

## ALTERNATIVE STABLE STATES IN EUTROPHIC, SHALLOW FRESHWATER SYSTEMS: A MINIMAL MODEL

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**KEYWORDS:** model; fish; vegetation; eutrophication; stability.

### ABSTRACT

A simple mathematical model was constructed, describing the relationships between pike, bream, aquatic macrophytes and the nutrient loading of shallow lakes. The model is analyzed with the use of zero-isoclines. It is concluded that, over a certain range of nutrient concentrations, the ecological relations incorporated in the model can give rise to the existence of two alternative stable equilibria; viz. a turbid bream-dominated one, and a clear state in which pike and aquatic vegetation are abundant. Under oligotrophic conditions, the clear-water state represents the only stable equilibrium; however, at high nutrient levels, the clear state is absent, or only locally stable. The response of the model to both increase and decrease of the nutrient level is characterised by hysteresis. The results indicate that manipulation of fish densities as a measure to improve water quality is only likely to produce long-term results when the nutrient level is below a certain threshold.

### INTRODUCTION

Recent experiments in small turbid lakes have shown that the removal of planktivorous and benthivorous fish, combined with the addition of predatory fish can lead to a dramatic improvement of water quality (MEIJER *et al.*, 1989; VAN DONK *et al.*, 1989). The short-term results of these and other biomanipulation experiments are encouraging. However, it is unclear whether on the long-term the manipulated system will return to the initial turbid condition, or stays in a new stable clear equilibrium. The latter possibility is suggested by the observation that both under clear and turbid conditions negative feedback mechanisms exist that tend to keep the system in its current state (TIMMS and MOSS, 1984; HOSPER, 1989). For shallow, eutrophic waters, characteristic for the Dutch situation, some relevant observations with respect to the possible equilibrium conditions can be summarised as follows (HOSPER, 1989).

Turbid, phytoplankton-dominated water generally contains large amounts of bream (*Abramis brama* L.) and other cyprinids, whereas pike (*Esox lucius* L.), the formerly important predator, is hardly found. Submerged vegetation is largely absent from such systems. Clear waters, on the other hand, are

generally characterised by relatively low populations of bream, and by the presence of a good pike stock and a well developed aquatic vegetation. In this paper, these two situations will be termed 'bream state' and 'pike state'. In the last century, most of the Dutch freshwater systems were in the clear pike state. The decline of pike and aquatic vegetation and the current dominance of bream and algae are generally considered to be caused by eutrophication as a result of increased nutrient loading. WILLEMSSEN (1980) showed that the pike/bream ratio is strongly correlated with water transparency, and that the separation between the pike and bream state is relatively distinct (Fig. 1).

In this paper a simple mathematical model is presented containing the ecological relations that are considered to be most important. The model is analyzed to determine whether these empirically derived relations are sufficient to allow the occurrence of alternative equilibria under the same external conditions. In addition the model is used to evaluate the relation between biomanipulation and reduction of nutrient loading as measures to improve water quality.

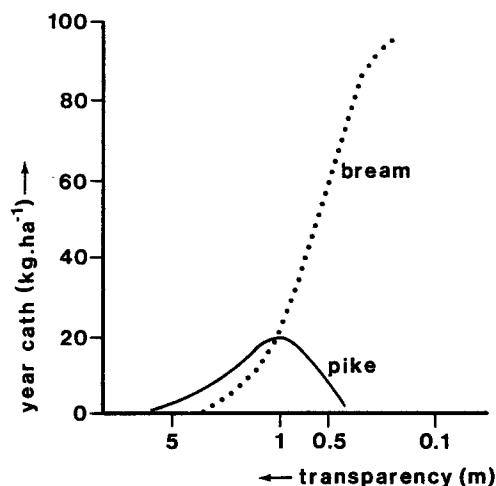


Fig. 1. Schematic representation of the relation between water transparency and the annual catches of pike and bream, based largely on Dutch data (after WILLEMSSEN, 1980).

## FORMULATION OF THE MODEL

The approach focusses on the interaction structure presented in Fig. 2. The components of this scheme are connected by four relations incorporated in the model as simple Monod and Hill functions (Fig. 3). Each of these relations is directly or indirectly supported by empirical evidence.

1. Populations of bream have a higher growth rate in more eutrophic waters. Enlarged production of planktivorous and benthivorous fish in artificially enriched waters is amply documented (for a review see *e.g.* GERKING, 1978).

2. High bream populations limit the development of aquatic vegetation. The effect of bream on aquatic vegetation is profound. In enclosure experiments, HILL *et al.* (1986) found a strong negative relation between stocked biomass of bream and the remaining biomass of aquatic macrophytes. If considered in detail the mechanism of the impact of bream on vegetation appears to be compound. The diet of bream consists mainly of zooplankton and of chironomid larvae and other bottom-dwelling invertebrates. When searching for the latter, bream disturbs the sediment. In experiments where this impact has been prevented by means of fish enclosure cages placed on the bottom, a regrowth of submerged macrophytes is observed within a few weeks (TEN WINKEL and MEULEMANS, 1984). Beside the mechanical impact that can be derived from this observation, a more indirect

