

## Seasonal dynamics of *Daphnia* and algae explained as a periodically forced predator-prey system

Marten Scheffer, Sergio Rinaldi, Yuri A. Kuznetsov and Egbert H. van Nes

Scheffer, M., Rinaldi, S., Kuznetsov, Y. A. and van Nes, E. H. 1997. Seasonal dynamics of *Daphnia* and algae explained as a periodically forced predator-prey system. – *Oikos* 80: 519–532.

The classical seasonal sequence of events in lake plankton is an early spring bloom of algae followed by a peak of zooplankton, typically of the genus *Daphnia*, grazing down algal biomass resulting in the spring clear-water phase around early June. Subsequently, *Daphnia* numbers usually remain low and algal biomass increases until autumn when a second small *Daphnia* peak can cause another drop in algal biomass. In this paper we show that this entire scenario with the right timing of events comes out naturally from a minimal model of the *Daphnia*–algae interaction if we simply vary the parameters of the model sinusoidally over the year to mimic the effect of seasonal variation in temperature, light and predation pressure from planktivorous fish. The model also reproduces the observation that in lakes where fish biomass is low, *Daphnia* peaks can continue to occur regularly throughout the summer, while in lakes with very high fish biomass *Daphnia* can be virtually absent throughout the season.

*M. Scheffer and E. H. van Nes, Inst. for Inland Water Management and Waste Water Treatment, PO Box 17, NL-8200 AA Lelystad, The Netherlands (marten@cc.ruu.nl). – S. Rinaldi, CIRITA, Politecnico di Milano, Via Ponzio 34/5, I-20133 Milano, Italy. – Y. A. Kuznetsov, CWI, PO Box 4079, NL-1009 AB Amsterdam, The Netherlands.*

One of the most distinctive events in the seasonal cycle of lake plankton communities is the clear-water phase that often occurs at the end of spring. This dip in algal biomass can be partially caused by depletion of the available nutrients (Reynolds 1984, Sommer et al. 1986, Vynhánek 1989), but heavy grazing on algae by large zooplankton species that peak after the spring algal bloom is usually the main mechanism causing the clear-water phase (Lampert et al. 1986, Luecke et al. 1990, Carpenter et al. 1993, Rudstam et al. 1993, Sarnelle 1993, Hanson and Butler 1994, Townsend et al. 1994, Jurgens and Stolpe 1995). The phenomenon can be especially spectacular in eutrophic lakes where this short clear period contrasts strongly with the turbid situation in the rest of the growing season. Although the spring clear-water phase is a common phenomenon, it does not always occur. Hypertrophic lakes can simply

remain turbid throughout the year (Berger 1975, Hosper and Meijer 1986, Sas 1989). On the other hand, there are lakes that show several clear-water phases during the summer (Lair and Ayadi 1989, Lampert and Rothhaupt 1991). Also, the timing of the clear-water phase can vary. It may, for instance, come relatively early in years when predation pressure from planktivorous fish on zooplankton is low (Temte et al. 1988, Rudstam et al. 1993).

In the first section of this paper we present a short review of case studies on clear water phases and a systematic analysis of 257 time series of chlorophyll concentrations to characterize the occurrence and timing of clear-water phases. Subsequently, we show that the bestiary of behaviour observed in the field, can be largely explained as the result of periodic forcing of a simple predator-prey system. Zooplankton is the preda-

Accepted 5 May 1997

Copyright © OIKOS 1997

ISSN 0030-1299

Printed in Ireland – all rights reserved

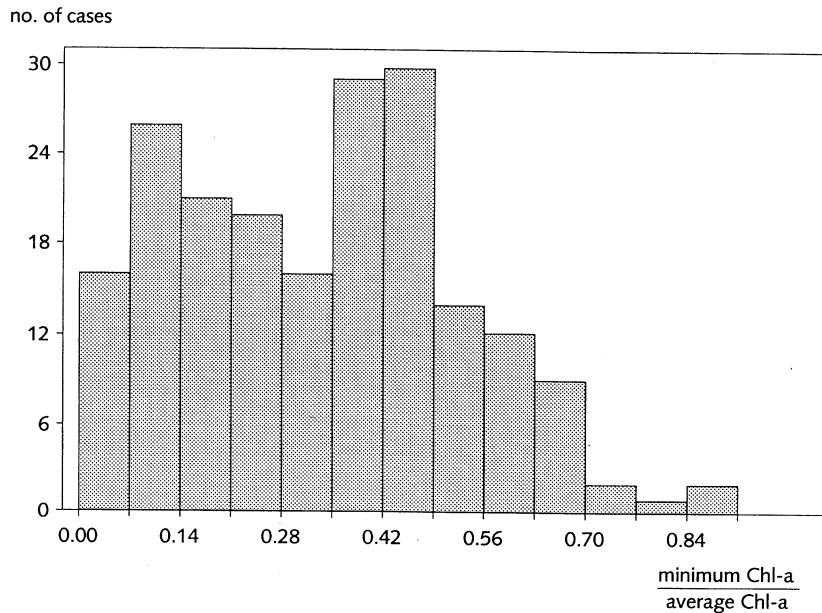


Fig. 1. Frequency distribution of the relative depth of the deepest dip (minimum/average of recorded values) in 257 time series of chlorophyll-*a* from 71 Dutch lakes. Each time series covers the period from 1 April to 1 November of a given year.

tor, algae are the prey, and temperature, light and the grazing pressure from zooplanktivorous fish vary sinusoidally with a one-year period. The notion that periodic forcing greatly influences the dynamics of predator-prey systems has only recently been established (see Hastings et al. (1993) for a review). Even the simplest predator-prey models can show a bewildering range of behaviours, including multiplicity of attractors, quasiperiodicity and deterministic chaos, when they are periodically forced (Schaffer 1988, Kuznetsov et al. 1992, Rinaldi and Muratori 1993, Gragnani and Rinaldi 1995). This dramatic effect on the qualitative behaviour suggests that periodic forcing should be an essential ingredient of the study of predator-prey models if we want to use them for understanding the dynamics of their real world counterparts in seasonal environments. The current results exemplify how intriguing dynamic patterns can arise simply from the interference of the rhythm of the seasons with that of the biological processes. Because the dynamics of the seasonally forced model can best be understood from the properties of the constant parameter case, we start the model analysis with a brief treatise on the latter.

### Seasonal dynamics in the field

While accurate field data on *Daphnia* dynamics and fish densities are relatively rare, there are many detailed time series of algal biomass. As a first step to characterize the occurrence of clear-water phases in the field, we analysed a database with 257 seasonal patterns of chlorophyll-*a* concentrations from 71 Dutch lakes that were sampled on a routine basis at least once every

month in the period from April to October of the analysed years. To check if clear-water phases can be distinguished from normal fluctuations in algal concentrations, we computed the relative depth of the deepest dip in algal biomass for each annual pattern (lowest Chl-*a*/average Chl-*a* over the April–October period). Indeed, this dip-depth has a distinct bi-modal distribution (Fig. 1). The main peak in the figure shows that the minimum is often about 40% of the average chlorophyll level, but the hump on the left indicates that there is another set of cases in which a dip to about 10% of the average concentration occurs. Arbitrarily we classify dips deeper than 25% of the average concentration as clear-water phases for further analysis. Such deep dips occur in 98 of the 257 analysed time series.

A plot of the relative depth of the dip in chlorophyll against the average concentration (Fig. 2), reveals that clear water phases are almost absent in lakes with an average chlorophyll level higher than  $150 \mu\text{g l}^{-1}$  ( $\chi^2$ ,  $p < 0.0001$ ). In such lakes, the chlorophyll level is not only high, but also relatively constant. This result is in line with earlier analyses by Gulati (1983) showing that strong peaks in zooplankton grazing and associated clear-water phases are largely restricted to oligomesotrophic situations.

To analyse the timing of clear-water phases, we checked the date of occurrence of the dips deeper than 0.25. Deep dips in algal biomass appear to occur at any time of the studied period of the year, although the majority of the clear-water phases are found around May, with another peak of occurrences in autumn (Fig. 3). This data-set does not allow a check whether grazing is really the cause of the deep dips in algal biomass, as zooplankton densities are not available. Recent Dan-

