



Why plankton communities have no equilibrium: solutions to the paradox

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Abstract

In a classical paper, Hutchinson (1961) argued that the large number of species in most plankton communities is remarkable in view of the competitive exclusion principle, which suggests that in homogeneous, well-mixed environments species that compete for the same resources cannot coexist. Few ideas in aquatic ecology have evoked more research than this 'paradox of the plankton'. This review is an effort to put the main solutions to the paradox that have been proposed over the years into perspective. Hutchinson himself already suggested that the explanation could be that plankton communities are not in equilibrium at all due to weather-driven fluctuations. Subsequent research confirmed that such externally imposed variability can allow many species to coexist. Another important point is that in practice the homogeneous well-mixed conditions assumed in the competitive exclusion principle hardly exist. Even the open ocean, for instance, has a spatial complexity resulting from meso-scale vortices and fronts that can facilitate coexistence of species. Perhaps most excitingly, theoretical work on species interactions has given a counter-intuitive new dimension to the understanding of diversity. Various competition and predation models suggest that even in homogeneous and constant environments plankton will never settle to equilibrium. Instead, interactions between multiple species may give rise to oscillations and chaos, with a continuous wax and wane of species within the community. Long-term laboratory experiments support this view. This chaotic behavior implies among other things that plankton dynamics are intrinsically unpredictable in the long run when viewed in detail. Nonetheless, on a higher aggregation level, indicators such as total algal biomass may show quite regular patterns.

Introduction

Plankton are a crucial component of aquatic foodwebs, and a popular object of study for experimental as well as theoretical ecologists. The (seemingly) homogeneous nature of plankton communities and the (seemingly) simple character of the participating organisms suggest that they are easy to understand in comparison to spatially complex terrestrial ecosystems. Indeed, plankton are often proposed as a useful 'paradigm'

for more complex ecosystems (McCauley & Murdoch, 1987). However, even these relatively simple communities appear to be of a dazzling complexity when viewed in detail. In practice, algal dynamics are mostly studied at highly lumped levels. Although usually a distinction between the major taxonomical groups is made, neither eutrophication models nor descriptive studies of lake phytoplankton do often go down to the species level. The reason for lumping algal species is obvious. At a high aggregation level, the

response of the communities to events such as a bio-manipulation is quite predictable (Gulati et al., 1992). However, when viewed in detail, the algal community of the average lake consists of hundreds of different species, and dynamics on the species level are usually very erratic (Cottingham, 1996).

In a classical paper entitled *The paradox of the plankton*, Hutchinson (1961) drew attention to the fact that the high diversity of phytoplankton is really remarkable. There seems not much room for niche specialization in this relatively homogeneous environment where everyone is competing for a few limiting nutrients and light. Indeed, simple competition models and laboratory competition experiments suggest that the number of species that can coexist in equilibrium cannot be greater than the number of limiting resources unless additional mechanisms are involved (Tilman, 1977, 1981; Sommer, 1985, 1986; Rothhaupt, 1988, 1996; Scheffer et al., 1997a; Huisman et al., 1999). Hutchinson himself already offered an outline of potential explanations of his paradox. Importantly, he suggested that, in general, the plankton community might not be in equilibrium at all:

“Twenty years ago in a Naturalists’ Symposium, I put (Hutchinson 1941) forward the idea that the diversity of the phytoplankton was explicable primarily by a permanent failure to achieve equilibrium as the relevant external conditions changed.” [Hutchinson, 1961, p.138].

Although, with this non-equilibrium argument, the issue of Hutchinson’s paradox may seem solved, the question remains what actually drives the non-equilibrium dynamics. Indeed, Hutchinson’s suggestion, namely the continuous variation in environmental conditions, due to the seasonal cycle and less predictable factors like the change in weather and hydraulic conditions, is the most obvious explanation (Hutchinson, 1961; Richerson et al., 1970). However, intrinsically generated non-equilibrium dynamics are likely to make a major contribution as well (Armstrong & McGehee, 1980; Scheffer, 1991; Huisman & Weissing, 1999). On top of that, spatial heterogeneity is an important reason to expect coexistence of species. Even in seemingly homogeneous environments such as the open ocean, meso-scale vortices and fronts generate transport barriers preventing complete mixing and competitive exclusion (e.g. Bracco et al., 2000). Here, we neglect the extensive literature on spatial aspects, but review the field of chaos, disturbance and diversity in plankton communities in an attempt to put

the various arguments in the ongoing discussion into perspective.

