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Energy flow and community structure in freshwater ecosystems

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Abstract. The goal of this article is twofold: 1) It aims at providing an overview on some major results obtained from energy flow studies in individuals, populations, and communities, and 2) it will also focus on major mechanisms explaining community structures. The basis for any biological community to survive and establish a certain population density is on the one hand energy fixation by primary producers together with adequate nutrient supply and the transfer of energy between trophic levels ('bottom-up effect'). On the other hand, predator pressures may strongly control prey population densities one or more trophic levels below ('top-down effect'). Other interpopulation effects include competition, chemical interactions and evolutionary genetic processes, which further interact and result in the specific structuring of any community with respect to species composition and population sizes.

Key words. Ecosystem; biological community; energy flow; energy budget; plankton; daphnids; *Ancylus*; snails; benthic invertebrates; threshold concentration; 'bottom-up' vs 'top-down effects'.

Ecosystems, communities, and energy flow: a short historical survey

Natural aggregations of different species in a common habitat that interact with each other within this area, are called a (biological) community. Ever since freshwater systems have been considered as ecosystems or communities (e.g. refs 29, 16, 17), scholars of freshwater ecosystems (i.e., limnologists) have been looking for general principles underlying structure and function of communities. It was the notion of 'productivity', which has been forwarded by various early limnologists some 60 to 70 years ago (e.g. refs 14, 83) and which later led to the concepts of energy budgets[28] and energy flows in ecosystems. In 1942, R. L. Lindeman[39], following collaboration with G. E. Hutchinson, emphasized the general principle of productivity changes (and thereby energy flow changes) in ecosystems over time and argued for a combined study of abiotic and biotic aspects of energy-based ecosystem research.

Ecosystem energy flow is mostly driven by the fixation of light energy by autotrophic organisms (plants or bacteria), followed by the transfer of biochemically usable energy (energy-rich organic bonds) through heterotrophic populations of various species. Along the path from autotrophs to various consumers, a dissipation of energy is observed at each step. The series of steps or trophic levels is referred to as a food chain, and the number of trophic levels is designated as the length of a food chain, disregarding the fact that most food 'chains' are actually part of more complex (non-linear) food webs. Empirical assessments, especially from freshwater biota, indicated that the ecological efficiencies, based on ingestion rates between consecutive trophic levels, are roughly on the order of 10%, explaining energetically what had long been known as the Eltonian pyramid (for more detailed analyses of efficiencies, see below). The most widespread number of trophic levels, not only in freshwater, but also in marine and above-ground terrestrial food chains is from three to four, with variations from one to six levels (e.g. ref. 57). However, it should be noted that various freshwater systems are not directly based on sunlight fixation, but rather on the supply of fixed organic energy from outside the system. This holds true, for example, for forest rivers and ponds with a strong supply of dead leaves, for aquatic systems with anthropogenic organic debris, and for underground aquatic systems.

Another important compartment of aquatic energy flow – studied only for about twelve years in more detail – is dissolved organic matter ('DOM'), released from algal (especially phytoplankton) exudation or leakage. The return of DOM to the conventional or classic food chain (e.g., phytoplankton – zooplankton – fish) has been termed the 'microbial loop' and was first studied in the ocean by Azam and coworkers[5]. According to these authors, the carbon and nutrient flows within the microbial plankton community are tightly coupled, and the dynamic behavior of the loop is basically the result of three processes: commensalism (production of DOM by phytoplankton and utilization by bacteria), competition (for nutrients between bacteria and phytoplankton, which is influenced by substrate availability), and predation (by flagellates, ciliates and other microzooplankton, which provides the feedback of nutrients and some DOM). Various factors may strongly influence pathways of carbon flow (and thereby energy flow) within microbial components of pelagic communities in freshwater and marine ecosystems. One of these factors is temperature (e.g. refs 69, 22), another one is presence or absence of certain keystone herbivores, like *Daphnia* vs. *Diaptomus* (e.g. ref. 64).

Although there were attempts to quantify energy budgets for whole freshwater systems as early as 1940[28], energy-based concepts of ecosystems have been predominantly theoretical for a long time[39] and not really based on detailed energy flow studies within communities or populations. First profound empirical investigations appeared in 1957. One was by Teal[82] on a temperate cold spring system, the other and more well-known one by H. T. Odum[52] on a subtropical large flowing spring, the Silver Springs in Florida.

Energy flow as an important ecological determinant and the correlations found between energy flow analyses and various parameters of successional and (so-called) 'mature' stages led to the notion of community and ecosystem 'strategies'. For instance, E. P. Odum[51] pointed out that communities tend to change during their physical existence from simple food chain-based ones to complex food-web structures, and from less stable to more stable communities. This probably represented the final period in which ecosystems were considered as 'community organisms' with features like individual growth, mature stages, and age. The 'superorganismic school', initiated by Forbes' later papers, and influencing also the European limnologists E. Naumann and A. Thienemann, had a long tradition[54]. The increased complexity (and stability) of mature ecosystems and communities was considered to be linked to an increased information content of the systems, and hence to increased feedback loops, leading to a high level of self-organization within the community[41,42]. This basically holistic approach proved useful for heuristic reasons[1], and strongly favored a systems approach to ecological theory.

The weakness of this approach became obvious after it was shown that increased complexity does not necessarily mean increased stability against external disturbances, and that the analogy between trophic interrelationships and mechanical webs is inadequate (see May[43]). Nonlinearity in interrelationships may easily result in an unpredictable behavior of a system in space and time. Further, genetic processes had been completely overlooked so far in ecosystem analyses. Thus, it became clear that interacting processes of the ecosystems would have to be studied in much more detail, as external forces may influence subsystems with unpredictable consequences for the whole system. Therefore, beside the holistic approach, an analytical or reductionist approach to ecosystem analysis is equally necessary and must include intra- and interspecific competition, herbivore-plant and predator-prey interactions, parasite-host relationships, chemical interferences, genetic heterogeneity, selection and hybridization processes, and impacts from invading species of other geographical areas.

Table 1. Examples of classical energy flow studies from the late 1950's to the late 1970's.