minimum Chl-a  
average Chl-a

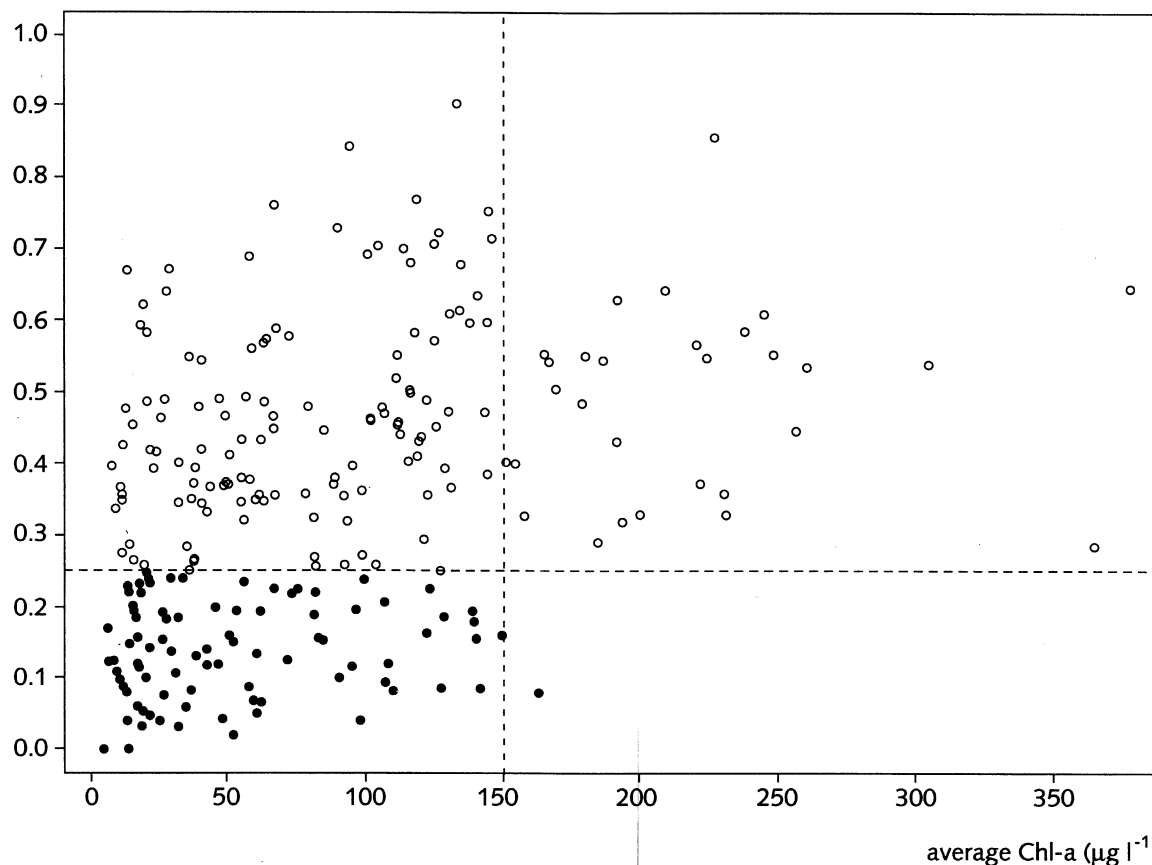


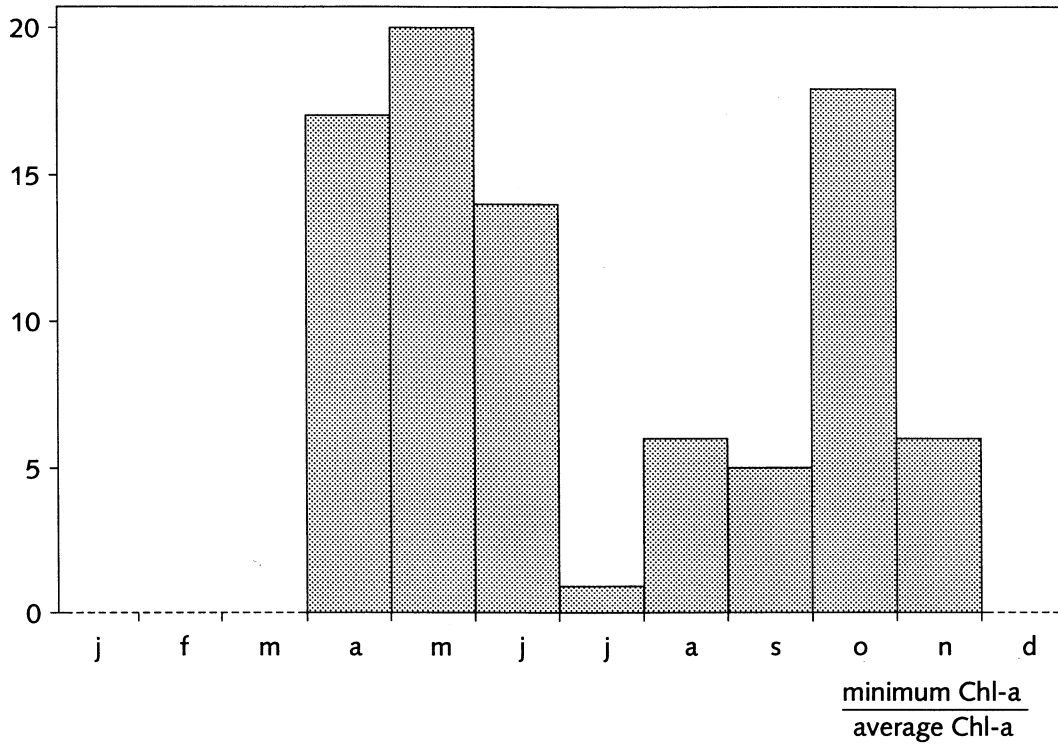
Fig. 2. Relative depth of the deepest dip in chlorophyll-*a* plotted against the average chlorophyll concentration in each of the analysed time series (see Fig. 1). Drops in chlorophyll to less than 25% of the average value of that time series (filled circles) are practically absent in lakes where the average level exceeds  $150 \mu\text{g l}^{-1}$ .

ish results (Jeppesen et al. 1997), however, indicate that in moderately eutrophic lakes (TP  $0.05\text{--}0.1 \mu\text{g l}^{-1}$ ) the peaks in potential grazing pressure of zooplankton on phytoplankton occur precisely in the same periods as the clear-water phases observed in the Dutch data-set (Fig. 3). The Danish analysis also shows that grazing pressure tends to be low during the entire year in very eutrophic lakes.

There are also many case studies of *Daphnia* dynamics and their effect on algal biomass. Especially the *Daphnia* peak and the resulting clear-water phase in spring are often described (Lampert et al. 1986, Luecke et al. 1990, Rudstam et al. 1993, Sarnelle 1993, Hanson and Butler 1994, Townsend et al. 1994, Jurgens and Stolpe 1995), but also a repetition of the spring pattern in autumn appears to be very common in lakes. Indeed, an international assemblage of lake plankton specialists (the Plankton Ecology Group, PEG) described the pattern with a spring and a fall peak as the typical scenario for eutrophic lakes (Sommer et al. 1986) (Fig. 4A).

There also are several case studies that demonstrate that recurrent *Daphnia* peaks can cause several clear-water phases during the summer. Examples are the French Lake Aydat where three *Daphnia* peaks and corresponding clear-water phases are found in one year (Lair and Ayadi 1989), and the German Lake Grosser Binnensee where four *Daphnia* peaks occurred in one season, three of which led to a conspicuous clear-water phase (Lampert and Rothhaupt 1991). It is likely that such repeated outbreaks of large *Daphnia* are only possible in lakes with few planktivorous fish in summer. An example that supports this idea is the development of the community dynamics in Bough Beech Reservoir, a newly created water reservoir in south-east England from which all coarse fish was removed in the first year (Munro and Bailey 1980, Harper and Ferguson 1982). Fish populations established slowly and planktivorous young-of-the-year individuals became abundant only after several years. Recurring *Daphnia* peaks were among the most striking features of the plankton dy-

no. of cases



Potential grazing (% d<sup>-1</sup>)

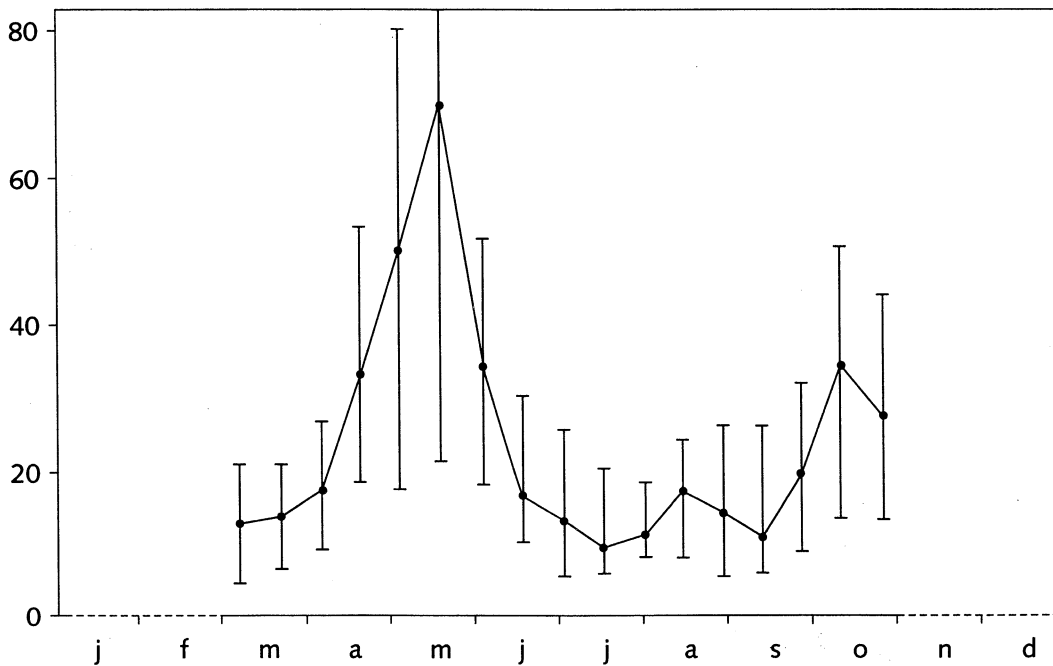


Fig. 3. Top graph. Frequency distribution of the moment of occurrence of drops in chlorophyll concentration below 25% of the average of a time series (see Fig. 1) (filled circles in Fig. 2). Bottom graph. Seasonal variation in the zooplankton grazing pressure on phytoplankton (% of the phytoplankton biomass ingested per day) for moderately eutrophic Danish lakes (TP 0.05–0.10  $\mu\text{g l}^{-1}$ ). The curve indicates the median, the bars represent the 25–75% percentiles. (From Jeppesen et al. (1997).)