Seasons and the weather; the external noise

Seasons are an obvious reason why there can never be a real ‘equilibrium of nature’ in most ecosystems. The role of seasonality has been neglected largely by theoretical ecologists working with simple models. However, field biologists have analyzed seasonal patterns in great detail. As pointed out by Sommer and Reynolds, the seasonal succession of algal species is comparable in many aspects to succession in terrestrial vegetation, although the time scales differ widely (Sommer, 1991; Reynolds, 1993). The typical generation time of algae is about a thousand times shorter than that of terrestrial plants. Therefore, one summer in plankton dynamics is comparable to many centuries of terrestrial succession. In fact, Reynolds (1993) argues that what happens between two winters in plankton is comparable to what happened since the Weichselian glaciation period in temperate forests. Indeed, there are remarkable similarities between seasonal succession in algae and the succession patterns described for terrestrial plant communities. The ‘colonizers’ that start off the succession sequence are small rapidly growing species, while the species that dominate at the end of the succession in summer are large, shade-tolerant algae that grow slow, but are well able to conserve biomass and nutrients. The sequence of algal groups that appear in the course of the seasonal succession depends on aspects like lake depth and nutrient status. Although there can be differences from year to year, the overall pattern of biomass and succession of dominant groups is more or less predictable in most lakes (Sommer et al., 1986).

On top of the regular annual cycle driven by the gradual change of temperature and light during the year, there is a continuous weather related ‘disturbance’. Meteorological events like heavy rainfall, hot weather periods and stormy days can have a pronounced impact on hydraulics, light conditions, water temperature and nutrient supply. Such short-term variability can be thought of as setting back succession, and thus preventing one species from outcompeting the rest. Indeed, fluctuating nutrient and light conditions suffice to prevent equilibrium conditions leading to competitive exclusion in the lab (Van Gernerden, 1974; Sommer, 1985; Grover, 1989; Litchman, 1998). Thus, also in real lakes, weather related disturbances

are thought to be important in keeping algal communities diverse and dynamic (Padišák et al., 1993; Flöder & Sommer, 1999).

Chaos; the internal noise

It is usually thought that in the absence of any externally imposed disturbance the algal succession should in one or two months lead to a stable state in which most species have been outcompeted by one or a few dominants: “. . . undisturbed successions should eventually approach competitive exclusion and ecological equilibrium” (Reynolds et al., 1993). However, as we explain in this review, recent model analyses and laboratory experiments point out that plankton would probably remain fluctuating erratically even if, by some miraculous event, the environment would become completely constant and uniform. This is because, as discussed further in the next section, feedback in the plankton system itself generates complex dynamics preventing the system from coming to rest.

Consequently, what we see in real lakes may well be the behavior of an intrinsically chaotic system in a fluctuating environment. It may be argued that in the end there is not much difference between intrinsic chaos or the effect of fluctuations in the environment, since for all practical purposes the result is just some sort of noise. Conceptually, however, the phenomenon of intrinsic chaos has important theoretical implications: Firstly, the final state (‘asymptotic regime’) to which a chaotic system settles in the absence of perturbations is a so-called strange attractor. Simulations with most dynamical systems that had been studied before tended to a stable equilibrium point (‘point attractor’) or a regular cycle (‘cyclic attractor’). A chaotic system, however, tends to a state of continuous change in which the same pattern is never exactly repeated (‘strange attractor’) although a rough periodicity is clearly detectable. A second important feature of a chaotic system is that small differences in initial state blow up exponentially with time. This implies that the long-term time course is unpredictable. Even if we would know exactly the rules that govern the plankton community, the time course of the community remains unpredictable, because we can never precisely determine the current state and even if we could, the slightest perturbation has huge effects on the long term. Thus, if plankton systems are indeed chaotic, the discussed weather effects will tend to blow up with time, and long-term predictab-

ility on the species level seems unlikely. To phrase it otherwise: chaotic systems are ‘noise amplifiers’ that magnify perturbations; non-chaotic systems are ‘noise mufflers’ that dampen perturbations (Ellner & Turchin, 1995).