- measurements of primary and secondary production of whole ecosystems[52,82]
- measurements of energy budgets of individuals and populations and relating them to the overall ecosystem energy flow[62,45,9,37,15,60,84,50,53,71,72,73,87,44]
- calculating ecological efficiencies within and between populations[59,91,10,71]
- studies on the use of primary production by consumers as well as the use of food by each consecutive trophic level[19,71]

A great many detailed studies of individual- and population-based energy budgets (see table 1), general ecophysiology, of theory and field observations on population density regulation, as well as various aspects of community ecology have been performed in the past decades, which allow us to draw detailed pictures and quantitative estimates of interactions in freshwater populations, although many fundamental principles remain unresolved or under debate. In the following, I will first focus on some selected topics of classical energy flow studies, and then relate the results to aspects of population biology and community analyses.

Bioenergetics of planktonic and benthic invertebrates in an ecological context

Freshwater communities and their ambient water solution represent a highly dynamic ecological system, where physical, chemical, and biological interactions occur. Not only are the relative positions of particles and chemical substances in the plankton and benthon changing over time, but also numerous chemical and biological interactions are going on simultaneously. Biological interactions occur through contact, predation, parasitism, and various kinds of biochemical effects.

In order to analyze biological and ecological systems from a systems theory approach, compartmental theory has turned out useful, and became generally used in the late 60's. An important introductory book at that time was 'Multicompartment models for biological systems' by Atkins[4]. By the mid-70's, compartmental theory had come into general use in ecological turnover studies of organisms (e.g. refs 34, 71), and was soon applied to the study of uptake of nutrients and xenobiotics by freshwater organisms (see also Streit[78] for a general overview).

Systems were divided into a series of compartments for the purpose of studying fluxes of elements or energy between them. Energy-based compartment analyses frequently used trophic levels as compartments or subsystems of the whole community. The system could thus be characterized by the number of compartments, and the fluxes of energy between them. The energy compartment approach, however, will always be but one side of a combined energy and nutrient flux approach. In an ideal autonomous ecosystem, nutrients are actually cycling (in contrast to the energy flow), whereas in river systems it is more adequate to talk of elemental 'spiralling'.

The energetic approach helps explain, how many organisms, in terms of individuals and biomass, are sustainable by the energy input, and the successive transfer and splitting up of the energy flow. However, it is the species assemblage itself that determines the direction of the energy flow from the primary producers, either towards primarily herbivorous or primarily detrivorous species. Specialized consumer species, especially among the top carnivores, can often exert strong influence on the species assemblage and the numerical dominance or destruction of populations within the community (top-down effect). Normally, bottom-up and top-down effects are interrelated in a complex way and not easily separable. Therefore, it may be more useful to look at the food web as an entire topological figure[38], where the interrelationships are variable functions of various other parameters, such as temperature, food patchiness, activity of predators, and genetic shifts (as observed, for example, in temporal hybridization processes in zooplankton[81]).

Traditionally, freshwater ecologists have focused their studies on either plankton organisms, which are more

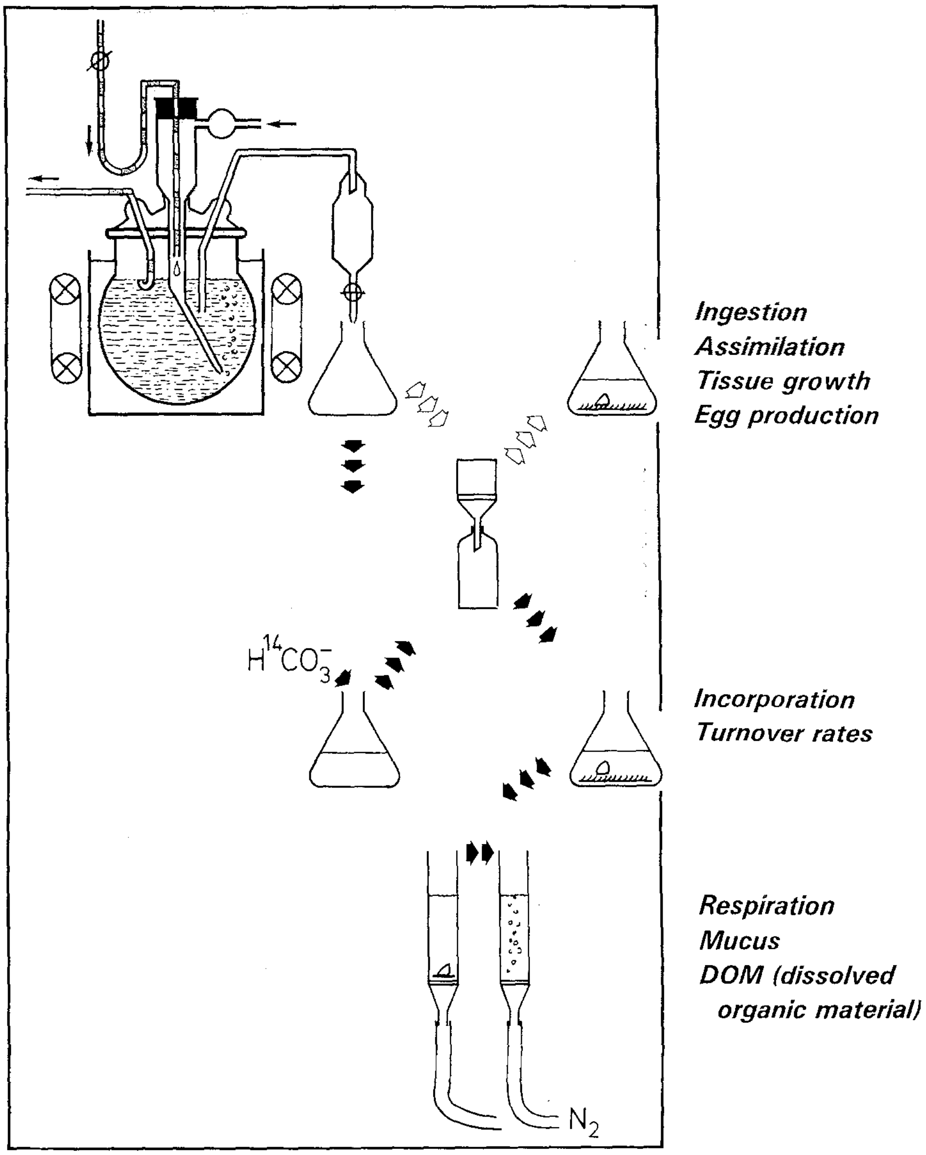

Figure 1. Diagrammatic representation of an experimental design to study energy budgets of benthic grazers (ancylid limpets) using ^{14}C labelled and non-labelled algae. *The upper part* shows cultivation of algae in a chemostat and offering algal layers attached on millipore™ filters to limpets within 100 mL wide-mouth Erlenmeyer flasks. Comparing ingestion, assimilation, growth of soft body and shell, and egg production allows calculation of an energy budget for various sizes and temperatures. *Middle part*: ^{14}C labelled algae demonstrate allocation of organic material into individual organs and into eggs, and also allow estimation of organic carbon turnover rates in whole animals and in single organs. *Lower part*: Tracing the fate of ^{14}C released by the animal into the water allows estimation of the relative importance of respiration, mucus secretion, and passive loss of soluble organic substances. Adapted from Streit[76].