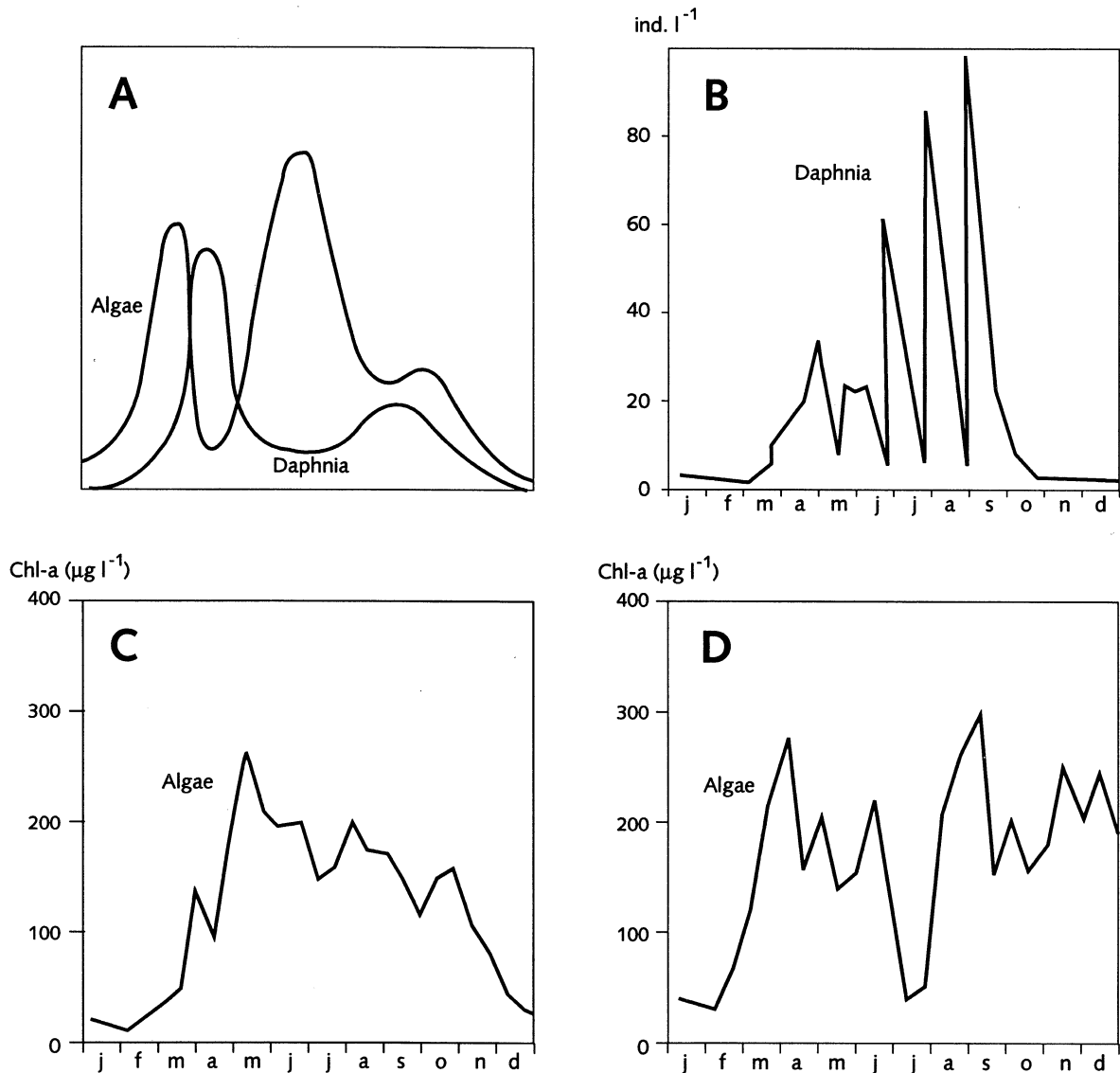


Fig. 4. A selection of patterns of seasonal dynamics observed for lake plankton. A) A seasonal cycle with a spring and an autumn peak of large *Daphnia* and corresponding dips in algal biomass, considered the typical pattern for eutrophic lakes (after Sommer et al. 1986). B) A sequence of peaks in *Daphnia* numbers observed in the newly created Bough Beech Reservoir, UK, before the development of a significant fishstock (redrawn from data of Harper and Ferguson (1982)). C) Time series of chlorophyll-*a* concentrations for 1980 in Lake Tjeukemeer, the Netherlands, illustrating the absence of pronounced clear-water phases typical of many hypertrophic lakes. D) A mid-summer clear-water phase in 1975 in Lake Tjeukemeer.

namics during the first years (Fig. 4B), while in later years, when planktivorous fish established, *Daphnia* oscillations were greatly reduced.

The analysis of the chlorophyll time series (Fig. 2), indicates that pronounced clear-water phases are often entirely absent, especially in hypertrophic lakes. Indeed, algal biomass is known to follow a more or less smooth seasonal pattern in many of the relatively shallow and eutrophic Dutch lakes (Fig. 4C). Interestingly, isolated clear-water phases are sometimes observed in such lakes

which do not necessarily occur in spring, but take place in the middle of the summer (Fig. 4D) or in autumn as well.

### The model

The basic model of plankton dynamics that we use consists of two differential equations, one for edible algae (*A*) and one for large herbivorous zooplankton (*Z*):

$$\frac{dA}{dt} = rA \left( 1 - \frac{A}{K} \right) - Zg \frac{A}{A + h_A} + d(K - A) \quad (1)$$

$$\frac{dZ}{dt} = egZ \frac{A}{A + h_A} - mZ - F \frac{Z^2}{Z^2 + h_Z^2} \quad (2)$$

Algal growth is basically logistic with a maximum growth rate of  $r$  and a carrying capacity of  $K$ . Losses are due to grazing by zooplankton following a simple saturating (type-II) functional response formulated as a Monod function of algal density with a half saturation value of  $h_A$ , and a maximum per capita grazing rate of  $g$ . A small diffusive inflow,  $d$ , proportional to the concentration difference between the algae in the studied part and those in an ungrazed refugium where algae are at carrying capacity is also added. This is a simple and straightforward way to account for the stabilizing effect of spatial heterogeneity in the distribution of algae and zooplankton (Scheffer et al. 1995).

Food intake by zooplankton is converted into growth with an efficiency of  $e$ . In addition to a fixed mortality,  $m$ , zooplankton suffers losses from predation depending on the planktivorous capacity,  $F$ , of the fish community, and the value of the sigmoidal (type-III) functional response of fish with a half saturation value of  $h_Z$ . Reference values and dimensions of all parameters are summarized in Table 1.

This or comparable formulations have often been used to describe the interaction of *Daphnia* and algae (Rosenzweig 1971, Gilpin 1972, Caughley and Lawton 1981, Scheffer 1991, Scheffer et al. 1995). The incorporation of planktivory is less classical and deserves some explanation. Firstly, it should be noted that we do not model fish dynamically. We will analyse the effect of varying fish predation pressure over the season, but we do not model fish growth as a function of zooplankton consumption (see Doveri et al. (1993) for an example where fish is modelled dynamically). Although fish will benefit from the consumption of *Daphnia*, this food is for most individuals just a part of their diet. Therefore, overall fish density depends on the productivity of the

lake, but does not react as directly to *Daphnia* density as *Daphnia* dynamics respond to phytoplankton. Therefore, it is reasonable to study the impact of fish on *Daphnia* dynamics without directly considering the effect of *Daphnia* on the population dynamics of fish.

Secondly, it should be noted that the predation loss term in the zooplankton equation represents the impact of the fish community as a whole. In reality, different groups of fish forage on *Daphnia* with different functional responses. Therefore, this term is really just a pragmatic solution to mimic the effect of many different animals switching to forage on *Daphnia* at different moments with different efficiencies. Since most of the larger individuals usually switch to *Daphnia* only when it is not too scarce (Lammens 1985, Lammens et al. 1985), the predation pressure is likely to increase more than linearly with *Daphnia* density over this initial range. Because of this prey switching behaviour of fish, the overall functional response is likely to be sigmoidal. The maximum consumption rate ( $F$ ) is set directly, rather than as the product of the fish biomass and their weight specific maximum intake. The latter is not easily defined for a whole community, since large animals consume less per gram of body weight than small ones.

## Equilibria and cycles in a constant environment

An extensive analysis of the properties of the unperturbed version of the model will be presented elsewhere. Here we briefly point out the main characteristics. Since the model has only two differential equations (it is a 'second order model'), its asymptotic modes of behaviour (for  $t \rightarrow \infty$  or  $t \rightarrow -\infty$ ), i.e. its attractors, repellors and saddles, can only be equilibria or limit cycles if the parameters are kept constant. In the case of a stable equilibrium, the populations settle to constant values, while in the case of a stable limit cycle they settle to a periodic regime.