Causes of chaos

Trophic interactions and the coupled oscillator analogy

The idea that the dynamics of natural communities are intrinsically chaotic stems mainly from the results of analyses of simple models. It is known long since that chaotic dynamics can arise from a variety of trophic interactions, such as a consumer exploiting two competing preys (Vance, 1978; Gilpin, 1979; Takeuchi & Adachi, 1983), two consumers exploiting two separate but competing prey species (Alekseev & Kornilovsky, 1985; Vandermeer, 1993), and a predator on top of a simple consumer-food system (Hogeweg & Hesper, 1978; Hastings & Powell, 1991; Kuznetsov & Rinaldi, 1996; DeFeo & Rinaldi, 1998). Although all of these interactions are potentially seeds of chaos, models for each of them only produce chaotic behavior for a restricted range of parameter settings. Some specific plankton models such as a model of *Daphnia* preying on competing cyanobacteria and green algae (Gragani et al., 1999) indicate that chaos may indeed be expected for realistic conditions. However, it is difficult to extrapolate such findings for plankton interactions in general. Going into the details for any specific model appears not to be very illuminating, but there is an interesting generic rule to be learned from physics in this context: systems that contain interacting oscillators can easily show chaotic dynamics (Rogers, 1981; VanBuskirk & Jeffries, 1985). As predator-prey interactions have a strong tendency for cyclic dynamics, oscillators may be considered abundant in communities based on multiple phytoplankton species and zooplankton species. Obviously, these predator-prey oscillators are coupled since there are large overlaps in food among the different zooplankton species (Brooks & Dodson, 1965; DeMott, 1982; Boersma, 1995). Hence, it seems reasonable to expect plankton dynamics to be intrinsically chaotic, just because there are many ‘oscillators’ around.