or less easy to handle, or have predominantly studied benthic organisms. Both, empirical handling and conceptual development seem to be somewhat less established for freshwater benthic communities than for plankton communities. A very general experimental design frequently employed to measure energy uptake and conversion through individuals of aquatic grazers in the laboratory is depicted in figure 1.

Among major plankton animal taxa studied in detail are: water fleas (e.g., the pond-dwelling *Daphnia pulex*, *Daphnia magna*, the lake-inhabiting small-sized *Daphnia longispina* group) and other crustaceans (*Diaptomus*, *Cyclops*); rotifers (e.g., *Brachionus*, *Keratella*, *Synchaeta*, *Polyarthra*, *Asplanchna*), ciliates; and various groups of heterotrophic and mixotrophic flagellate algae/protozoans.

Major benthic groups, which have been studied, include, e.g., freshwater limpets (especially *Ancylus* and *Ferrissia*) and the zebra mussel (*Dreissena polymorpha*), several species of aquatic insect larvae (e.g., *Ecdyonurus*, *Stenonema*, *Acroneuria*, *Potamophylax*, *Agapetus*, *Stenonema*, *Dinocras*, *Perlodes*, *Pteronarcys*, *Lestes*, *Pyrrhosoma*, *Hydropsyche*, *Odagmia*), as well as crustaceans (*Gammarus*, *Hyalella*, *Asellus*), annelids (*Tubifex*) and others.

Despite the structural and functional complexity of interactions encountered in all ecosystems and additional unique features in each single system, a number of generally-applicable parameter estimates characteristic of different kinds of population interactions has been worked out. Those most widely used are 1) assimilation efficiencies of herbivore, detritivore and carnivore species, indicating the ratio between assimilated energy (i.e., absorbed energy through the gut wall) compared to ingested energy; 2) ecological efficiencies (comparing corresponding parameters in populations of consecutive trophic levels, such as ingestion, assimilation, or production of the two levels); 3) productivity-to-biomass ratios (P/B ratios) for various populations.

Primary productivity figures of natural freshwater lakes and rivers (though in part polluted or eutrophicated) vary between ca. 5 and 6400 mg carbon per square meter and year, i.e. more than one thousendfold (see, e.g., Pimm[57] for an extended survey). Assuming 1 mg $C/(m^2 \times yr)$ organic carbon to correspond to about 60 $J/(m^2 \times yr)$, this would correspond roughly to 0.3–380 $kJ/(m^2 \times yr)$. The lower figures represent ecosystems with severe nutrient deficiency (i.e., extreme oligotrophic conditions), the upper figures represent the physiologically maximal photosynthesis rate under high nutrient supply (i.e., under highly eutrophic conditions). (Note that energy fluxes are often expressed in carbon units in limnology, abbreviated as 'C', as measurements are frequently based upon dry or wet combustion techniques. These include heating in an oven and transferring organic carbon into CO_2, or oxidation of organic carbon by means of dichromic acid or another reducing chemical. The general use of carbon units instead of pure energy units, such as joule, is adequate also, because there is a good correlation between biochemically usable energy content of an organic compound and its percentage of carbon.)

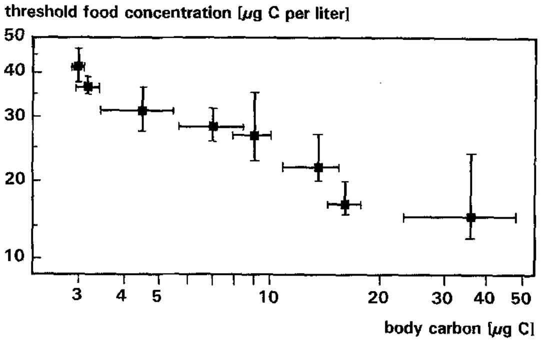

Figure 2. Threshold food concentrations for various species of Daphnidae (Genera *Daphnia* and *Ceriodaphnia*) taken as the intercepts of the regression lines with the zero growth level plotted against species-specific body size expressed as body carbon of 6-day-old animals grown at high food concentrations (green algae). Adapted from Gliwicz[21].

Secondary production naturally varies at least as much as primary productivity figures, and food-web structures are naturally highly diverse, in that other species of algae or macrophytic plants will dominate in systems with a high nutrient (eutrophic systems) supply, compared to those with a low nutrient supply (oligotrophic systems). A general relationship between primary productivity of aquatic ecosystems and food chain length has not been established, and may not exist. The change in the food-web structure, including both the primary producer and consumer populations, will in any case be the prominent difference between eutrophic vs. oligotrophic conditions. In lakes, it has generally been found that under low nutrient conditions, copepods dominate over other planktonic forms, whereas under eutrophic conditions, one finds primarily cladocerans, especially daphnids.

In a very general sense, there is an extensive niche overlap between species especially in the plankton (but also in the benthon) communities, because all algae have basically similar nutrient requirements and many planktonic grazers have similar preferences for food particle sizes. Hutchinson has called this the paradox of the plankton[27]. There is, however, at least a partial separation between different species of algae as well as between different species of grazers: Whereas the phytoplankton species may exhibit species-specific preferences for nutrient concentrations (e.g., high or low phosphate concentration) and vary in their competitive capacity against other species, the zooplankton grazers may prefer slightly different food items in terms of size (e.g., maximum length of diatoms), quality (e.g., excluding cyanobacteria), and quantity (different threshold concentrations).