Usually, the position of equilibria and the shape of limit cycles depend upon the parameters of the model in a smooth way. Varying the parameters slightly, equilibria and limit cycles shift gradually in the state space. For second order systems, a geometric representation of this dependency can be produced if we fix all parameters but one. Here we employ this approach to show the response of the model to changes in fish predation pressure ( $F$ ) (Fig. 5).

For zero fish we have the classical case of an unstable equilibrium point, surrounded by a stable limit cycle where both populations oscillate. The small diffusive inflow ( $d$ ) prevents the period and amplitude of the oscillations to be unnaturally large as in the classical 'paradox of enrichment' models (Rosenzweig 1971, Gilpin 1972). Increasing the predation pressure on zooplankton by fish ( $F$ ), we first arrive at a fold of an equilibrium curve called a saddle-node or fold bifurca-

Table 1. Reference parameter values and their dimensions. Maximum algal growth rate ( $r$ ) and carrying capacity ( $K$ ) are estimated to represent a typical eutrophic lake situation (Scheffer 1991). The functional response half-saturation coefficient of fish ( $h_Z$ ) is set quite arbitrarily (Scheffer 1991). The parameters for the zooplankton functional response, assimilation efficiency and mortality and respiration ( $g$ ,  $h_A$ ,  $d$ ,  $e$  and  $m$ ) are taken near the median of the ranges reported by Rose et al. (1988) for medium-sized *Daphnia*.

$r$	0.5	$d^{-1}$
$K$	10	mg DWT $l^{-1}$
$g$	0.4	day $^{-1}$
$h_A$	0.6	mg DWT $l^{-1}$
$d$	0.01	–
$e$	0.6	–
$m$	0.15	$d^{-1}$
$h_Z$	0.5	mg DWT $l^{-1}$
$F$	0.7	–

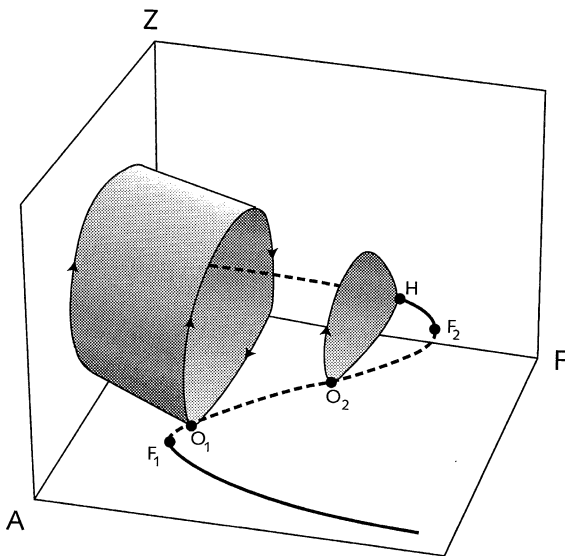


Fig. 5. Effect of fish predation pressure on the equilibria of the system. The limit cycle does not exist between the two homoclinic bifurcations ( $O_1$  and  $O_2$ ) where it collides with the saddle that marks the border of the basin of attraction of the stable algal dominated equilibrium.

tion ( $F_1$ ) (Arnold 1983, Guckenheimer and Holmes 1983, Kuznetsov 1995). Here, two new equilibria arise, a stable and an unstable one. The stable equilibrium point is a 'node' with almost no zooplankton and a high algal density. Because this corresponds to turbid water we refer to this equilibrium hereafter as 'the turbid equilibrium' for short. The unstable (dashed) equilibrium is a 'saddle'. Its stable manifold is the 'separatrix' that marks the limit of the basin of attraction of the turbid equilibrium (Fig 6A).

Increasing fish predation, the saddle and the node move further apart and consequently, the attraction area of the turbid equilibrium grows until the saddle collides with the limit cycle ( $O_1$ ) (see also Fig. 6B). This is a so-called homoclinic bifurcation (Kuznetsov 1995). This bifurcation implies the disappearance of the limit cycle, as beyond this bifurcation any trajectory ends up inevitably in the turbid equilibrium (Fig. 6C). A peculiarity of the homoclinic bifurcation is that the period of the limit cycle tends to infinity as it approaches the bifurcation. This 'saddle effect' occurs because the saddle is an equilibrium where, by definition, the derivatives of algae and zooplankton are zero. Hence, very close to it the system moves extremely slowly. Thus, in the vicinity of the homoclinic bifurcation, the system slows down, each time when it passes close to the saddle.

Note that the homoclinic bifurcation suggests an interpretation of the mechanism that causes the end of the spring clear-water phase. The development of a new cohort of young fish tends to cause a significant increase in planktivory in early spring. In terms of the

model this can bring the system from an oscillatory mode with episodes of low algal biomass and zooplankton-peaks into the stable turbid equilibrium. The homoclinic contact is at a point on the cycle with low zooplankton and high algal biomass (Figs 5 and 6). This implies that, following the limit cycle, first, zooplankton collapses due to food shortage while, subsequently, it is prevented to recover despite the high food concentration, because fish predation is too high. This is indeed what is found in recent careful examinations of the processes involved in lakes (Luecke et al. 1990).

If fish predation is raised further, a limit cycle reappears (Fig. 5) through a second homoclinic bifurcation ( $O_2$ ) and subsequently shrinks approaching the Hopf bifurcation ( $H$ ) (Guckenheimer and Holmes 1983, Kuznetsov 1995) where it collides with its unstable focus to become a stable equilibrium point. The last qualitative change with increasing fish density is a fold bifurcation ( $F_2$ ) again. The stable point that was formed through the Hopf bifurcation collides with the saddle in the point where the equilibrium curve is folded back. This whole right part, from the second homoclinic to the second fold, is mainly of theoretical interest, as the system will normally not arrive there. To see this, imagine a slow increase in fish density, starting from zero. The populations will show oscillations until the homoclinic ( $O_1$ ) is reached. Here the system jumps to the turbid equilibrium, where it will stay when fish predation is increased further. Lowering the amount of fish from this point will keep the system in the turbid equilibrium until the fold bifurcation ( $F_1$ ) is reached. At this point it will jump back to the oscillatory mode. Only a disturbance could potentially bring the system on the attractors around the Hopf. However, since their basins of attraction are rather small this is unlikely to happen. For all practical purposes we can therefore neglect this part of the picture.

### Seasonal forcing of the model

The simplest way to include the effect of the seasonal cycle of light, temperature and fish predation in the model, is to impose a sinusoidal variation of the value of the relevant model parameters over the year.

In eutrophic lakes, light limitation tends to set an upper limit to algal biomass. We therefore assume the carrying capacity ( $K$ ) to be a function of light. The parameters related with the metabolism of algae, zooplankton and fish ( $r$ ,  $g$ ,  $m$ ,  $F$ ) will depend upon temperature. The summer maximum in the temperature of a lake is usually delayed compared to the maximum in irradiation. For simplicity we neglect this phase shift and many other subtleties like the exact shapes of temperature and light dependence of the organisms and

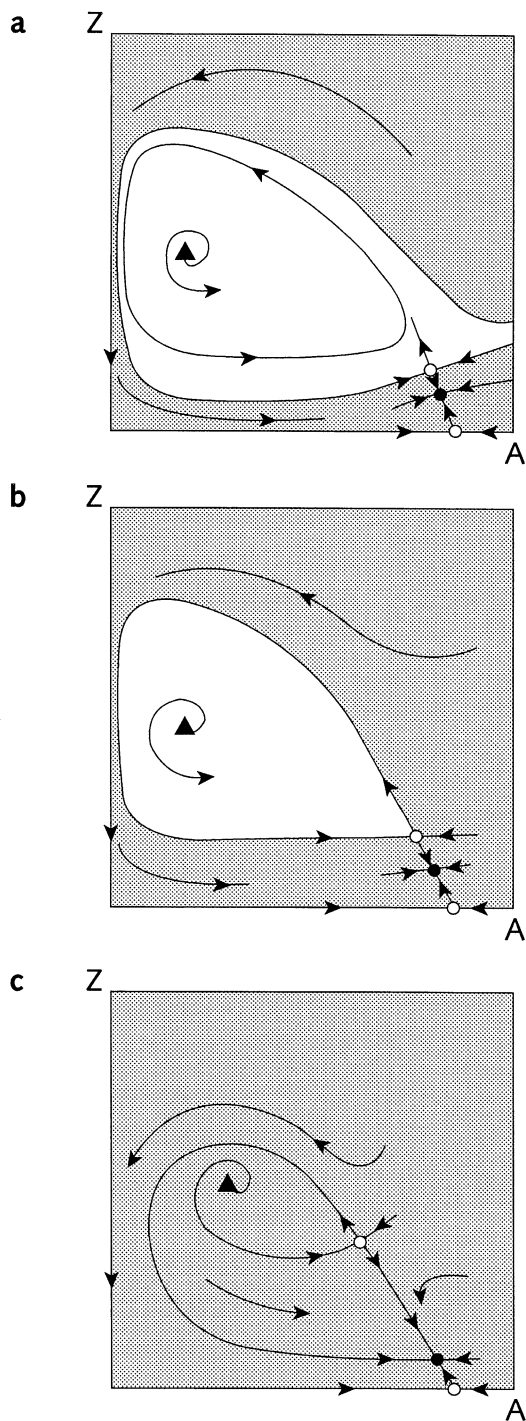


Fig. 6.

simply mimic the effect of seasons by multiplying each of those parameters by a seasonal impact,  $\sigma_{(t)}$ , which is a periodic function of time  $t$ :

$$\sigma_{(t)} = \frac{1 - \varepsilon \cos\left(\frac{2\pi t}{365}\right)}{1 + \varepsilon} \quad (3)$$

where  $t = 0$  stands for the first of January. Notice that the minimum value of each parameter (i.e. the value in the middle of the winter) is equal to its maximum in summer multiplied by  $(1 - \varepsilon)/(1 + \varepsilon)$ , and that the summer maximum corresponds to the reference value given in Table 1.