effect of bream on vegetation exists. Various studies have shown that the presence of bream and other planktivorous and benthivorous fish causes an increase of water turbidity (*e.g.* CRONBERG, 1982; MEIJER *et al.*, 1989; SHAPIRO, 1980; VAN DONK *et al.*, 1989). This is partly an effect of the whirling up of sediment, causing an increase in particulate matter and nutrient concentrations in the water, and partly an effect of the grazing pressure of bream on zooplankton which in turn reduces the grazing on algae by zooplankton. The resulting high algal biomass and suspended matter concentration both contribute to an increase of water turbidity and eventually to a decrease in aquatic vegetation as a result of light limitation. In view of this mechanism, it is likely that the amount of aquatic vegetation in a lake will decrease with bream density in a nonlinear way for two different reasons. In the first place, there is some evidence that the effect of fish on the planktonic community is discontinuous (McQUEEN and POST, 1988; MILLS *et al.*, 1987). A collapse of populations of large zooplankton species coinciding with an elevation of phytoplankton abundance typically occurs at a certain threshold density of planktivorous fish. Secondly, since the maximum depth inhabited by plants is directly related to water turbidity (SPENCE, 1982), the depth profile of the lake will finally determine the shape of the relation between turbidity and the percentage of the lake covered by vegetation. In shallow lakes of homogeneous depth, aquatic macrophytes may be expected to disappear from the largest part of the lake quite suddenly if turbidity exceeds a certain value at which the average depth is becoming unsuitable for plant growth. Since, as argued, turbidity is directly related to fish density, the area covered with vegetation will probably decrease with increasing bream density in such lakes in a sigmoidal way.

3. Pike preys upon bream. Pike is considered as the most important predatory fish for the regulation of

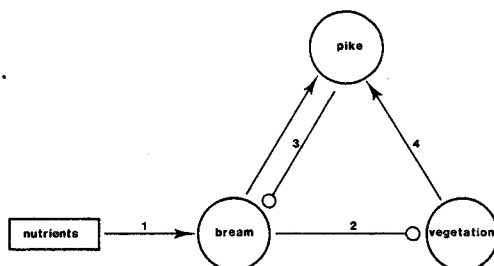


Fig. 2. The interaction structure used in the model. Positive effects are denoted by arrows, negative effects by open circles.

prey fish densities in shallow vegetated lakes (GRIMM, 1985). The predation efficiency of pike supposedly increases with prey density in a sigmoidal way approaching an upper limit at high prey availability. This type III functional response is generally considered to be a common feature of predators (e.g. HASSEL *et al.*, 1977).

4. Pike populations need vegetation for successful recruitment. There is a well documented positive relation between the standing stock of pike and the presence of aquatic vegetation (GRIMM, 1981, 1983; HAKKARI and BAGGE, 1985; RAAT, 1988). Pike is dependent on aquatic macrophytes for its reproduction. Furthermore, intraspecific predation is reduced by the presence of vegetation. The net effect of vegetation on the pike recruitment is generally reflected in the contribution of young pike to the total pike density. In the absence of aquatic vegetation young pike is hardly found (HAKKARI and BAGGE, 1985; WRIGHT, 1987).

For modelling purposes these four complex relations are reduced to simple Monod and Hill functions (Fig.

3). The whole system can now be represented by the following predator-prey model describing a complex pike-bream interaction:

$$dB/dt = ib + r \cdot \text{nutr} / (\text{nutr} + H_1) \cdot B - cb \cdot B^2 - \text{prmax} \cdot \text{FR} \cdot P$$

$$dP/dt = ip + ce \cdot \text{prmax} \cdot \text{FR} \cdot P \cdot \{V / (V + H_2)\} - mp \cdot P - cp \cdot P^2$$

where:  $V = K \cdot \{H_3^2 / (H_3^2 + B^2)\}$

$$\text{FR} = B^2 / (B^2 + H_4^2)$$

and where

B = bream density (g.m<sup>-2</sup>),

P = pike density (g.m<sup>-2</sup>),

V = percentage of lake covered with vegetation,

FR = functional response of pike,

ib = immigration rate of bream

$$(2 \cdot 10^{-5} \text{ g.m}^{-2} \cdot \text{day}^{-1}),$$

ip = immigration rate of pike (2 · 10<sup>-5</sup> g.m<sup>-2</sup> · day<sup>-1</sup>),

r = maximum growth rate of bream

$$(7.5 \cdot 10^{-3} \text{ day}^{-1}),$$

nutr. = nutrient level

(dimension irrelevant; see text),

H<sub>1</sub> = half saturation constant

(0.5; dimension irrelevant; see text),

H<sub>2</sub> = half saturation constant (10%),

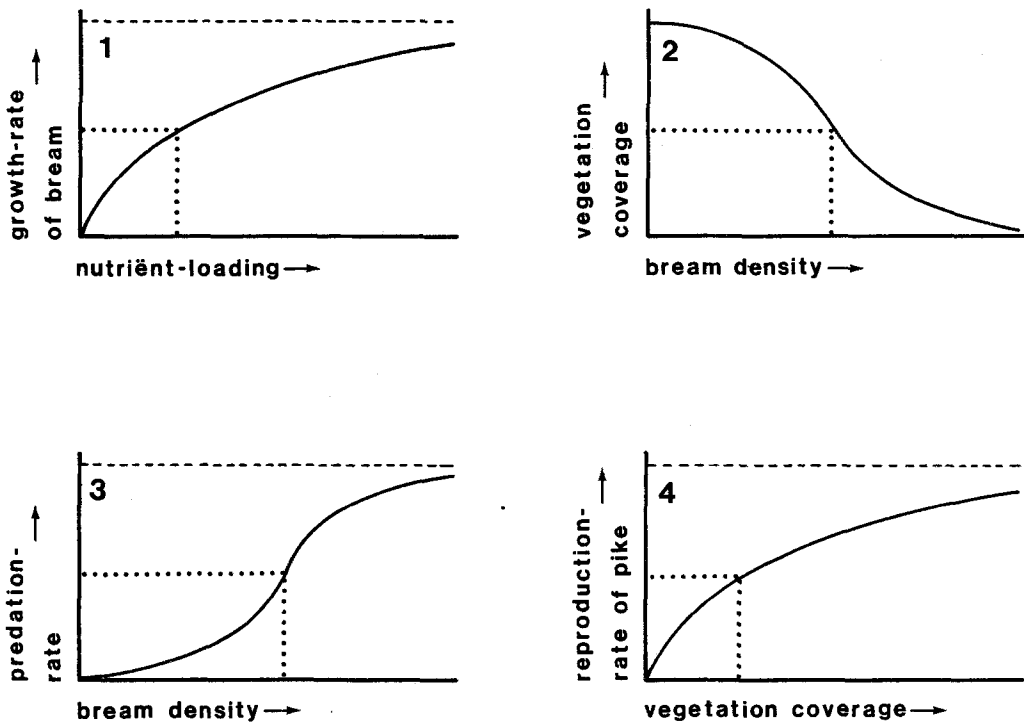


Fig. 3. Translation into Monod and Hill functions of the four main relations incorporated in the model.