For planktonic grazers, such as diaptomids, daphnids and the majority of rotifers, there exist characteristic threshold concentrations, the minimal concentrations needed to sustain a population. Under steady-state and low-mortality conditions, this concentration is approximately 0.01 to 0.04 mg C per liter for *Daphnia*/*Ceriodaphnia* species of different body sizes (*Daphnia magna* being the largest, *Ceriodaphnia reticulata* the smallest species[21]; fig. 2). For planktonic rotifers, the corresponding figures range from 0.03 mg C per liter in *Keratella cochlearis* to 0.4–0.5 mg C per liter in *Keratella crassa* and *Brachionus rubens*; thus the range for rotifers is shifted toward more eutrophic conditions. Especially when considering the range of preferred food sizes, there is a partial niche separation between the different groups: Rotifers belong to the microzooplankton preferring small particles as a consequence of their specific filtering mechanism, similar to ciliate protozoa and nauplii larvae of copepods. Cladoceran and the post nauplian stages of copepods belong to the macrozooplankton, posessing a filtering apparatus adapted for larger food particles.

The grazers among the zooplankton are actually omnivorous, rather than purely herbivorous, and typically feed on a variety of food particles of adequate size, including various heterotrophic forms such as flagellates or even detrital particles. Bacteria will also be taken up passively, as they are frequently attached on these detrital particles. Nevertheless, various zooplankton species are capable of actively rejecting individual items, e.g., cyanobacteria, which are usually of low nutritional value.

In addition to herbivore body size, which is usually important in separating food preferences of closely related species or between juveniles and adults, the difference in special food-gaining mechanical structures is important. Some members of the zooplankton can thus actually mechanically destruct large algae. In the benthic community of lotic environments, limpets (*Ancylus*) may be able to feed from lower concentrations of periphyton than Ecdyuronidae larvae[77].

Table 2. Parameters of individual energy budgets for four different freshwater invertebrates: *Daphnia* (water-flea), *Hyalella* (a North American amphipod), and *Ancylus* (a European limpet)

units	*Daphnia* [µg C/h]	*Hyalella* [µg C/h]	*Ancylus* [µg C/h]
food source	green algae	detritus	diatoms
ingestion	0.90 µg C/h	4.4 µg C/h	6.7 µg C/h
defecations	0.16 µg C/h	3.6 µg C/h	3.3 µg C/h
assimilation	0.74 µg C/h	0.8 µg C/h	3.4 µg C/h
loss through respiration etc.	0.18 µg C/h	0.68 µg C/h	3.0 µg C/h
production	0.56 µg C/h	0.012 µg C/h	0.4 µg C/h
assimilation efficiency	82%	18%	51%
production/ingestion efficiency	62%	3%	6%
production/assimilation efficiency	76%	15%	12%

Data from *Daphnia* and *Hyalella* are based both on figures found in[35]; original source of *Daphnia values* not indicated; those of *Hyalella* based on data by Hargrave[23]. As the latter author did not provide direct assimilation estimates, some assumptions had to be made. Data from *Ancylus* are based on Streit[77]. Energy equivalents of *Hyalella* have been transformed in this table to organic carbon (to allow comparison with *Daphnia* and *Ancylus*) by assuming a conversion factor of 1 J (= 0.24 cal) = ca. 20 µg C.

Table 2 summarizes energetic parameters of individual energy budgets for three different freshwater invertebrates: *Daphnia* (a filter-feeding cladoceran), *Hyalella* (a deposit-feeding amphipod), and *Ancylus* (a periphyton feeding pulmonate snail). As can be seen, not only the absolute values differ between species, but also the respective efficiency coefficients, which are frequently used for ecological considerations: The high production/assimilation efficiency for daphnids (76%) can be considered as the result of the experimental conditions, where only the parthenogenetic stage was considered, which is very efficient in growth. In contrast, benthic invertebrates with more complex environmental conditions show considerably lower figures, as high energy requirements are necessary for locomotion, mucus secretion, reproduction etc.. Further, the life cycle of these latter individuals includes periods of strongly reduced growth, not the constant high growth rate typical for *r* strategy, of which the parthenogenetically reproducing *Daphnia* is one example; including the whole life cycle would reduce their efficiency as well.

Representatives of nearly the whole r-K continuum are found in both, planktonic and benthic communities. An example of an r strategist in the benthic environment is the stage of vegetative reproduction in the oligochaete worm *Stylaria lacustris* (fig. 3). In this species, a continuous ingestion is observed, similar to many parthenogenetic cladocerans and rotifers. The result is a high production efficiency of roughly 34%, hence closer to

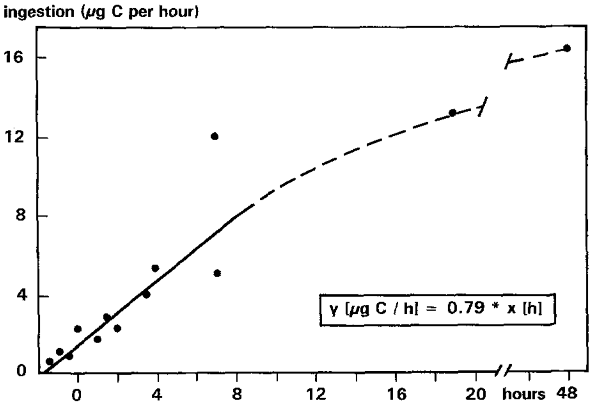

Figure 3. Carbon transfer from the periphyton into a single *Stylaria lacustris* (Naididae, Oligochaeta) chain after different periods of exposure. The linear part represents the ingestion rate per hour, the non-linear part results from partial loss of assimilated ^{14}C through respiration and others means. Note the continuous feeding behaviour of this species. Adapted from Streit[74].