Usually, there is a considerable seasonal variation in the amount of planktivorous fish. Fish reproduction in spring sets off the development of an often massive cohort of young animals that feed preferentially on zooplankton. The biomass development of the new cohort is a function of individual growth and mortality. Initial growth is very fast but only a small fraction of the individuals survive to recruit into the second year-class next spring. The consumption by the 'young-of-the-year' animals comes on top of that of the rest of the community to produce a maximum in planktivorous activity somewhere in the summer. Thus in addition to the temperature induced variation, fish predation pressure ( $F$ ) should show a seasonal variation due to the reproductive cycle. Assuming this cycle to be again sinusoidal and in phase with the variation in temperature and light we can include the effect simply by multiplying  $F$  with an extra seasonal impact ( $\sigma$ ). Thus the complete seasonal model becomes:

$$\frac{dA}{dt} = \sigma_{(t)} r A \left(1 - \frac{A}{\sigma_{(t)} K}\right) - Z \sigma_{(t)} g \frac{A}{A + h_A} + d(\sigma_{(t)} K - A) \quad (4)$$

$$\frac{dZ}{dt} = e \sigma_{(t)} g Z \frac{A}{A + h_A} - \sigma_{(t)} m Z - \sigma_{(t)} \sigma_{(t)} F \frac{Z^2}{Z^2 + h_Z^2} \quad (5)$$

Note that in this minimal model, we have assumed the amplitude  $\varepsilon$  and timing of the seasonal forcing to be equal for all parameters. Obviously, this implementation of seasonality is rather rudimentary, but, as pointed out later, numerical experiments show that inclusion of realistic time shifts between the seasonal variation in fish, temperature and light and adjustment of their amplitudes does not significantly alter the behaviour of the model.

Fig. 6. Phase portraits of model (1, 2) for increasing values of the fish predation pressure  $F$ . The triangle denotes the unstable equilibrium point that is the focus of the limit cycle. The open circles denote the trivial equilibrium with only algae (on the axis) and the positive saddle point. The filled circle is a stable equilibrium referred to in the text as the turbid equilibrium. The grey region is the basin of attraction of the turbid equilibrium. a) Situation with two attractors (a cycle and the turbid equilibrium), whose basins of attraction are demarcated by the stable manifold of a saddle also called separatrix; b) Situation with one attractor (the turbid equilibrium) and a homoclinic contact of the cycle with the saddle; c) Situation with a single global attractor (the turbid equilibrium).



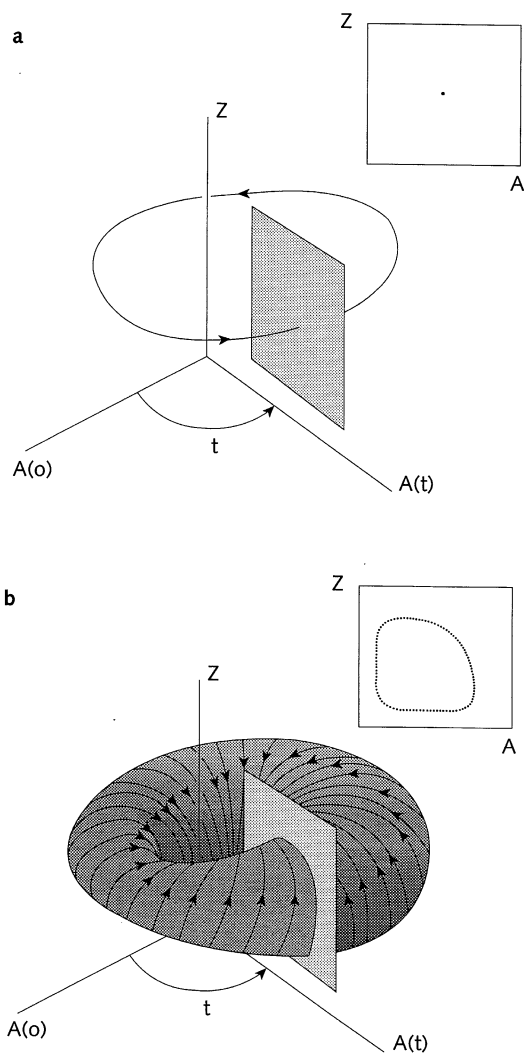


Fig. 7. Representation of the seasonally perturbed patterns in a three-dimensional state space with angular time ( $t$ ). The algal axis ( $A(t)$ ) turns  $360^\circ$  in one year. The depicted transverse frames are so-called Poincaré sections. They represent annual samples of the amount of algae and zooplankton on a fixed day of the year. A period-one cycle (a) shows up on the Poincaré section as a single point, while a torus (b) is represented by a closed regular curve of points.

### The nature of seasonal attractors

If the seasonal forcing is small (i.e. if  $\varepsilon$  is small) the attractors of the model can be interpreted as a simple distortion of the attractors of the constant parameter model (Fig. 5). The stable equilibrium point becomes a small stable cycle with a period of one year, and, likewise, unstable equilibria of the constant parameter case change into unstable cycles. On the other hand, the stable limit cycle (Fig. 5) becomes a so-called torus. The reason for this name can be seen if the attractors of the system are plotted in a three-dimensional space (Fig. 7) where time is represented by the angle between the axis

$A(0)$  and a rotating axis  $A(t)$  which returns to  $A(0)$  in one year. A one-year periodic regime will be represented in this space by a single cycle (Fig. 7a). A torus resembles a doughnut (Fig. 7b). A trajectory on this attractor never comes back to the initial point, thus covering the torus densely as time goes on.

This representation (Fig. 7) also shows the so-called Poincaré section of the two attractors. Poincaré sections are obtained by cutting the attractors transversally with a plane. This corresponds to the figure one obtains by sampling algae and zooplankton annually at the same day for a long series of years. Obviously, a periodic regime with a period of one year will be revealed by a unique point on the Poincaré section, while a periodic solution of period two years will give rise to two points which are visited in odd and even years respectively, and so on. A quasi-periodic regime, however, will generate an infinite series of data points that fill a closed regular curve.

Like in the constant parameter case, the shapes of all attractors will smoothly change as parameter values are varied and incidentally they collide with repellers and saddles at bifurcation points. If, for example, fish predation ( $F$ ) decreases, the turbid regime can disappear when the two cycles outside the torus collide. This is analogous to the fold bifurcation in the constant parameter case ( $F_1$  in Fig. 5). Also the torus can disappear. This happens when it "collides" with the saddle cycle. The resulting "torus destruction" is analogous to the homoclinic bifurcation of the constant parameter case ( $O_1$  in Fig. 5). Actually, the torus destruction is a sequence of bifurcations, through which the torus loses its smoothness before finally disappearing. Just before this happens, the torus is very close to the saddle cycle, so that from time to time the trajectories on the torus remain very similar to the saddle cycle for a long period. Varying a parameter, the saddle cycle approaches the torus and the phase of turbid water becomes longer and longer. Thus, the transition from a clear-water regime to a turbid regime is not characterized by gradually less pronounced clear-water episodes but, instead, by increasingly rare clear-water phases. This kind of transition, called intermittency, has been observed experimentally in different phenomena and characterizes many non-linear dynamic systems (Grebogi et al. 1987, Vandermeer 1993).

In order to clarify the behaviour of the seasonal model we need to consider one more phenomenon, namely frequency locking. When a periodically forced non-linear system has a torus, it can happen that, for a particular value of the parameters, a cycle exists on that torus which attracts all other nearby trajectories. This implies that the behaviour of the system becomes periodic (on torus) and will show up as such on the Poincaré section. A trajectory will no longer cover the torus densely, as it converges to the periodic cycle. Remarkably, such periodic solutions on the torus per-

sist when the values of parameters are varied slightly. This is because the external frequency tends to 'lock' the system, in the sense that the system is forced to behave periodically with the same period as the forcing function or with a period that is an integer multiple of it. In our case, seasons can force the algae-zooplankton communities to behave periodically with a period of 1, 2, 3, . . . years, even though the system would have the tendency to cycle at another frequency in the absence of seasons. In general, the regions of the parameter space in which the system is locked are larger if the amplitude of the season is larger.

### Behavioural repertoire of the seasonal model

The best overview of the behavioural repertoire of the seasonal model can be obtained from a bifurcation diagram (Fig. 8). The presented diagram is an approximation that has been constructed using the software package LOCBIF (Khibnik et al. 1992) to produce segments of bifurcation curves and Poincaré sections on many points in the parameter space. On the vertical axis ( $\varepsilon = 0$ ) there are the two bifurcation points  $F_1$  and  $O_1$  corresponding to the fold and homoclinic bifurcations shown in Fig. 5. These points are the roots of the two bifurcation boundaries separating regions 1, 2 and 3 in which the model has qualitatively different asymptotic behaviours.