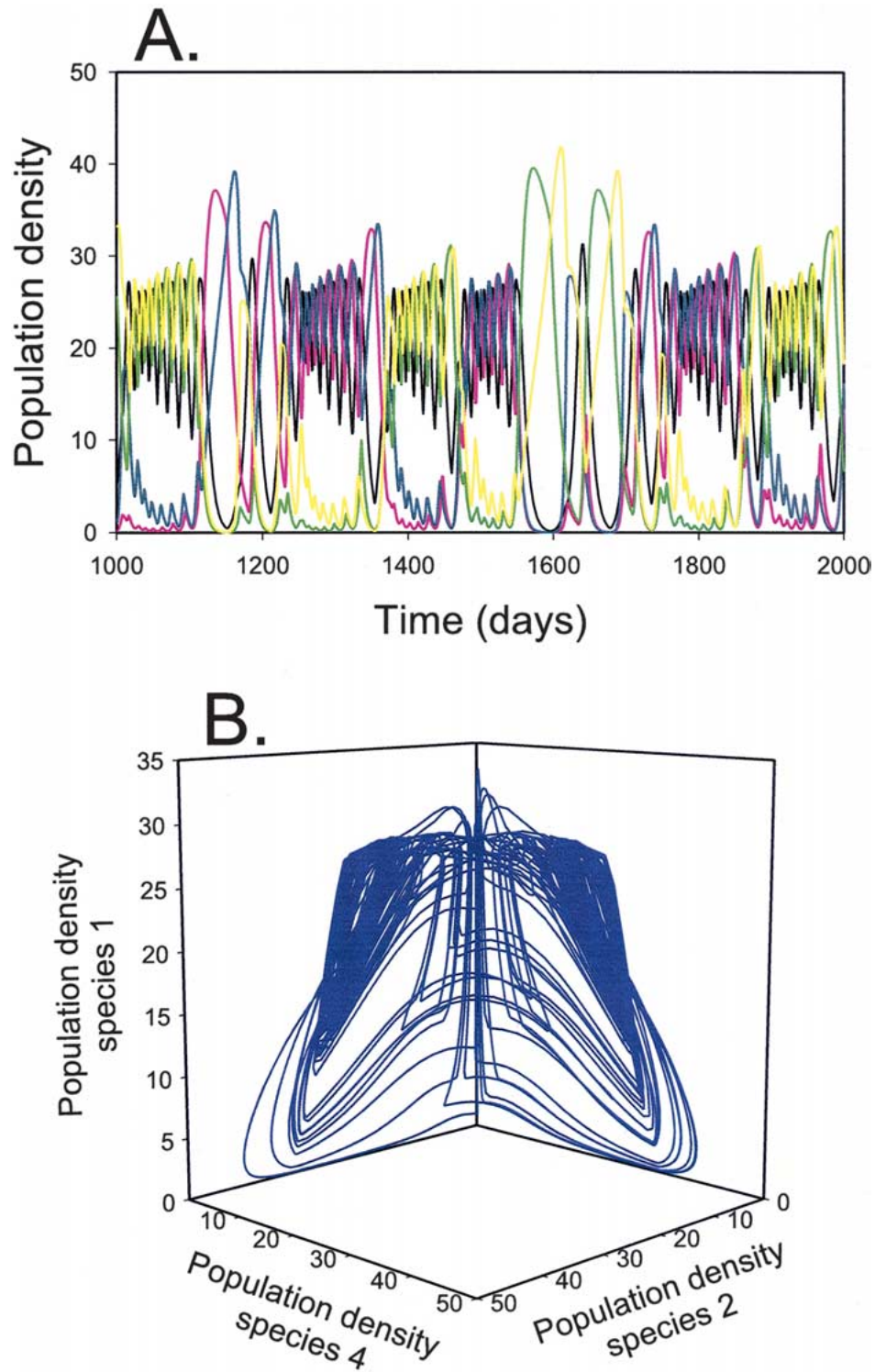


Figure 1. Competitive chaos of five species competing for three resources. (A) Time series of population densities of the species. (B) The corresponding chaotic attractor, shown by plotting the population densities of three of the species. Redrawn from Huisman & Weissing (2001a), with permission from University of Chicago Press.

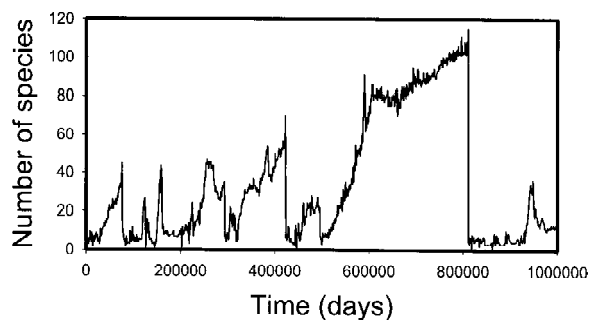


Figure 2. Competitive chaos of multiple species competing for three resources. The simulation starts with a single species at day 0, and a new species is added once every 50 days. The species parameters are drawn randomly under the constraint that species have a cyclic relation in their competitive abilities. The graph shows the resulting diversity. Redrawn from Huisman et al. (2001), with permission from Blackwell Science Ltd.

Competition

In addition to trophic interactions, it has been shown that multispecies competition can lead to chaos as well. The minimum number of interacting populations required if simple Lotka-Volterra competition is assumed is four (Arneodo et al., 1982). Although a full-fledged strange attractor can be produced for the four species case, the chaotic behavior in this Lotka-Volterra model appears to be rather fragile (Scheffer, 1991). The basin of attraction of the strange attractor is small so that a disturbance might easily kick the system out of its chaotic behavior in which case it degenerates into a stable one-species case. Furthermore, the chaotic behavior is easily lost if parameters are modified. Therefore, it does not seem very likely that a four-species system like this will display chaotic behavior in the real world. It has, however, been proved that competitive interactions of five and more species can lead to any type of behavior including chaos, and that complex dynamics become more likely if more competing species are involved (Smale, 1976). Obviously, the number of algal species in an aquatic system is generally much larger than four or five, and it might, therefore, well be that even if there is no detectable impact of zooplankton, algal communities can behave chaotically.