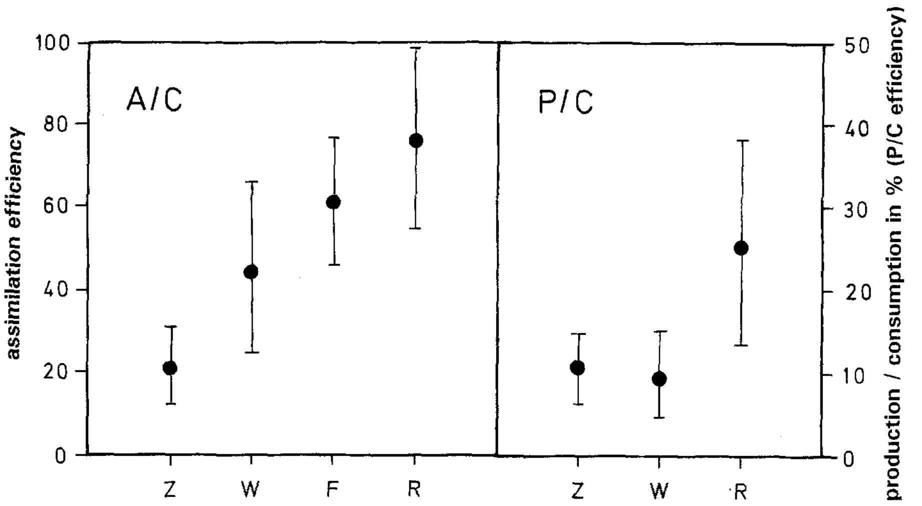

Figure 4. Energetic parameters for benthic freshwater invertebrates of different feeding mechanisms. The two parts of the figure correspond to the assimilation/consumption efficiency (indicating the effectiveness of the digestion process) and the production/assimilation efficiency (indicating the effectiveness of tissue production from ingested food). Adapted from Streit[73].

Left side: Z: Shredders acc. to[2,11,45,50,53,59,86,90]. W: Grazers acc. to[10,33,67,71,84]. F: Filter feeders acc. to[44,66,87]. R: Carnivores acc. to[7,15,25,32,36].

Right side: Z: Shredders acc. to[56,53,60]. W: Grazers acc. to[6,67,71,84]. R: Carnivores acc. to[15,18,25,31,37].

the daphnids' figures than the ancylid/amphipod figures[74].

In general, much of the energy assimilated by an animal is used for respiration; the range of production efficiencies (production to assimilation efficiency, P/A) thus reflects energetic costs. P/A ratio typically ranges from 1%–5% in endothermic birds and mammals (aquatic and terrestrial ones), through approximately 10% in long-lived ectotherms like fish or molluscs, extending even to about 40% for short-living herbivorous invertebrates (episodically even higher; see table 2) and perhaps to 50–60% for some carnivorous invertebrates[47,71,26]. P/A ratio is thus clearly related to general metabolism, to life history traits, and to the food uptake mechanisms, which may use up more or less energy per unit energy absorbed. Further, assimilation efficiency (assimilation/ingestion ratio) will naturally differ in different feeding types, as animal food will often be more easily digestible than plant food. It should be possible therefore to find general properties for efficiencies in different ecological groups of invertebrates. Such groups have been defined for benthic invertebrates by Streit[77] (fig. 4).

In addition to energetic efficiency parameters calculated for within and between populations or trophic levels, other parameters, based on mean biomass of the individual or the populations have been defined and calculated. These ratios are usually called 'specific rates' (specific ingestion, specific assimilation, and specific growth rates of individuals or populations) and are frequently based on a daily period. The most widespread are specific production rates of individuals and populations, for which extensive tables have been compiled[91]. Production to biomass ratios (P/B ratios) on an annual basis have been called 'annual biomass turnover ratios', those on a life-cycle basis of the respective population 'life cycle biomass turnover ratios' (e.g. ref. 9). Annual biomass turnover ratios in freshwater gastropods with an annual life cycle are on the order of 2.6–6.5. Multivoltine species show higher rates, biennial species lower rates[73].

A case study: energy flow in benthic pulmonate snails

Many major studies on individual energy budgets and energy flow in populations were performed during the 1970's, although some go back as far as the late 50's[62,52]. In particular, the energetics of various zooplankton groups (rotifers, cladocerans) have been intensively studied and related to community ecology and life history strategies. I would therefore like to confine myself here to benthic invertebrate studies chosen from extensive experiments with freshwater limpets (Ancylidae). These molluscs are spread all over the world; the polyploid species *Ancylus fluviatlis*, however, is basically limited to Europe. This chapter will first highlight some individual-based results on resource utilization and energy allocation, then focus on ecologcial aspects of bioenergetics, and finally discuss some benthic community interrelationships. The general method employed for individual energy budgets was similar to those used for aquatic invertebrate studies in general, and is shown in figure 1.

Environments for benthic invertebrates are not at all uniform. There are patches of adequate substrate and food supply, and patches that are unsuitable for one reason or the other. Limpets need a firm substrate with an adequate layer of palatable periphyton, consisting either of diatoms, uni- or oligocellular green algae, or other suitable food items, such as lichens[68]. Too low a

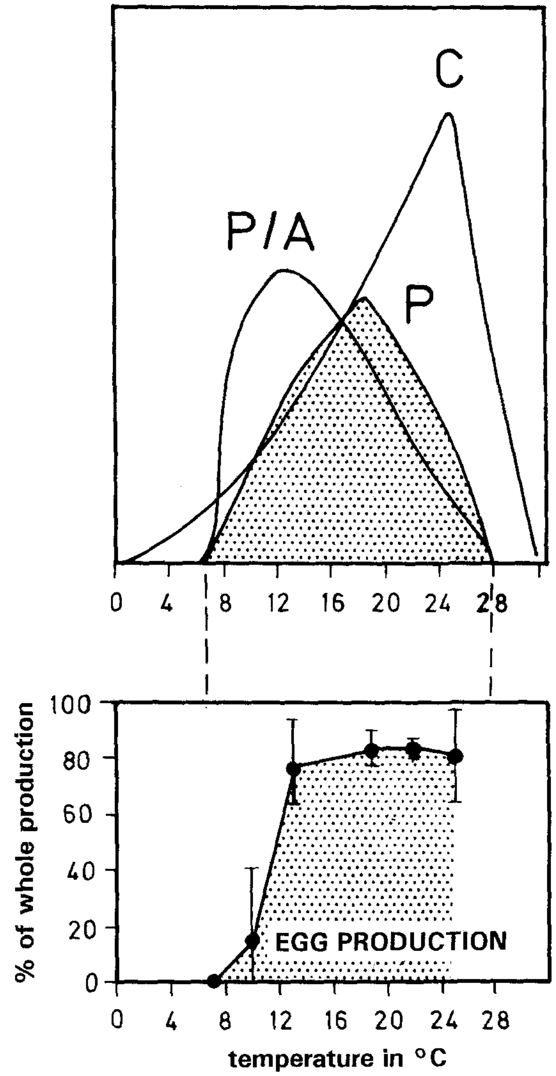

Figure 5. *Top*: Consumption (C), net production (P; growth and egg production), and net growth efficiency (P/A; production/assimilation) as a function of temperature. Scales for the three plots differ. Allocation of production energy into eggs as a function of temperature. The difference to 100% is growth production. Values are for adult limpets. (Streit[72], based on Streit[71]).
Bottom: Allocation of production ('P' in top figure) into maternal growth and egg production in adult *A. fluviatilis* as a function of temperature. Note: The difference to 100% corresponds to the scope for maternal growth at each temperature. Above 13 °C, an average 81.2% is used for egg production, the remainder for growth. Below 7 °C, no eggs are produced. Adapted from Streit[72], based on Streit[71]).