$H_3$  = half saturation constant ( $20 \text{ g.m}^{-2}$ ),  
 $H_4$  = half saturation constant ( $15 \text{ g.m}^{-2}$ ),  
 $cb$  = intraspecific competition constant for bream  
 ( $7.5 \cdot 10^{-5} \text{ m}^{-2} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ ),  
 $cp$  = intraspecific competition constant for pike  
 ( $2.75 \cdot 10^{-4} \text{ m}^{-2} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ ),  
 $prmax$  = maximum predation rate of pike  
 ( $5 \cdot 10^{-2} \text{ day}^{-1}$ ),  
 $ce$  = pike food conversion efficiency to growth  
 (0.1),  
 $mp$  = mortality rate of pike ( $2.25 \cdot 10^{-3} \text{ day}^{-1}$ ),  
 $K$  = maximum vegetation coverage (100%).

#### Determination of parameters

Since no seasonality is incorporated in the model, parameters should reflect average annual situations. The values of the parameters concerning maximal growth rates, attainable standing stocks, and predation efficiency are estimated using data from the literature.

**r.** Assuming constant growth, a growth rate of  $0.01 \text{ .day}^{-1}$  can be derived from data for carp under optimal conditions in fish ponds (BACKIEL and LECREN, 1978). For bream under natural (and hence supposedly suboptimal) conditions a growth rate of  $0.005 \text{ .day}^{-1}$  can be derived from data for several eutrophic Dutch waters (CAZEMIER, 1982). The value for  $rbmax$  is arbitrarily set between these values.

**prmax.** Food consumption of pike is reported to average  $0.03 \text{ g.g}^{-1} \cdot \text{day}^{-1}$ . Arbitrarily 0.05 is taken as an estimate of maximum potential food consumption under optimal conditions.

**ce.** Pike's annual ratio of weight gain to consumed food is reported to be 0.11 by POPOVA (1978). The value of 0.1 is assigned to  $ce$  in the model.

**cb.** The ratio of  $r$  to  $cb$  sets the maximum standing stock for bream. Since the highest fish stocks in eutrophic waters are about  $100 \text{ g.m}^{-2}$ , the value of  $cb$  is computed as  $r/100$ .

**mp.** The largest annual decline in the Windermere pike population (KIPLING, 1983) is 40%, which is  $0.00125$  on a daily basis. Two times this value is taken as an estimate of mortality in complete absence of food, as should be reflected in  $mp$ .

**cp.** The intraspecific competition factor for pike sets the upper limit to pike density together with  $ce$  and  $prmax$ . Very high pike densities ( $P_{MAX}$ ) are about  $10 \text{ g.m}^{-2}$  (e.g. GRIMM, 1983). From the steady state solution of the pike equation the value of  $cp$  is estimated as:  $ce \cdot (prmax \cdot mp) / P_{MAX} = 2.75 \cdot 10^{-4}$ .

In the absence of suitable field data, all other parameter values are arbitrarily set. Half saturation constants of Monod and Hill functions should be evaluated in their context, viz. the parameters  $nutr$  and  $H_1$  only have a meaning relative to each other. The same applies to  $H_2$  and  $H_3$  relative to  $V$ , and to  $H_4$  relative to  $B$ . Immigration rates  $ip$  and  $ib$  are small and only serve to prevent irreversible extinction.

#### Method of analysis

The properties of the model are analyzed in a graphical way with the use of zero-isocline representations. Zero-isoclines, or isoclines for short, are lines on which the derivative of either of the state variables is zero. The net increase of bream biomass is zero on the bream isocline. The same applies to the net growth of the pike population on the pike isocline. The typical isocline picture of the presented model is given in Fig. 4. By definition, isoclines divide the state space (here the bream/pike plane) into areas where a state variable is increasing, and areas where a state variable is decreasing. The direction of change in pike and bream densities is marked in Fig. 4 by means of arrows. More thorough explanations of the use of zero-isoclines can be found for instance in MAY (1976). The isocline representations shown in this paper are derived from the model by means of the computer program GRIND (DE BOER, 1983).

## RESULTS

#### Alternative stable states

The general features of the model are reflected by the shape of the isoclines. The low position of the pike isocline at high bream densities is explained by the decrease of vegetation in these situations. The rise of the bream isocline at low bream densities is a result of the functional response used in the model. The isoclines intersect at three points. Since the net growth of both pike and bream is equal to zero at these points, they represent equilibrium points of the model. Points I and III are stable equilibria. However, point II represents an unstable equilibrium. The slightest perturbation will cause the system to shift away from this point with increasing speed. Unstable equilibria are merely of theoretical interest since they will not occur in fluctuating natural environments. The stable equilibria are of more interest for the current analysis. The two stable states of the modelled system appear to be analogous to the pike waters (I) and bream waters (III); subsequently, these points will be termed pike equilibrium and bream equi-