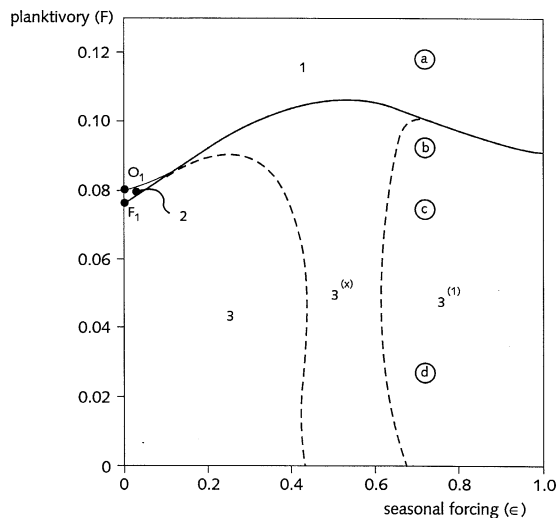


Fig. 8. Bifurcation diagram of the model. The bifurcation boundaries merging from points  $O_1$  and  $F_1$  divide the parameter space into three distinct regions where the asymptotic behaviour of the model is different (see text). In region (1), clear-water phases are absent, while in region (3) clear water phases occur. In region (2) the asymptotic behavioural regimes of region (1) and (3) co-exist. On the left side of the dashed curves the dynamics in region ( $3^{(\omega)}$ ) are not locked with the rhythm of the seasons (see text), on the right side of these curves (region  $3^{(1)}$ ) the system behaves periodically with a period of one year. The dynamic behaviour at the parameter settings marked as a, b, c and d is illustrated in Fig. 9.

The top boundary corresponds to torus destruction and, as already pointed out, is actually not a curve but a very narrow band with complex structure. Crossing this band from below the torus disappears through homoclinic contacts. The boundary rooted at  $F_1$  is a tangent bifurcation curve. Crossing this curve from above a stable cycle and a saddle cycle collide and disappear. Thus, region 1 contains a unique attractor, namely a stable cycle characterized by high algal biomass (Fig. 9a) corresponding to the 'turbid equilibrium' of the constant parameter case. In region 2, this turbid regime coexists with a torus characterised by clear-water episodes. All the numerical experiments we have carried out indicate that region 2 is very small. Region 3 is characterized by the existence of an invariant torus, although in many subregions ( $3^{(i)}$ ) the regime is locked to be purely periodic with a period of  $i$  years (see below). In our case all of those subregions are small with the exception of region  $3^{(1)}$  where the behaviour on the torus is locked to a period of one year. The bifurcation line demarcating the border of region  $3^{(1)}$  corresponds to a tangent bifurcation of cycles on torus. Although numerical experiments have shown in which zone of the parameter space it occurs ( $3^{(2)}$ ) the exact position could not be detected due to numerical problems. In this parameter zone ( $3^{(3)}$ ) several small islands occur where cycles with a period of more than one year exist.

A value of 0.7 for  $\varepsilon$  is probably the best choice for mimicking seasonal forcing in temperate regions. At this forcing amplitude the frequency of oscillations in the plankton tends to be locked with that of the seasons, in such a way that the same pattern of plankton dynamics repeats each year (Fig. 9). If fish predation on zooplankton is very high (region 1) the seasonal cycle is simple (Fig. 9a). *Daphnia* biomass remains low throughout the year and algal biomass develops smoothly with a minimum in winter and a maximum in summer. If the predation pressure from fish is less extreme, the spring bloom of algae is followed by a zooplankton peak which causes a clear-water episode with low algal density (Fig. 9b, c, d). What happens after this clear-water phase depends on the predation pressure by fish. At high fish density the spring dip is the only clear water phase of the season (Fig. 9b). If planktivory is lower, a second *Daphnia* peak occurs at the end of the summer (Fig. 9c). At very low fish densities, the number of *Daphnia* peaks that occur over the summer can increase up to four (Fig. 9d). Note that the first clear-water phase occurs remarkably constantly around May, although there is a dependency on fish predation pressure ( $F$ ). With increasing fish the spring clear-water phase tends to occur later (Fig. 9).

Although relevant from a biological point of view, the increase in the annual number of clear-water phases with decreasing planktivory is not characterized by real bifurcations in the system's behaviour. Only, the transi-

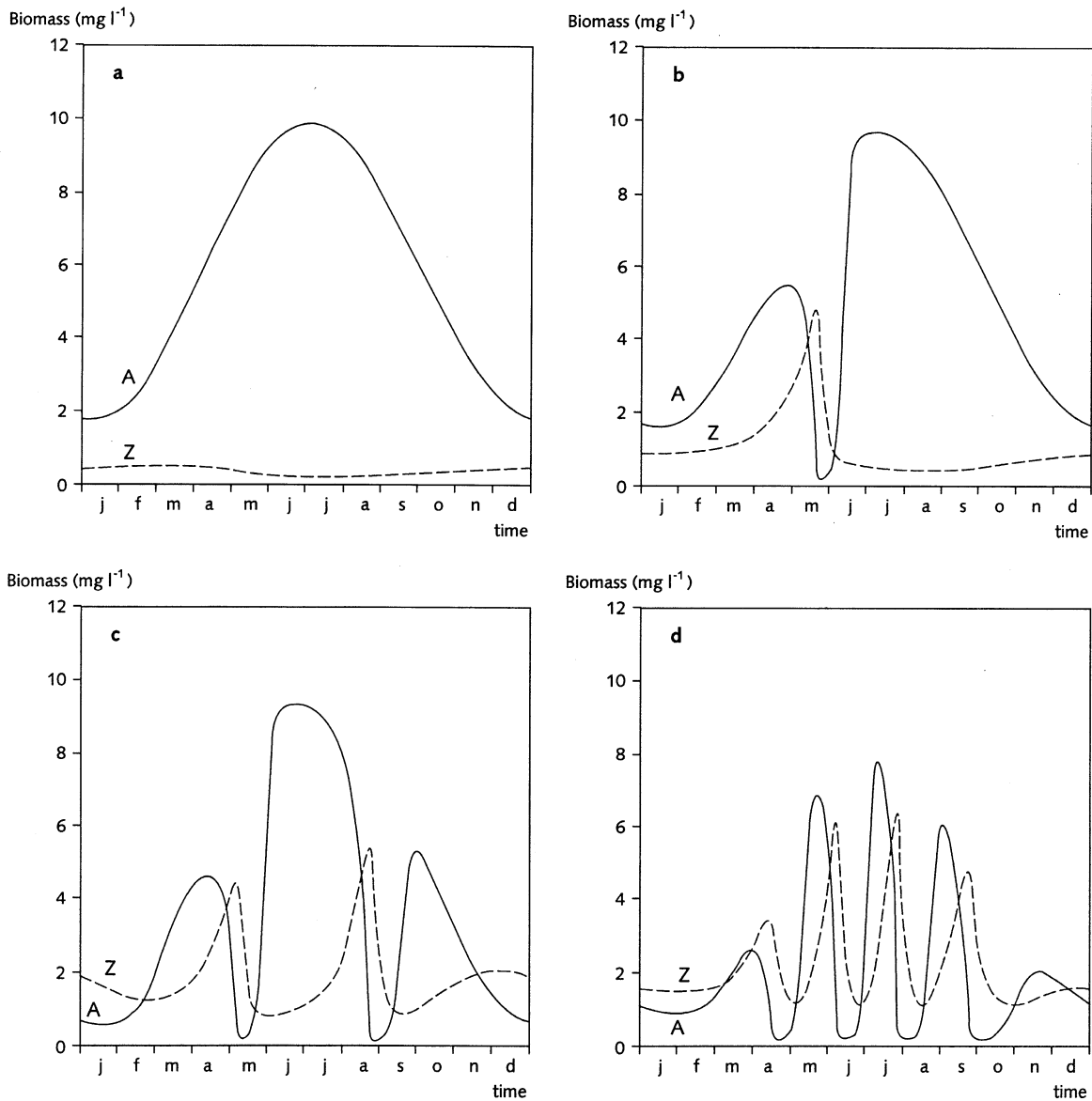


Fig. 9. Cyclic plankton dynamics corresponding to points a, b, c, and d in Fig. 8 ( $\epsilon = 0.7$ ,  $F = 0.12, 0.09, 0.075$  and  $0.025$ , respectively).

tion from the permanently turbid regime (region 1) to the regime with one or more clear-water phases (region 3) is marked by bifurcations (Fig. 8). More precisely, regions 1 and 3 are separated by a very narrow band in which there are many bifurcation curves delimiting tiny bands of frequency locking. Increasing the fish biomass over this parameter band, the clear-water phase does not become gradually less pronounced but rather increasingly rare. In each individual year, the clear-water phase is either fully present or completely absent, but with increasing fish density we go gradually from a situation in which the clear-water occurs every year (region 3<sup>(1)</sup>) to a situation in which it never happens

(region 1). In this narrow transition zone regular cycles with a length of more than one year are found. Clear-water phases may occur, for instance, two out of three years, or two out of four years. However, this parameter band also contains very long cycles that, judging from the time series, can be considered erratic for all practical purposes. Obviously, such multi-year cycles are unlikely to be found in nature since they only occur over a very small region in the parameter space. Taking environmental variability into account, however, lakes which are 'close' to the border of having-or-not-having clear-water phases should be expected to behave in a rather unpredictable way. They may or may not display

a clear-water phase in any given year. The simulation results suggest that in such lakes, also the timing of clear-water phases can be rather erratic. Isolated clear-water episodes can occur in summer or even in autumn.