An important recent contribution to the discussion about chaos in communities of competing species comes from model analyses by Huisman & Weissing (1999, 2001a). They found that competition for limiting resources easily leads to chaotic dynamics if multiple species compete for at least three resources

(Fig. 1). This is obviously a common condition in nature, and may therefore apply to a wide range of situations. A major point is that this behavior is quite robust, in the sense that it occurs over a relatively wide range of parameter values (Huisman & Weissing, 2001b) and for different mathematical formulations of resource competition (Huisman & Weissing, 2002). The authors also confirmed by means of simulation experiments that the strange attractor can indeed facilitate coexistence of many more species (Huisman et al., 2001). Competing species can persist in great numbers in this chaotic situation (Fig. 2).

Interestingly, for certain species combinations, the multispecies system may collapse after a long period of transient chaos, so that in the end only one or a few species survive. In this case, it might be fundamentally impossible to predict which of the species will be among the survivors (Huisman & Weissing, 2001a). The reason for this complexity is that there might be multiple potential winners present within a diverse community. Which of these potential winners takes the lead, depends on infinitesimally small differences gained during the period of transient chaos. In technical terms, there are multiple attractors, and the basins of attraction that determine which attractor wins are intermingled in a fine-grained fractal geometry ('fractal basin boundaries'). An example is shown in Figure 3. Here, eight species compete for three resources. Among these eight species, there are three potential winners. In the end, only one of the species wins. But which one? It turns out that, due to the fractal nature, the tiniest change in initial conditions may lead to a different winner. Thus, in practice, if such fractal structures govern competition, it is fundamentally impossible to predict in advance which of the potential winners finally becomes dominant.

Seasonal forcing

Since, as argued, interactions of oscillators can lead to chaos, it is not surprising that inclusion of the seasonal oscillation of light and temperature in models that already generate cycles under constant conditions may generate chaos. Indeed, seasonal forcing can cause even a simple predator-prey model to behave chaotically (Rinaldi & Muratori, 1993; Rinaldi et al., 1993). Models of seasonally forced plankton dynamics confirm that chaos can be expected for parameter values that reasonably mimic natural situations (Doveri et al., 1993; Scheffer et al., 1997b). However, such models also indicate that over a large range of parameters