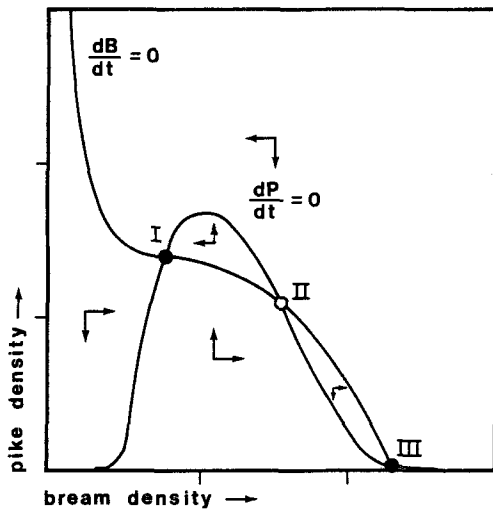


Fig. 4. Zero-isoclines of bream ( $dB/dt=0$ ) and pike ( $dP/dt=0$ ) (see text for explanation).

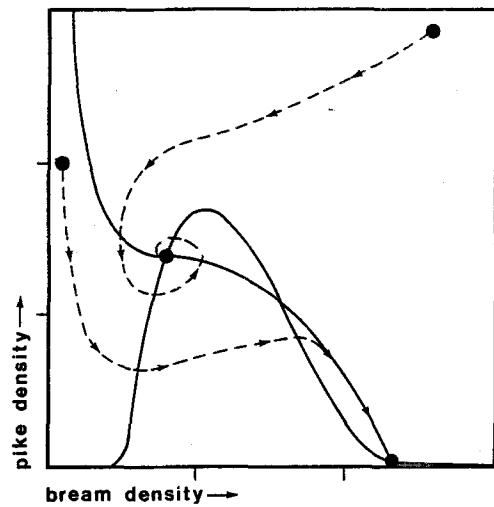


Fig. 5. Trajectories of two simulation starting from different initial states.

brum, respectively. Simulation runs end in either of the two equilibria depending on the initial conditions (Fig. 5).

**Hysteresis**

The effect of eutrophication on the system can be visualised by plotting isoclines for different values of the parameter NUTR (Fig. 6). The position of the pike isocline is not affected by the nutrient status. However, the position of the bream isocline changes with the nutrient level. The behaviour of an oligotrophic system subject to a eutrophication process can be easily derived from Fig. 6. The lower bream isocline applies to the oligotrophic state. A low pike-type equilibrium is the only possible steady state under these conditions. During the first stages of eutrophication the equilibrium will shift upwards slowly. Pike density increases but bream density does not change much. This type of response continues until the bream isocline reaches a position where the intersection point that represents the pike equilibrium disappears. At this point the pike population collapses to a level set by the immigration rate, and bream density, in the absence of its predator, increases approximately to the carrying capacity of the environment. A turbid bream equilibrium without vegetation is achieved. If subsequently the nutrient level is reduced to intermediate values, the system will stay in a bream type of equilibrium although bream density slightly decreases due to a reduced carrying capacity. Only at a very low nutrient status the intersection point representing the bream equi-

brum disappears and the system returns to a pike state.

Clearly this type of behaviour is analogous to that described by catastrophe theory as frequently applied to biological systems (e.g. MOHN and MILLER, 1987; ROSE and HARMSSEN, 1981). It should, therefore, be possible to visualise these properties of the model by means of an isocline showing a so-called catastrophe fold. Indeed, this can be produced from the

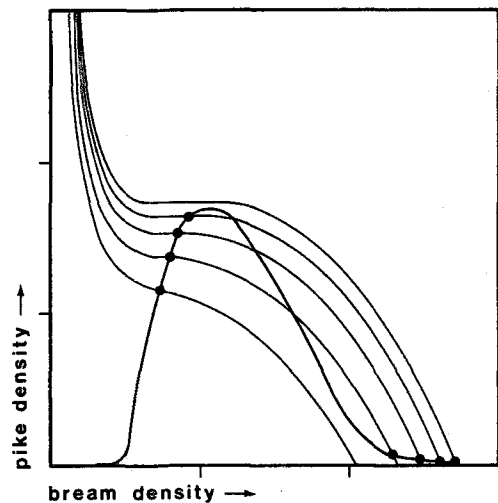


Fig. 6. The position of isoclines and stable equilibria at different nutrient levels. The highest position of the bream isocline corresponds to the highest nutrient concentration.

model (Fig. 7) by plotting a bream isocline in the bream-nutrients plane under the assumption that pike is in steady state. The nutrient status of the system is added as a third dimension to the bream-pike isocline representation. The intersection line of the two resulting isocline planes is an equilibrium line of the system. When this line is projected on the bottom of the cube (the nutrient-bream plane), the desired isocline is produced. The isocline consists of the stable parts I and III and an unstable part II (Fig. 7). Their interpretation is

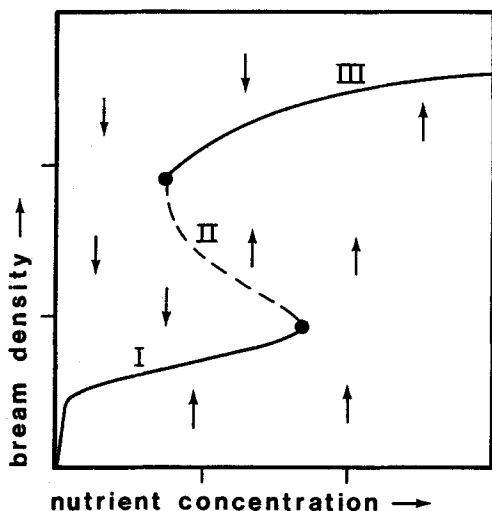
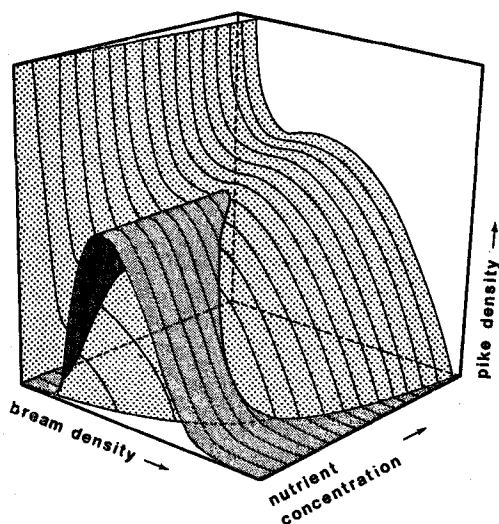