concentration of suitable algae would be below the energetic requirements (as the mass input rate per surface unit is limited), too high a concentration may be unpalatable due to mechanical properties of the radular apparatus.

Selecting four populations from small rivers with slightly different geological and trophic conditions[73] revealed the limpets to occur only on certain areas on rocks and gravels, where algal concentrations were neither too low nor too high[75]. Previous experimental results had shown that optimal concentrations were between about 0.25 and 2 μg C per square millimeter. Suitable rock patches were thus inhabited by a great many individuals at any one time in all of the populations studied; other patches were only transiently occupied by individual migrating between more suitable areas.

Another crucial niche dimension, in addition to food concentration, is ambient temperature. Extensive studies have revealed that the maximum consumption rate in *Ancylus fluviatilis* is found at roughly 25 °C (ref. 71). However, this is not the temperature for maximum growth, which is close to 19 °C; respiration requirements at higher temperatures increase more rapidly than ingestion, in a non-linear fashion. Maximum production efficiency (P/A), however, is still lower and shows its upper value at around 13 °C. (Note that the original measurements were performed in 3 °C intervals; so results should be viewed with this uncertainty; fig. 5, top). The range around 13 °C is actually the temperature observed for many natural habitats of *Ancylus fluviatilis* in the spring, when limpets reach maturity and reproduce. It is this temperature where competition with other grazers (in terms of eggs produced per ingested algal mass) may be strong. Egg production only starts at around 7 to 10 °C and remains at an equal percentage of total production (egg and tissue production) from about 13 °C up to the maximum tolerated temperature of ca. 25 °C (i.e., the allcation between growth and egg production remains constant, fig. 5, bottom).

Autecological aspects, including energy requirements, could thus help to explain the natural occurrence of limpets with respect to environmental factors, such as temperature and food concentration (which is related also to the trophic status and to lotic characteristics of the aquatic ecosystem). But it remained unclear from the data reported so far, why a species with such a low production efficiency compared to various planktonic grazers (cf. table 2) could be a successful grazer in the benthic community.

Later studies[76] revealed, that the low production efficiency seemed to be the result of high energy expenditure for locomotion. The energetic requirements for slugs, limpets and others, is extremely high when compared to other moving animals, since the continuous production and secretion of slime entails a high energy cost (fig. 6). The high locomotion costs are obviously part of the general stuctural and physiological properties of the snail group, as locomotion always is accompanied by simultaneous loss of energy-rich mucus. We currently think that these costs may be outcompeted by a long-time advantage in survivorship. Limpets tend to adhere from time to time on vertical surfaces. This 'stop-and-go' behavior[75] may favor occasional phoretic transport by adequate hosts, such as water beetles or birds and allow colonization of adequate new habitats.

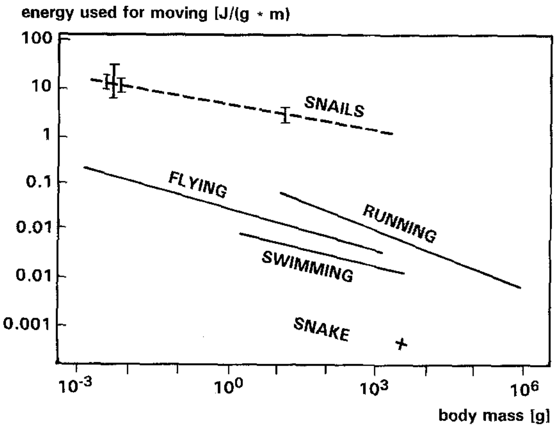

Figure 6. Comparison of energetic costs in terms of J/(g × m) of moving a unit body weight 1 m for different modes of locomotion in multicellular animals of varying fresh weights. The figure summarizes experimental results for snake motility[55], running, flying, and swimming[65], and snail crawling[55,76]. Adapted from Streit[77].

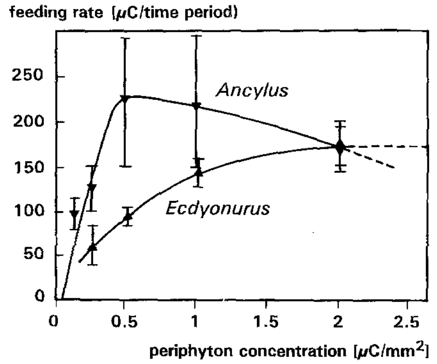

Figure 7. Niche separation between benthic grazers: Feeding rates from *Ancylus fluviatilis* (given as consumption rate per day for a standard limpet of 450 μg C) and for *Ecdyonurus venosus* (given as consumption rate per hour for a standard larva of 2750 μg C) for different algal concentrations. Although the two curves cannot be compared in absolute terms due to the different experimental design and calculation, it is obvious from the general shape of the curves that *Ancylus fluviatilis* is better at exploiting the lower concentration range than *Ecdyonurus venosus*. (Adapted from Streit[73]).