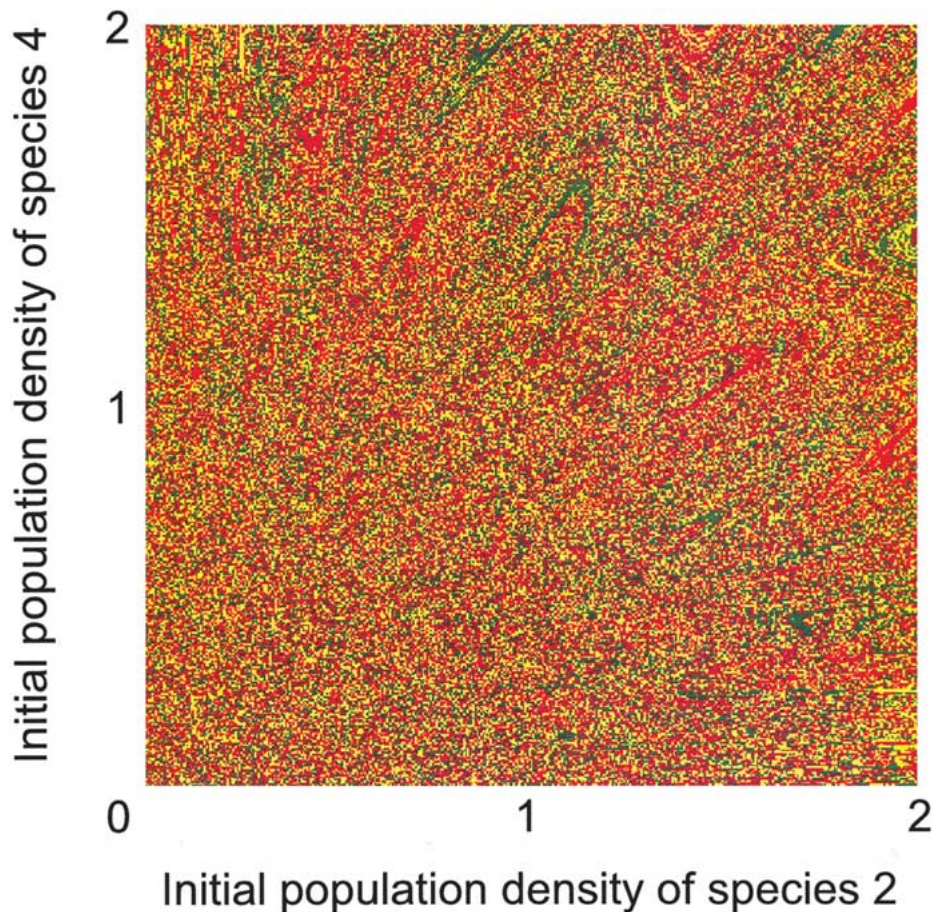


Figure 3. Fractal basin boundaries, generated by eight species competing for three resources. The colors indicate which of the eight species will win if a simulation is started from the corresponding initial condition. Yellow = species 6 wins; red = species 7 wins; green = species 8 wins. Redrawn from Huisman & Weissing (2001a), with permission from University of Chicago Press.

simple phase locking occurs. This means that the seasonal forcing is strong enough to let the biological system become ‘locked’ into the seasonal cycle, in the sense that the same dynamics repeat each year with the same timing. This suggests that, at least at the high aggregation level used in such models, seasonal dynamics should be rather predictable. Indeed, seasonal dynamics of chlorophyll *a* and large herbivorous zooplankton can be quite regular (Sommer et al., 1986; Gulati et al., 1990). Also, response of total algal biomass and *Daphnia* to a large-scale climatic oscillation of the North Atlantic System (NAO) show a predictable pattern which can be reproduced by rather simple models (Fig. 4) (Scheffer et al., 2001). The idea that predictability increases with the aggregation level is in line with empirical observations (Cottingham, 1996; Tilman, 1996; McGrady-Steed et al., 1997; Naeem & Li, 1997), and with results from chaotic plankton

competition models that produce an almost constant total algal biomass despite erratic fluctuations at the species level (Huisman & Weissing, 1999).

Empirical evidence for the role of chaos

Obviously, in the real world the ever unpredictable weather always affects patterns of population dynamics quite strongly. Although the weather system itself is chaotic too (Lorenz, 1964), its effects are usually considered as ‘noise’ or ‘random disturbances’ from the ecological point of view. Since intrinsically chaotic systems blow up small effects exponentially with time, it is not surprising that it is far from easy to show the fragile fractal structure of strange attractors in real field data. Over the past decade, an impressive suite of techniques has been proposed to detect the signs

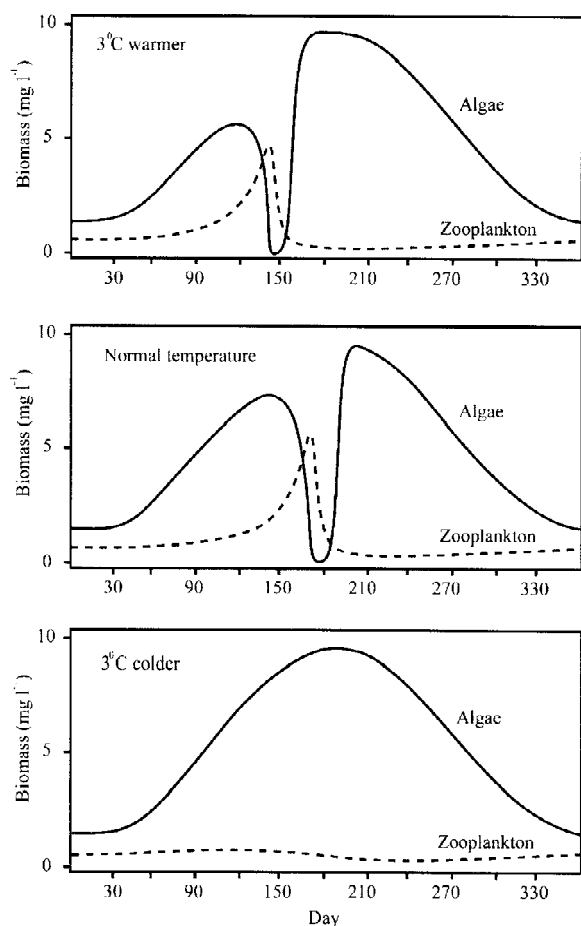


Figure 4. On a higher level of aggregation, plankton dynamics are probably more predictable than on the species level. A simple seasonally forced model of total algal biomass and large herbivorous zooplankton predicts that the spring clear water phase (dip in algae) comes earlier in a warm year (upper panel), and can disappear in a cool year (lower panel). Redrawn from Scheffer et al. (2001), with permission from the American Society of Limnology and Oceanography, Inc.