Fig. 7. A catastrophe fold is visualised by means of the projection of the intersection line of isocline planes of bream and pike on the nutrient-bream plane (the bottom of the cube, seen from below).

analogous to that of the equilibrium points in Fig. 4. A similar figure can be drawn in the nutrient-pike plane. The discontinuous response to increase and decrease of the nutrient level that was derived from Fig. 6 can easily be seen from this new representation of the model. The trajectory of a simulation run in which the nutrient level is slowly raised from very low to very high and consecutively in reverse is shown in Fig. 8.

It may be seen from these analyses that the existence of two alternative equilibria will only occur over a certain range of nutrient levels.

### Predator-prey cycles

If the response of the model to different changes in the parameter setting is scanned, the type of hysteresis shown in the foregoing appears to be not the only behaviour that can be produced by the model. If the value of the half saturation constant in the functional response of pike ( $H_4$ ) is decreased, thus increasing the predation efficiency of pike at low prey densities, the original shape of the bream isocline (Fig. 4) changes into a humped one (Fig. 9). Generally spoken such a humped form of the bream isocline arises if the half saturation constant is small relative to the carrying capacity of bream. In addition, this single-parameter change has increased the height of the pike isocline as could be intuitively expected. The new form of the bream isocline gives rise to a qualitatively different model behaviour (Fig. 10). At low nutrient levels the bream isocline resembles its original form and a stable pike equilibrium

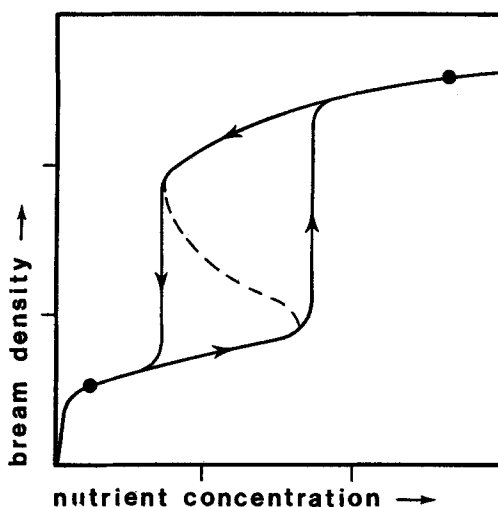


Fig. 8. Simulation of the systems response to gradual increase and decrease of the nutrient level, respectively.

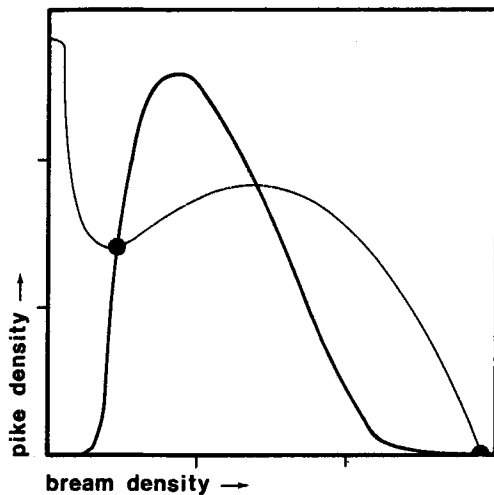


Fig. 9. Humped form of the bream isocline arising from a decrease in the half saturation constant of the functional response of pike (see text).

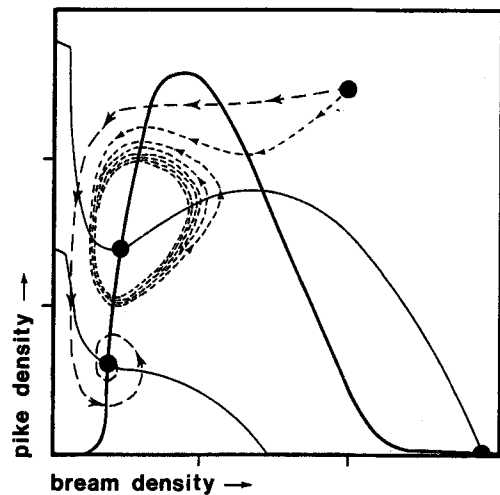


Fig. 10. Simulation runs departing from the same initial state at two different nutrient levels. A limit cycle occurs at the higher nutrient level.

exists. However, at higher nutrient levels the bream isocline has a positive slope at the intersection point that represents the pike equilibrium, and as a result the point-equilibrium changes into a so-called stable limit cycle.