Population-derived energy budgets differ both between species and between populations of the same species. The reason may be genetic differences in energy allocation between populations[46]; other reasons may be found in variable abiotic and nutritional environmental conditions with variable production efficiencies or in variable interactions with competitors and predators. Population-based energy budgets include demographic factors such as mortality rates, and therefore represent part of an ecosystem analysis. A general conclusion from studies like those presented in table 3 is that the results from one population or from one generation (in a multivoltine species) cannot be easily applied to others, but may allow rough estimates from one locality to another. Ancylidae are but one of several grazing species in many river systems; other grazers coexist, including larvae of ephemeropterans and trichopterans as well as other insects. Studies with the larvae of the Ephemeropteran *Ecdyonurus venosus*, conducted by Schweder[67], revealed a somewhat different preference of algal thickness (fig. 7). These larvae pick up algae fast, often at dusk with the help of their maxillae. Consequently, they are capable of living in environments of higher food concentration, are more mobile, and can collect food faster. It is probable, although not proven, that their threshold concentration is higher compared to that of *Ancylus*. Also, ecdynuronid larvae may be more susceptible to organismic drift in rivers compared to ancylid limpets. It is the interface of population biology, physiological ecology, and evolution theory, where we will need more information to understand the whole benthic grazer system.

Synthesis and outlook

Species assemblages and population densities are not fixed structural characteristics of an ecosystem but are subject to temporal variations, which in turn also influence energy paths. A more detailed analysis of energy

Table 3. Population-derived bioenergetics of various populations of ancylid species: *Ancylus fluviatilis*, *Laevapex fuscus*, and *Ferrissia rivularis*, presented as carbon budgets.

		Assimilation mg C/(m² × life span)	Production mg C/(m² × life span)	Eggs produced per adult limpet
Ancylus (Europe)	I	1526	171	66
	II	719	-	-
	III	617	-	-
	IV	1934	229	113
Laevapex (N-America)	A	702	157	27
	B	92	23	13–42
	$C^{1st\ gen}$	408	186	22–34
	$C^{2nd\ gen}$	170	88	55–85
Ferrissia (N-America)	AL	-	-	35
	BC	1250	-	8

From Streit[73]; original figures for *Laevapex fuscus* from McMahon[46], those for *Ferrissia rivularis* from Burky[9]. Note that in *Laevapex fuscus* population C, there was a short-living summer generation (1st gen) and an overwintering generation (2nd gen).

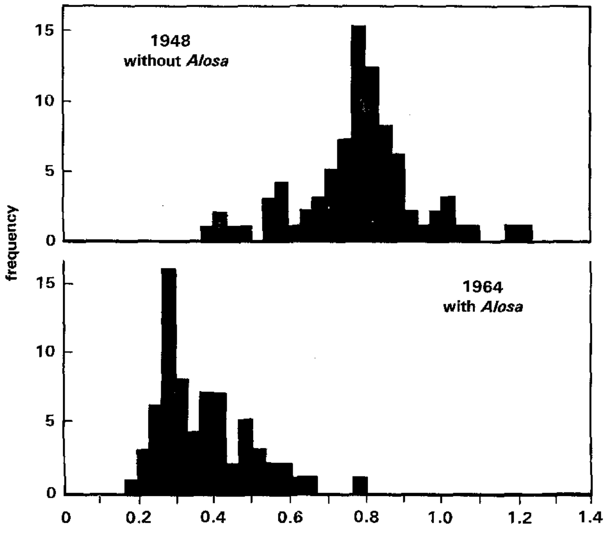

Figure 8. Size distribution of the mainly crustacean zooplankton of Crystal Lake, Connecticut (USA) before (1942) and after (1964) introduction of a planktivorous fish, *Alosa aestivalis*. The effect of the fish has been to replace a community of large species by one comprised of smaller species. (Adapted from Brooks & Dodson[8]).

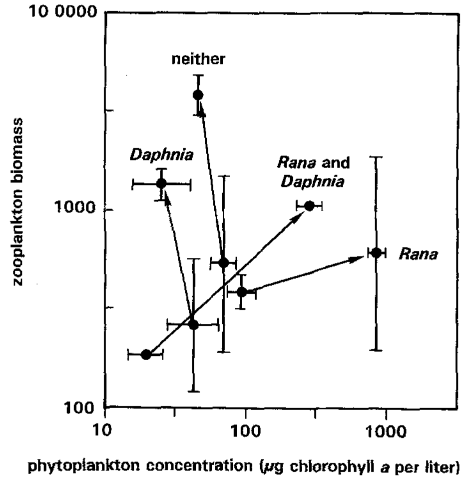

Figure 9. $\log_{10}$ of phytoplankton density vs. $\log_{10}$ of zooplankton density (exclusive of *Daphnia*) in each food-web at both nutrient levels. Arrows point from low nutrient to high nutrient conditions for each of four webs. Each arrow is labelled by indicating the occurrence of *Rana* and *Daphnia*. Hatchling *Rana ultricularia* tadpoles and 100 *Daphnia laevis* were introduced in all four combinations of occurrence. Populations were allowed to develop for 30 days in order to attain substantial zooplankton populations before the addition of nutrients to the high nutrient tanks. (After Leibold & Wilbur[38]).

flow will therefore have to be based on selected concepts of population biology and community ecology. One possible approach is to consider communities and energy flow as fluctuating arrangements, which may be modified into new structural assemblies, caused by, e.g., abiotic changes, by invading species, or simply for stochastic reasons. In the following I will give examples:

Among zooplankton, seasonal patterns of relative species abundance and size distribution are frequently encountered. A common shift is from predominance of large species early in spring to smaller ones as the summer progresses. Explanations include different grazing efficiencies between various forms and variable predator pressures: The predominance of smaller taxa seems to be related to selection by planktivorous fish species for the larger prey, which they can visually localize more easily when feeding. In 1965, Brooks & Dodson[8] introduced the so-called 'size-efficiency hypothesis', based on observations of plankton communities after the introduction of a planktivorous fish species into a lake where there had been no planktivorous fish (fig. 8). They believed that all zooplankters competed for the 1–15 μm particulate matter in the water, but that the larger zooplankters were more successful. Small animals were thus thought to be excluded by starvation if large ones were present. Fish (and also amphibians) select the larger Crustacea (cladocerans, calanoid copepods), and, depending on the intensity of predation, smaller zooplankters (smaller crustaceans, rotifers) could co-exist up to the state of complete elimination of the large forms where predation was intense.