## Discussion

Obviously, our plankton model is a crude simplification of reality. Like all minimal models, it neglects many of the mechanisms that are known to operate in the field. Rather than attempting to be complete, however, the aim is to check which part of the bestiary of behaviour that is observed in the field, can in theory be explained by the few ingredients included in the model. The ingredients in our case are a classical predator-prey model with fish as a super-predator and a sinusoidal variation of the parameters with time to mimic the effect of the change of seasons. The analysis shows that these ingredients are indeed sufficient to generate an array of seasonal patterns of plankton dynamics that corresponds surprisingly well to the patterns observed in the field.

Like in the field, a clear-water phase can be absent or occur up to four times a year. Scenarios with more than two *Daphnia* peaks and clear-water phases in a year are predicted only for a small parameter range at low fish densities. For a larger range of parameter settings the model predicts the clear-water phase to be either entirely absent (Fig. 9a), or to happen in spring (Fig. 9b) with a possible repetition in autumn (Fig. 9c). Indeed, in the field these three scenarios seem to be the most common ones also (Figs 3, 4A and 4C). The timing of the simulated patterns corresponds remarkably well to the field observations as well. Without any special tuning the spring clear-water phase occurs around May (Figs 9b, c, d) as it does in lakes (Fig. 3). The model suggests that the timing of the spring clear-water phase should depend on fish density, coming later if fish density is higher (Figs 9b, c, d). Suitable data to check this prediction are rare, but in Lake Mendota where the relationship between fish and plankton dynamics has been analysed for many years, it has indeed been noted that the spring clear-water phase can come earlier when the density of planktivorous fish is low (Temte et al. 1988, Rudstam et al. 1993). Even the peculiar prediction that incidental isolated clear-phases can occur in other periods than spring in lakes that normally show no clear-water phase is supported by data (Fig. 4D).

Although the correspondence between generated patterns and field observations is encouraging, it does of course not imply that the modelled mechanisms need to be responsible for these patterns in the field. Other mechanisms may cause the same patterns, or what is probably very common, help to cause the pattern (Scheffer et al. 1994). Here, we briefly highlight some of the more conspicuous discrepancies between our simple model and reality.

The model suggests that the absence of clear-water phases can be explained as the effect of a high density of planktivorous fish (region 1 in Fig. 8). Our time series analysis shows that the absence of clear-water phases is especially frequent in hypertrophic lakes with high algal biomass (Fig. 2). Indeed, fish biomass is typically very high in such lakes, and may therefore well explain the lack of clear-water phases. Importantly, however, hypertrophic lakes are also frequently dominated by cyanobacteria (Sas 1989). Since these algae are not well edible (Arnold 1971, Schindler 1971) and *Daphnia* growth can be severely reduced in their presence (Gliwicz 1990, Gliwicz and Lampert 1990), this may well contribute to the absence of clear-water phases in hypertrophic lakes. The zooplankton community of such lakes is typically dominated by small species. This is thought to be due to several mechanisms. Selective predation of fish removes the larger individuals (Brooks and Dodson 1965, Shapiro and Wright 1984, Hambright 1994, Seda and Duncan 1994), but *Daphnia* also tends to change its life history strategy, becoming smaller in response to chemical clues released by fish (Weider and Pijanowska 1993, Engelmayer 1995). However, it has also been shown that larger *Daphnia* species are less able to forage and grow in a mixture of filamentous blue-greens and other algae (Gliwicz 1990, Gliwicz and Lampert 1990) which may contribute to the absence of efficient grazers like large *Daphnia* species from hypertrophic lakes. Nonetheless, an extensive analysis of data from many Danish lakes indicates that top-down control by fish is probably the dominant mechanism preventing large zooplankters from peaking and grazing down algal biomass in most hypertrophic lakes (Jeppesen et al. 1997).

A conspicuous deviation between the predictions of this and other minimal zooplankton-algae models and the patterns observed in nature is that the amplitude of population oscillations in the field is usually much smaller than predicted by the models (McCauley and Murdoch 1987, McCauley et al. 1990). Also, contrary to the predictions *Daphnia* populations are sometimes reported to oscillate while the density of (edible) algae remains rather constant (McCauley and Murdoch 1987). These discrepancies between model predictions and field patterns may be largely explained from the fact that, especially when predators are present, *Daphnia* individuals are usually aggregated rather than dispersed randomly throughout a lake (Scheffer et al. 1995). If phytoplankton is depleted only locally in *Daphnia* aggregations, average algal densities can remain relatively unaffected by *Daphnia* peaks. Our model considers only the local dynamics in the part of the lake volume where *Daphnia* is present. The connection with the ungrazed part of the lake where algae are assumed to be approximately at carrying capacity is mimicked by the diffusive inflow term  $d(K - A)$  in eq. (1). Obviously, if *Daphnia* is concentrated in a small portion of the lake volume and exchange rates ( $d$ ) are small, large oscillations in their

population size may cause only a small ripple in overall algal biomass as is often observed.

The way in which the effect of seasons is mimicked in our model is another crude simplification of what happens in nature. It is remarkable that even with this minimal version of seasonality much of the observed dynamics can be produced. On the other hand it is not unusual that inclusion of more realistic details destroys the desired behaviour instead of enhancing it. Especially the assumption that the effects of temperature, light and fish predation all vary exactly sinusoidally, in phase and with the same amplitude is a conspicuous over-simplification. We have played extensively with more realistic time lags and variation in amplitudes, and found that the behaviour is very robust to such changes in the forcing regime. The robustness of the main patterns is illustrated well by the analysis of a comparable but much more elaborate model by Doveri et al. (Doveri et al. 1993). In that model, nutrient recycling and the dynamics of young-of-the-year fish are modelled dynamically, the role of adult fish that prey on zooplankton facultatively is modelled explicitly, and realistic temperature and light scenarios at different latitudes are analysed. The dominant dynamic patterns produced by this elaborate model are very similar to the repertoire of our minimal model.

Obviously, there are still many more mechanisms involved in driving plankton dynamics in reality. Depletion of nutrients, for instance, is probably contributing to the collapse of the spring bloom of algae in many cases (Reynolds 1984, Sommer et al. 1986, Vyhánek 1989), although *Daphnia* grazing on algae is usually considered the main mechanism causing the spring clear-water phase (Lampert et al. 1986, Luecke et al. 1990, Rudstam et al. 1993, Sarnelle 1993, Hanson and Butler 1994, Townsend et al. 1994, Jurgens and Stolpe 1995). Also, many organisms are able to time the start of a new cohort on the basis of temperature or light clues. *Daphnia*, for instance, tends to produce inert resting stages (ephippia) during periods of food shortage (De Stasio 1990). In spring those ephippia can emerge massively to form the off-set of the spring population peak that grazes down the spring bloom of algae. It could be argued, however, that the fact that largely the same population dynamics can be generated without such biological timing mechanisms, suggests that they are 'post-hoc' adaptations to optimize the reproductive moment with respect to food availability, rather than the prime forces driving the seasonal pattern.

In conclusion, the current results indicate that surprisingly much of the observed seasonal dynamics of *Daphnia* and algal biomass can be interpreted simply as the result of their predator-prey interaction if we account for the fact that everything, including planktivory, speeds up in summer and slows down in winter.

*Acknowledgements* – We want to thank the STOWA for allowing us to use the data presented in Figs 1, 2 and 3. The centre for limnology of the NIOO kindly allowed us to use the data presented in Figs 4C and D. Part of this work was carried out at the International Institute of Applied Systems Analysis, Laxenburg, Austria, and has been partially supported by the Italian Ministry of Scientific Research and Technology, contract MURST 40% Teoria dei sistemi e del controllo.