Simulations starting close to the intersection point of the isoclines (the formerly stable equilibrium point) will show predator-prey oscillations that increase in size until the stable cycle is reached. Simulations starting from outside the cycle (but inside the attraction area of the pike equilibrium) will approach the stable limit cycle with damping oscillations (Fig. 10). (For further reading, see *e.g.* MAY, 1976). If the nutrient value is raised further, the size of the limit cycle increases until it reaches the attraction area of the other equilibrium. The system then collapses into the bream state. The way back at reduced nutrient levels is equal to that in the situation without cycles. This situation can also be depicted by means of a catastrophe fold (Fig. 11). Because of the increased height of the top of the pike-isocline (see next section), the parts I and II of this fold (Fig. 7) are no longer connected within the considered nutrient range. Therefore, at first sight it is impossible to escape from the lower part of the isocline representing the pike equilibrium even at high nutrient levels. However, if a simulation run of a slowly eutrophying system is plotted in this picture it appears that at a certain nutrient level oscillations start to occur. The amplitude of the oscillations follows the size of the limit-cycle, and consequently increases with the

nutrient level until the bifurcation line is hit. The system then switches to a bream equilibrium. The occurrence of limit cycles as a result of enrichment has been demonstrated to be a common feature of most predator-prey models where the growth rate of prey is dependent on the trophic state of the system (ROSENZWEIG, 1971; and discussion: McALLISTER *et al.*, 1972; ROSENZWEIG, 1972).

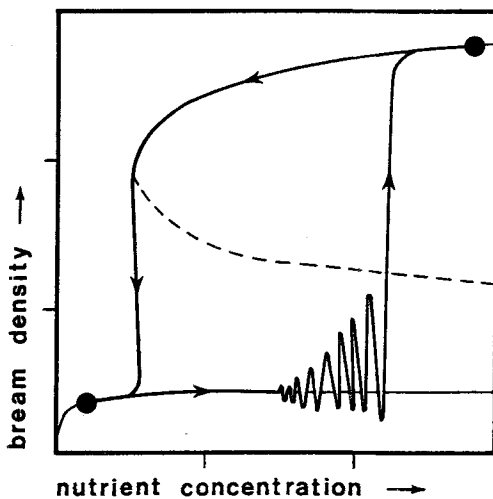


Fig. 11. Simulation of the systems response to a gradual increase in nutrient level shows the occurrence of intrinsic fluctuations preceding the switch (see text).

### Sensitivity to parameter changes

Hysteresis and the occurrence of alternative equilibria can easily be produced by the model presented. However, these phenomena will not arise under all conditions. Obviously, changes in parameter settings can change the qualitative behaviour of a model, as illustrated by the occurrence of a limit cycle in response to a change in just one parameter. The sensitivity of the model properties to changes in parameter values has been tested for all parameters. The results (not shown here) indicate that moderate changes in parameter values do not affect the occurrence of alternative equilibria. Nonetheless, some aspects deserve attention.

It is shown that the existence of two alternative equilibria is restricted to some range of nutrient levels. The length of this range depends on the value of the other model parameters. The left-hand limit of the range may be interpreted as the nutrient level at which the carrying capacity for bream is low enough to enable sufficient vegetation growth for the development of a pike population. Below this nutrient level, only one equilibrium exists. The upper limit is predominantly set by the height of the pike isocline. As a result of the built-in Monod formulation, the bream isocline rises asymptotically to a defined maximum height at increasing nutrient levels. If the top of the pike isocline lies above the highest possible bream isocline, nutrient levels can be increased unlimited without causing a spontaneous collapse of the system, although the alternative bream equilibrium still may exist. Note that, interestingly, the height of the pike isocline is no longer essential for the occurrence of an intrinsic switch of the system state if, as a response to increased nutrient levels, the pike equilibrium changes into a limit cycle.

The range of nutrient values over which two stable states exist, can decrease to zero if the top of the pike isocline is low relative to the bream isocline at an intermediate nutrient status. Here the slope of the right hand side of the bream isocline exceeds that of the pike isocline and only one intersection point will exist at any nutrient level. The system responds to eutrophication under such conditions without showing hysteresis.

The height of the top of the pike isocline relative to the possible positions of the bream isocline plays a central role in these considerations. The height of the pike top depends largely on the model parameters for 'non-food intraspecific competition' and mortality of pike ( $cp$  and  $mp$ ). The top of the pike isocline represents the maximum possible stable pike density that can be expected. Put in general terms, the behaviour of the system is dependent on the extent to

which the predator can increase its own density as a response to enlarged productivity of its prey.

### Stability analysis

Under conditions where two alternative stable states exist, the bream-pike plane is necessarily divided into two parts, *viz.* the attraction zone of the pike equilibrium and the attraction area of the bream equilibrium. The line that separates the two regions is called the separatrix. A knowledge of the exact position of the separatrix would allow an easy determination of the final steady state given the initial conditions. By definition the unstable equilibrium of the system lies on the separatrix.

However, an analytical solution to the position of the whole line is not feasible. Since the information is judged highly relevant for our purposes, the potential behaviour of the model is scanned in another way. The model is run from a large number of initial points lying in a grid over the state plane. A run is stopped when the model has reached an equilibrium (this is defined as the moment when the value of the maximum derivative of a population has passed a certain lower threshold and the maximum eigenvalue is negative). The length of each run is marked in the grid point corresponding to its initial condition. The result is visualised by plotting this matrix of 'settle times' as grey tones in the state plane (Fig. 12). Dark areas now represent initial conditions from which it takes a long time for the system to settle in either of the two equilibria. Hence, the equilibrium line is the darkest in the plane, and the neighbourhood of the equilibria is light. Obviously, the position of the separatrix is dependent on the nutrient status of the system. Under eutrophic conditions the attraction region of the pike equilibrium is relatively small. With decreasing nutrient levels the size of this region increases at the cost of the attraction area of the bream equilibrium (Fig. 12). The view that there can be a range of nutrient values at which two stable states exist should thus be extended; local stability of either of the two equilibria gradually changes over this range between the extremes of global stability and zero stability.

