latter case the predacious cyclopoids live mainly on other zooplankton and gain less than 10% of their energy by cannibalism.

Perspectives

The typical experimental approach to community ecology are manipulations of single components of the food web in order to study the effects of the disturbance on other components. In lakes, for example, nutrients may be added to study bottom-up forces or predacious fish may be added to study top-down forces. The results are not always conclusive and sometimes difficult to interpret. Conclusions drawn from such experiments are *a posteriori* explanations.

Physiological models of interactions can be very useful to make *a priori* predictions of the effects of manipulations. Although there are «real difficulties in applying food web theories to the real world» (Power 1992), there is also some hope that we will be able to estimate which connections in a food web are possible or important and how these connections will change under temporal and spatial heterogeneity.

Including ideas of evolutionary ecology helps to reduce the degrees of freedom in constructing communities. The key is an approach to physiological ecology that follows the (slightly modified) definition of Krebs (1985): «Natural selection is ecology in action».

Hence there are close links between physiological ecology, evolutionary ecology and genetics. The optimality approach as used in the models presented here assumes that natural selection has already shaped all interactions. But we must not forget that evolutionary changes can take place very rapidly in ecological times. Quantitative genetics have been successful in modelling complex traits that are usually determined by many genes e. g., environmental tolerance and reaction norms (Gabriel and Lynch 1992). These models have a strong implicit connection to physiological ecology even if they are quite abstract at first glance. They may help to build a theoretical framework for a better understanding of the adaptability of organisms in an interacting community.

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