of chaos in noisy time series (Sugihara & May, 1990; Turchin & Taylor, 1992; Hastings et al., 1993; Wilson & Rand, 1993; Stone et al., 1996; Bjørnstad & Grenfell, 2001). Although each of these approaches has certain advantages over its predecessors, we are still faced with the disappointing conclusion that none of them is really powerful. Data requirements are simply very large, and noise in the measured data can easily give misleading results (Lloyd & Lloyd, 1995). Indeed, strict separation of noise and chaos in ecological systems is probably very difficult, and perhaps also unnecessary or even misleading (Ellner & Turchin, 1995).

The most obvious approach to answering the question if plankton communities would behave chaotically even if we would eliminate all external disturbances to a system is to just try it experimentally. Already in the 1970s and 1980s, scientists were starting up experiments with small aquatic model ecosystems ('microcosms') that have been kept undisturbed in the laboratory for as long as 10 years (Ringelberg, 1977; Kersting, 1985; Heerkloss & Klinkenberg, 1998; Fernández et al., 1999). These laboratory ecosystems generally consist of micro-organisms like bacteria, phytoplankton, and zooplankton. Apart from a few perturbations that are unavoidable over such long time periods, temperature and light are kept constant and the systems remain closed. Nonetheless, these systems typically do not settle to a stable state, but instead keep exhibiting irregular dynamics throughout the whole observation period (Fig. 5). The exact mechanisms that underlie the non-equilibrium dynamics in these laboratory experiments are not known. The fluctuations may be caused by multispecies competition for limiting resources. They may also result from predator-prey or host-parasitoid interactions. Most likely, the fluctuations are caused by interactions among a large ensemble of species, and it will be difficult to pinpoint a particular species interaction as the most responsible perpetrator. One thing is certain, though: these laboratory experiments clearly reveal strong fluctuations in species abundances, even though the external conditions are kept constant.

Conclusions

In summary, there are many reasons to believe that real-world plankton communities can never be at equilibrium. Firstly, theoretical analyses and laboratory experiments show that competition and predation in multi-species plankton communities are very likely to produce chaos. On top of that, the communities are subject to environmental fluctuations in the real world, and the effects of environmental variability are magnified rather than damped by the species interactions. It is, therefore, not surprising that plankton dynamics are usually highly erratic on the species level. If, as McCauley & Murdoch (1987) argue, the plankton serves as a paradigm for other ecosystems, it is tempting to suggest that complex dynamics may arise in a similar fashion in other ecosystems as well. Terrestrial vegetation (Rammert, 1991; Hubbell, 2001) and coral reefs (Jackson & Buss, 1975; Buss & Jackson, 1979) might