## DISCUSSION

### Interpretation of the model as a hypothesis

Clearly, the presented model is merely a complex hypothesis formulated in a mathematical way, and examined with the use of computer programs. According to PARTRIDGE and LOPEZ (1984), this is in fact the only means of thoroughly testing and



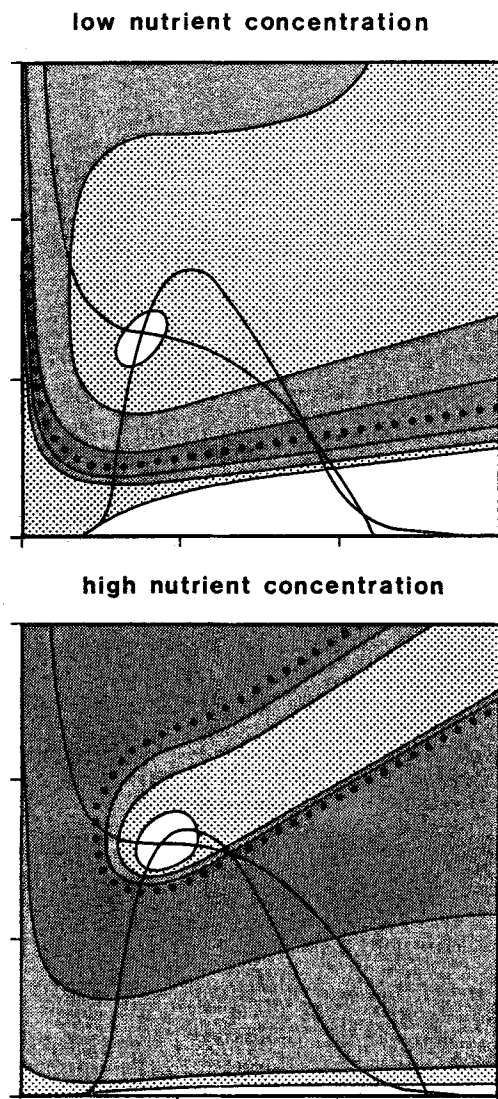


Fig. 12. The form of the attraction areas of both equilibria and the position of the separatrix (heavy dots) separating the areas, at two different nutrient levels.

examining a large and intricate theory. An obvious advantage of this approach is that implications of the theory can be generated in an unbiased way, although it should be noticed that translation of a more or less vague theory in a rigid mathematical form can introduce some artifacts. The fact that a model is analogous to a hypothesis should be carefully born in mind when interpreting the results. It can not be proved; it can only be falsified for a defined case; and its predictions are merely implications of the theory

under consideration. A review of some important results of the analysis of the model is useful in this light.

From the present analysis, it can be generalised that the ecological relations incorporated in the model are sufficient to allow the occurrence of two alternative stable states under the same external conditions. Obviously, this is not to be seen as a proof of the existence of this phenomenon in real ecosystems, but it may be inferred that it is reasonable to expect the occurrence of alternative equilibria in situations where the incorporated relations are valid.

The hysteresis followed by the catastrophic switch behaviour of the model as a response to a gradual increase of nutrient concentration is a characteristic result that is in line with observations from real systems. A catastrophic type of change in fresh water ecosystems has been reported frequently. DE NIE (1987) concludes from a review of literature that a shallow, eutrophic, relatively clear water that is rich in water plants, can change into a phytoplankton-dominated state within a short time and without remarkable increase in the actual nutrient loading. Obviously, although the model can supply an adequate explanation for this type of system change this can not be a proof of the validity of the underlying theory; other theories may be equally suitable. Nonetheless, additional available information (HOSPER, 1989) lends support to the relevance of the presented model for the situation in shallow eutrophic waters. Whether or not the assumptions underlying the model are valid in other aquatic systems as well remains to be seen. The essential mechanism in the model is that the considered predator can substantially reduce the density of its prey, whereas the prey species can, in high densities, render the environment unsuitable for its predator. This scenario may be applicable to other situations, but is probably quite specific to shallow water bodies where vegetation can be abundant and the vegetation-dependent predator pike is the dominant piscivore.

#### Bio-manipulation

The possibility of the existence of two alternative equilibria in freshwater ecosystems is of special interest from the viewpoint of bio-manipulation. If both equilibria exist, and the system is moved away from the current equilibrium as a result of some enforced change in a population density, it will consecutively settle in either of the two equilibria. Enforced density changes may result from human activities like bio-manipulation, but also from sto-

chastic, environmental effects like the occurrence of diseases or exceptionally warm or cold years. Although no quantitative predictions may be expected from this minimal model, the relative sensitivity to different kinds of density shifts may be derived from the presented settle time maps (Fig. 12). It may for instance be seen that biomanipulation in the form of an enforced decrease of bream density will generally not be enough to escape from a turbid bream state. Addition of the predator seems a required extra measure under these conditions.

As shown, the nutrient status has a pronounced effect on the form of the regions of local stability. The attraction area of the pike equilibrium gets smaller with increasing nutrient levels. This implies that, under eutrophic conditions, perturbations may easily bring the system from the pike state into the attraction region of the bream equilibrium, causing a collapse. The system is especially sensitive to a decrease in pike under these conditions. A decrease in bream density or an increase in pike density can also destroy the pike state. If the objective is to get

the system from a bream state into a pike equilibrium by means of a manipulation of pike and bream densities, it can be seen that the chance of success will be much larger at low nutrient levels than under eutrophic conditions. Above a certain upper threshold to the nutrient level no stable pike state can be achieved. This is similar to the conclusion drawn by BENNDORF (1987) from a review of biomanipulation experiments: "a lake-specific 'biomanipulation-efficiency threshold' of the phosphorous load should not be exceeded".