Recent studies have also revealed the direct influence of chemical interactions by invertebrate and vertebrate predators on the final size of *Daphnia* species[70]. *Daphnia hyalina* transferred into 'conditioned water' (previously in contact with predatory fishes) will allocate less energy into growth and thus remain smaller. Invertebrate predators, such as *Chaoborus* larvae, tend to elicit the opposite allocation shift. Such a physiological and life history response may be looked upon as adaptive, since the reduction in body size seems to be an adequate avoidance mechanism against fish predators; but the alternative strategy will probably be adaptive in defense against the relatively small-sized *Chaoborus* larvae, which do not filter, but catch prey items individually.

There are, however, not only interrelationships between the different trophic levels within the consumer food-web, but also between primary producers and the various consumer levels. An example of complex relationships between nutrients (and consequently primary production) and phytoplankton density was presented by Leibold & Wilbur[38], though only on a phenomenological basis: They found that the zooplankton biomass in mesocosms (tank experiments) could either increase or diminish after addition of nutrients, depending on the food-web structure. For instance, in those experiments where either *Rana* alone, or *Rana* and *Daphnia* together, were present, phytoplankton concentration increased, but when only *Daphnia* alone, or neither of the two grazers were present, phytoplankton concentration decreased, due to complex interactions with the other zooplankton representatives (fig. 9).

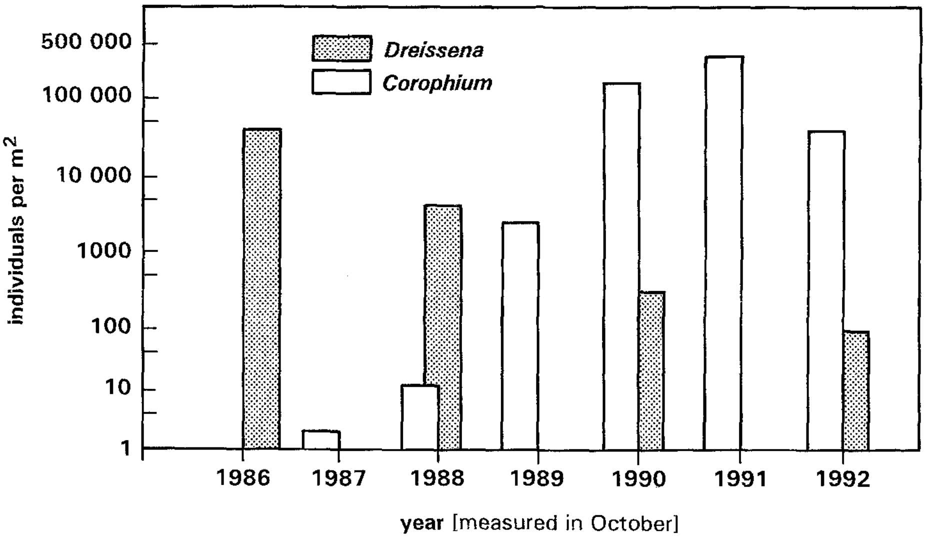

Figure 10. Population explosion of *Corophium curvispinum* in the lower Rhine (Lobith/Rees) and decrease in zebra mussels (*Dreissena polymorpha*) based on maximum densities per m^2 stone area. (From van der Velde et al.[85]; for 1989 and 1991 no data on the density of *D. polymorpha* were available).

These results illustrate that differences in food-web structure, similar to those documented in natural communities, can dramatically alter energy flow.

Another aspect of increasing complexity in freshwater systems is the colonization by species from other areas. Especially in major river and lake systems with high vessel traffic, invading species are changing communities fundamentally, and are frequently replaced themselves after some time by new invaders. For instance, zebra mussel (*Dreissena polymorpha*) invasions were recorded already in the late 19th century in central and western European rivers and lakes, and considerably increased in number in the 1970's. In North America, this ponto-caspian species invaded the Great Lakes system in 1985/86 and immediately became a pest, with densities in some cases of more than 700 000 individuals per square meter. In Europe however, especially in the Rhine River system, populations have started to decline in the 1980's, due to several factors: In the Lake Constance area, a high predator pressure has been reported, resulting from feeding by coots (*Fulica atra*). In the Lower and Middle Rhine, their densities have declined due to the invasion of a filter-feeding competitor, the amphipod species *Corophium curvispinum* (van der Velde et al. 1994; fig. 10).

Gammarus species composition has equally undergone changes in the Rhine River. The North American species *Gammarus tigrinus*, immigrant in Central Europe, has largely replaced autochthonous species, such as *G. fossarum* (and *G. pulex*, where originally occurring). The reasons for its colonization success may lie in the higher tolerance of temperature, salinity, and selected chemicals, like organophosphorous insecticides[79]. Currently, the invasion of still another *Gammarus* species (*G. ischnus*) seems to reduce *G. tigrinus* densities substantially – this time possibly caused by special features of life history of this last arriving species, such as a faster generation cycle.

In order to jointly study energy flow through communities with population biology, future research programms will usually have to include aspects that were often neglected in the past. Among them are the following:

1) The interrelationship between nutrients, phototrophic production, heterotrophic microbial production, and consumer ingestion rates. The complex interactions between bottom-up and top-down impacts on freshwater community structures may thus become more tractable (e.g. refs 48, 63, 38).

2) Studies on interactions between different taxonomic and ecological groups competing for resources should be extended, such as those between macrozooplankton and microzooplankton (e.g. refs 24, 89), daphnids and rotifers (e.g. ref. 12), rotifers and ciliates[20, 3], zooplankton and heterotrophic microorganisms (e.g. ref. 30), benthon and the pelagic food web[58]. Planktonic and benthic studies should be based on common models, hypotheses, and concepts.

3) Studies will have to focus on joint effects of chemical effects between species, individual energy allocation, and life history traits of interacting populations and species (e.g. refs 49, 13, 40, 70).

4) The use of non-equilibrium models in experiments may prove fruitful for future studies. Empirical studies will then have to take into account issues of the chaos theory when discussing heterogeneity in space and time. Spatial heterogeneity, genetic heterogeneity, genetic exchange at various levels (e.g., introgression), parasitism (parasitized vs. non-parasitized populations), and processes of selection and species rearrangements as the

consequence of invading species on a world-wide scale will be important (e.g. refs 88, 61, 85, 80).

5) From a methodological standpoint, successful studies in the future will make necessary the use of various levels of approach, combining experiments i) from detailed microcosm experiments in the laboratory, ii) mesocosm studies, iii) field studies, and iv) using novel methodologies, including molecular techniques, to allow new approaches to population ecology.

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