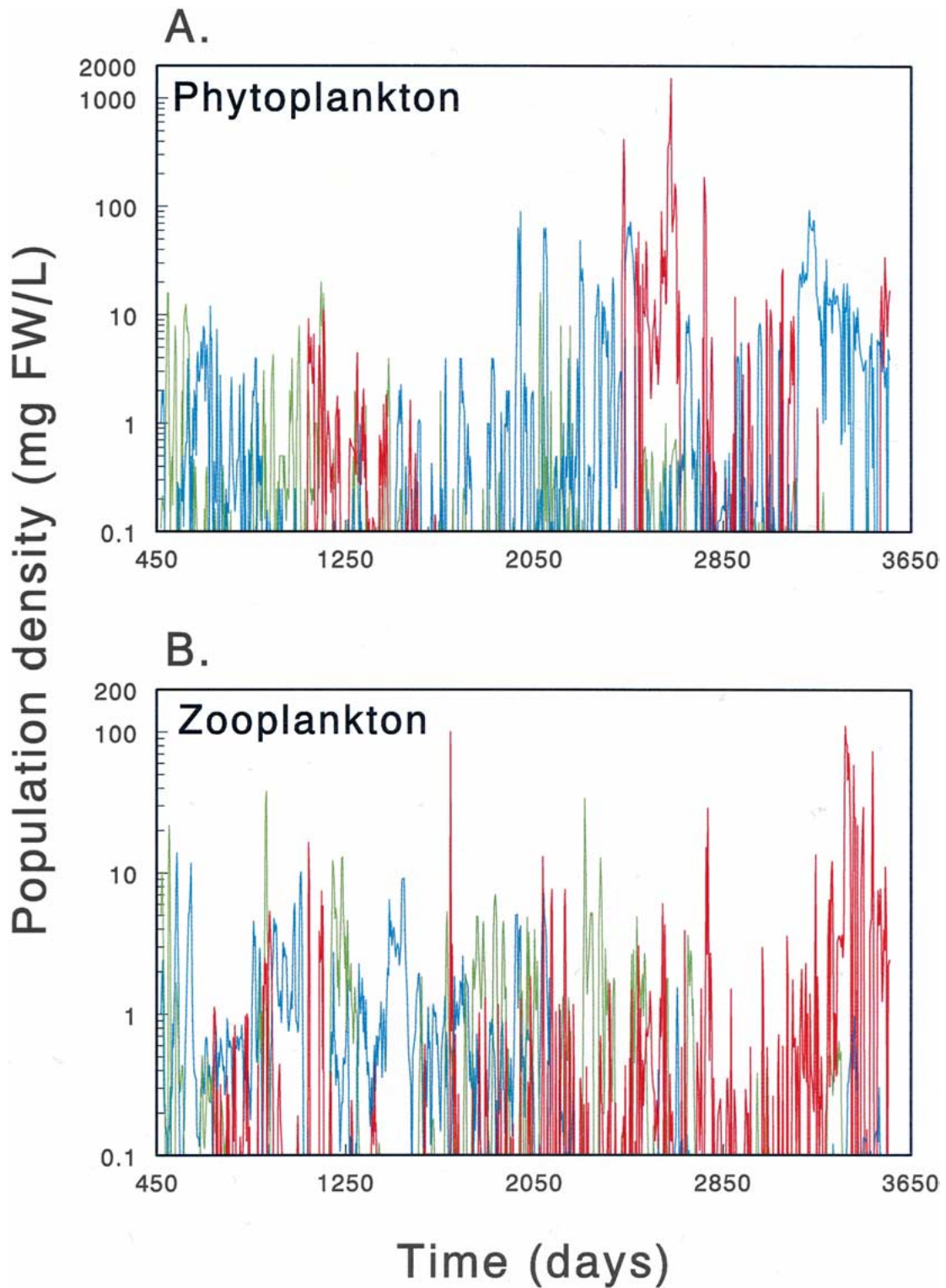


Figure 5. Non-equilibrium dynamics observed in an experimental multispecies community. The community developed in a long-term laboratory experiment under constant external conditions, and consisted of more than 20 different species. Data show the observed time course of (A) the dominant phytoplankton groups (green = green flagellates, blue = prokaryotic pico-phytoplankton, red = the diatom *Melosira*), and (B) the dominant zooplankton groups (green = the rotifer *Brachionus*, blue = the copepod *Eurytemora*, red = protozoans). Data were kindly provided by Heerkloss (unpublished), and by Heerkloss & Klinkenberg (1998), with permission from Schweizerbart'sche Verlagsbuchhandlung.

be intriguing examples. The only key difference with the plankton might be that the wax and wane of plankton species is more conspicuous for a human observer, simply because plankton generation times are much shorter than the generation times of, say, tropical trees. Indeed, Hutchinson (1961) was right when he suggested that the explanation for the unexpected biodiversity in plankton communities was most likely the fact that they are never in equilibrium. However, though it is always easy to blame the weather for its unpredictability, 40 years later we know quite a bit more about the fascinating internal mechanisms, within plankton communities, that can fuel non-equilibrium dynamics and thus enhance biodiversity.

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