## References

- Arnold, D. E. 1971. Ingestion, assimilation, survival, and reproduction of *Daphnia pulex* fed seven species of blue-green algae. – *Limnol. Oceanogr.* 16: 906–920.
- Arnold, V. 1983. Geometrical methods in the theory of ordinary differential equations. – Springer-Verlag, New York.
- Berger, C. 1975. Occurrence of *Oscillatoria agardhii* Gom. in some shallow eutrophic lakes. – *Verh. Int. Ver. Theor. Angew. Limnol.* 19: 2689–2697.
- Brooks, J. L. and Dodson, S. I. 1965. Predation, body size and composition of plankton. – *Science* 150: 28–35.
- Carpenter, S. R., Lathrop, R. C. and Munoz-Del-Rio, A. 1993. Comparison of dynamic models for edible phytoplankton. – *Can. J. Fish. Aquat. Sci.* 50: 1757–1767.
- Caughley, G. and Lawton, J. H. 1981. Plant-herbivore systems. – In: May, R. M. (ed.), *Theoretical ecology, principles and applications*. 2. Blackwell, Oxford, pp. 132–166.
- De Stasio, B. T., Jr. 1990. The role of dormancy and emergence patterns in the dynamics of a freshwater zooplankton community. – *Limnol. Oceanogr.* 1079–1090.
- Doveri, F., Scheffer, M., Rinaldi, S., Muratori, S. and Kuznetsov, Y. A. 1993. Seasonality and chaos in a plankton-fish model. – *Theor. Popul. Biol.* 43: 159–183.
- Engelmayer, A. 1995. Effects of predator-released chemicals on some life history parameters of *Daphnia pulex*. – *Hydrobiologia* 307: 203–206.
- Gilpin, M. E. 1972. Enriched predator-prey systems: theoretical stability. – *Science* 177: 902–904.
- Gliwicz, Z. M. 1990. Why do cladocerans fail to control algal blooms? – *Hydrobiologia* 200/201: 83–98.
- and Lampert, W. 1990. Food thresholds in *Daphnia* species in the absence and presence of blue-green filaments. – *Ecology* 71: 691–702.
- Gragani, A. and Rinaldi, S. 1995. A universal bifurcation diagram for seasonally perturbed predator-prey models. – *Bull. Math. Biol.* 57: 701–712.
- Grebogi, C., Ott, E. and Yorke, J. A. 1987. Chaos, strange attractors and fractal basin boundaries in non-linear dynamics. – *Science* 238: 632–638.
- Guckenheimer, J. and Holmes, P. 1983. *Nonlinear oscillations, dynamical systems and bifurcations of vector fields*. – Springer-Verlag, New York.
- Gulati, R. D. 1983. Zooplankton and its grazing as indicators of trophic status in Dutch lakes. – *Environ. Monit. Assess.* 3: 343–354.
- Hambright, K. D. 1994. Can zooplanktivorous fish really affect lake thermal dynamics? – *Arch. Hydrobiol.* 130: 429–438.
- Hanson, M. A. and Butler, M. G. 1994. Responses of plankton, turbidity and macrophytes to biomanipulation in a shallow prairie lake. – *Can. J. Fish. Aquat. Sci.* 51: 1180–1188.
- Harper, D. M. and Ferguson, A. J. D. 1982. Zooplankton and their relationships with water quality and fisheries. – *Hydrobiologia* 88: 135–145.
- Hastings, A., Hom, C. L., Ellner, S. and Turchin, P. 1993. Chaos in ecology – Is mother nature a strange attractor? – *Annu. Rev. Ecol. Syst.* 24: 1–33.
- Hosper, S. H. and Meijer, M.-L. 1986. Control of phosphorus loading and flushing as restoration methods for Lake Veluwe, the Netherlands. – *Hydrobiol. Bull.* 20: 183–194.

- Jeppesen, E., Jensen, J. P., Søndergaard, M., Lauridsen, T. L., Pedersen, L. J. and Jensen, L. 1997. Top-down control in freshwater lakes with special emphasis on the role of fish, submerged macrophytes and water depth. – *Hydrobiologia* 342: 151–164.
- Jurgens, K. and Stolpe, G. 1995. Seasonal dynamics of crustacean zooplankton, heterotrophic nanoflagellates and bacteria in a shallow, eutrophic lake. – *Freshw. Biol.* 33: 27–38.
- Khibnik, A. I., Kuznetsov, Y. A., Levitin, V. V. and Nikolaev, E. V. 1992. Continuation techniques and interactive software for bifurcation analysis of ODE's and iterative maps. – *Physica D* 62: 360–370.
- Kuznetsov, Y. A. 1995. Elements of applied bifurcation theory. – Springer-Verlag, New York.
- , Muratori, S. and Rinaldi, S. 1992. Bifurcations and chaos in a periodic predator-prey model. – *Int. J. Bifurcation Chaos* 2: 117–128.
- Lair, N. and Ayadi, H. 1989. The seasonal succession of planktonic events in Lake Aydat, France: a comparison with the PEG model. – *Arch. Hydrobiol.* 115: 589–602.
- Lammens, E. H. R. R. 1985. A test of a model for planktivorous filter feeding by bream *Abramis brama*. – *Environ. Biol. Fishes* 13: 289–296.
- , DeNie, H. W., Vijverberg, J. and Densens, W. L. T. 1985. Resource partitioning and niche shifts of bream (*Abramis brama*) and eel (*Anguilla anguilla*) mediated by predation of smelt (*Osmerus eperlanus*) on *Daphnia hyalina*. – *Can. J. Fish. Aquat. Sci.* 42: 1342–1351.
- Lampert, W. and Rothhaupt, K. O. 1991. Alternating dynamics of rotifers and *Daphnia magna* in a shallow lake. – *Arch. Hydrobiol.* 120: 447–456.
- , Fleckner, W., Rai, H. and Taylor, B. E. 1986. Phytoplankton control by grazing zooplankton: a study on the spring clear-water phase. – *Limnol. Oceanogr.* 31: 478–490.
- Luecke, C., Vanni, M. J., Magnuson, J. J. and Kitchell, J. F. 1990. Seasonal regulation of *Daphnia* populations by planktivorous fish implications for the spring clear-water phase. – *Limnol. Oceanogr.* 35: 1718–1733.
- McCauley, E. and Murdoch, W. W. 1987. Cyclic and stable populations: plankton as paradigm. – *Am. Nat.* 129: 97–121.
- , Murdoch, W. E. and Nisbet, R. M. 1990. Growth reproduction and mortality of *Daphnia pulex* Leydig life at low food. – *Funct. Ecol.* 4: 505–514.
- Munro, I. G. and Bailey, R. G. 1980. Early composition and biomass of the crustacean zooplankton in Bough Beech Reservoir, Southeast England, UK. – *Freshw. Biol.* 10: 85–96.
- Reynolds, C. S. 1984. The ecology of freshwater phytoplankton. – Cambridge Univ. Press, Cambridge.
- Rinaldi, S. and Muratori, S. 1993. Conditioned chaos in seasonally perturbed predator prey models. – *Ecol. Model.* 69: 79–97.
- Rose, K. A., Swartzman, G. L., Kindig, A. C. and Taub, F. A. 1988. Stepwise iterative calibration of a multi-species phytoplankton-zooplankton simulation model using laboratory data. – *Ecol. Model.* 42: 1–32.
- Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. – *Science* 171: 385–387.
- Rudstam, L. G., Lathrop, R. C. and Carpenter, S. R. 1993. The rise and fall of a dominant planktivore: direct and indirect effects on zooplankton. – *Ecology* 74: 303–319.
- Sarnelle, O. 1993. Herbivore effects on phytoplankton succession in a eutrophic lake. – *Ecol. Monogr.* 63: 129–149.
- Sas, H. 1989. Lake restoration by reduction of nutrient loading: expectations, experiences, extrapolations. – Academia Verlag Richarz, St. Augustin.
- Schaffer, W. M. 1988. Perceiving order in the chaos of nature. – In: Boyce, M. S. (ed.), *Evolution of life histories of mammals*. Yale University Press, New Haven, CT, pp. 313–350.
- Scheffer, M. 1991. Fish and nutrients interplay determines algal biomass: a minimal model. – *Oikos* 62: 271–282.
- , Van den Berg, M., Breukelaar, A. W., Breukers, C., Coops, H., Doef, R. W. and Meijer, M.-L. 1994. Vegetated areas with clear water in turbid shallow lakes. – *Aquat. Bot.* 49: 193–196.
- , Baveco, J. M., DeAngelis, D. L., Lammens, E. H. R. R. and Shuter, B. 1995. Stunted growth and stepwise die-off in animal cohorts. – *Am. Nat.* 145: 376–388.
- Schindler, D. E. 1971. Food quality and zooplankton nutrition. – *J. Anim. Ecol.* 40: 589–595.
- Seda, J. and Duncan, A. 1994. Low fish predation pressure in London reservoirs: 2. consequences to zooplankton community structure. – *Hydrobiologia* 291: 179–191.
- Shapiro, J. and Wright, D. I. 1984. Lake restoration by biomanipulation Round Lake, Minnesota, the first two years. – *Freshw. Biol.* 14: 371–384.
- Sommer, U., Gliwicz, Z. M., Lampert, W. and Duncan, A. 1986. The Plankton Ecology Group model of seasonal succession of planktonic events in fresh waters. – *Arch. Hydrobiol.* 106: 433–472.
- Temte, J., Allen-Rentmeester, Y., Luecke, C. and Vanni, M. 1988. Effects of fish summerkill on zooplankton and phytoplankton populations in Lake Mendota. – *Annual International Symposium on Lake and Watershed Management* 8: 8.
- Townsend, D. W., Cammen, L. M., Holligan, P. M., Campbell, D. E. and Pettigrew, N. R. 1994. Causes and consequences of variability in the timing of spring phytoplankton blooms. – *Deep-Sea Res. Part A Oceanogr. Res. Pap.* 41: 747–765.
- Vandermeer, J. 1993. Loose coupling of predator-prey cycles – Entrainment, chaos and intermittency in the classic McArthur consumer-resource equations. – *Am. Nat.* 141: 687–716.
- Vyhnálek, V. 1989. Growth rates of phytoplankton populations in Rimov reservoir (Czechoslovakia) during the spring clear-water phase. – *Ergeb. Limnol.* 435–444.
- Weider, L. J. and Pijanowska, J. 1993. Plasticity of *Daphnia* life histories in response to chemical cues from predators. – *Oikos* 67: 385–392.