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#### REFERENCES

- BACKIEL, T. and E.D. LE CREN, 1978. Some density relationships for fish population parameters. In: S.D. Gerking, Ed., Ecology of Freshwater Fish Production, p. 279-302. Blackwell, Oxford.
- BENNDORF, J., 1987. Food web manipulation without nutrient control: a useful strategy in lake restoration? *Schweiz. Z. Hydrol.*, 49: 237-248.
- CAZEMIER, W.G., 1982. The growth of bream (*Abramis brama* L.) in relation to habitat and population density. *Hydrobiol. Bull.*, 16: 269-277.
- CRONBERG, G., 1982. Phytoplankton changes in Lake Trummen induced by restoration. *Folia Limnologica Scandinavica*, 18: 1-119.
- DE BOER, R.J., 1983. GRIND Great Integrator Differential Equations. Bioinformatics group, University of Utrecht.
- DE NIE, H.W., 1987. The decrease in aquatic vegetation in Europe and its consequences for fish populations. EIFAC/CECPI, occasional paper no. 19, 52 pp.
- GASCON, D. and W.C. LEGGET, 1977. Distribution, abundance and resource utilization of littoral zone fishes in response to a nutrient/production gradient in Lake Memphremagog. *J. Fish. Res. Board Can.*, 34: 1105-1117.
- GERKING, S.D., Ed., 1978. Ecology of Freshwater Fish Production. Blackwell, Oxford.
- GRIMM, M.P., 1981. The composition of northern pike (*Esox lucius* L.) populations in four shallow waters in The Netherlands with special reference to factors influencing O<sup>+</sup> pike biomass. *Fish. Management*, 12: 61-79.
- GRIMM, M.P., 1983. Regulation of biomasses of small (<41 cm) northern pike (*Esox lucius* L.), with special reference to the contribution of individuals stocked as fingerlings (4-6 cm). *Fish. Management*, 14: 115-133.
- GRIMM, M.P., 1985. Pike. In: pike, pike perch and bream: biology, population development and control. Report of the working party on the evaluation of control methods. OVB, Nieuwegein. (in Dutch).
- HAKKARI, L. and P. BAGGE, 1985. On fry densities of pike (*Esox lucius* L.) in Lake Sainaa, Finland. *Verh. Internat. Verein. Limnol.*, 22: 2560-2565.
- HASSEL, M.P., J.H. LAWTON and J.R. BEDDINGTON, 1977. Sigmoid functional responses by invertebrate predators and parasitoids. *J. Anim. Ecol.*, 46: 249-262.
- HILL, D., R. WRIGHT and M. STREET, 1986. Survival of mallard ducklings (*Anas platyrhynchos*) and competition with fish for invertebrates on a flooded gravel quarry in England. *Ibis*, 129: 159-167.
- HOSPER, S.H., 1989. Biomanipulation, new perspectives for restoration of shallow eutrophic lakes in The Netherlands. *Hydrobiol. Bull.*, 23: 5-10.
- KIPLING, C., 1983. Changes in the population of pike (*Esox lucius*) in Windermere from 1944 to 1981. *J. Anim. Ecol.*, 52: 989-999.
- MANN, R.H.K., 1982. The annual food consumption and prey preferences of pike (*Esox lucius*) in the river Frome, Dorset. *J. Animal. Ecol.*, 51: 81-95.
- MAY, R.M., 1976. Theoretical ecology. Blackwell, London.
- McALLISTER, C.D., R.J. LEBRASSEUR and T.R. PARSONS, 1972. Stability of enriched aquatic ecosystems. *Science*, 175: 562-564.
- McQUEEN, D.J. and J.R. POST, 1988. Cascading trophic interactions: uncoupling at the zooplankton-phytoplankton link. *Hydrobiologia*, 159: 277-296.

- MEIJER, M.-L., A.J.P. RAAT and R.W. DOEF, 1989. Restoration by biomanipulation of the Dutch shallow, eutrophic Lake Bleiswijkse Zoom, first results. *Hydrobiol. Bull.*, 23: 49-57.
- MILLS, E.L., J.L. FORNEY and K.J. WAGNER, 1987. Fish predation and its cascading effect on the Oneida Lake food chain. In: W.C. Kerfoot and A. Sih, Eds., *Predation, direct and indirect impacts on aquatic communities*, p. 118-131. University Press of New England, Hanover.
- MOHN, R.K. and R.J. MILLER, 1987. A ration-based model of a seaweed/sea urchin community. *Ecological Modelling*, 37, 249-267.
- PARTRIDGE, D. and P. LOPEZ, 1984. Computer programs as theories in biology. *J. theor. Biol.*, 108: 539-564.
- POPOVA, O.A., 1978. The role of predacious fish in ecosystems. In: S.D. Gerking, Ed., *Ecology of freshwater fish production*, p. 215-249 Blackwell, Oxford.
- RAAT, A.J.P., 1988. Synopsis of biological data on the northern pike, *Esox lucius* L. FAO Fisheries Synopsis No. 30 Rev. 2. FAO, Rome.
- ROSE, M.R. and R. HARMSSEN, 1981. Ecological outbreak dynamics and the cusp catastrophe. *Acta Biotheoretica*, 30: 229-253.
- ROSENZWEIG, M.L., 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science*, 171: 385-387.
- ROSENZWEIG, M.L., 1972. Stability of enriched ecosystems; a reply. *Science*, 175: 564-565.
- SHAPIRO, J., 1980. The importance of trophic-level interactions to the abundance and species composition of algae in lakes. In: J. Barica and R. Mur, Eds., *Developments in Hydrobiology, Vol. 2, Hypertrophic ecosystems*, pp. 105-116.
- SPENCE, D.H.N., 1982. The zonation of plants in freshwater lakes, 12: 37-125.
- TEN WINKEL, E.H. and J.T. MEULEMANS, 1984. Effects of fish upon submerged vegetation. *Hydrobiol. Bull.*, 18: 157-158.
- TIMMS, R.M. and B. MOSS, 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing in the presence of zooplanktivorous fish in a shallow wetland ecosystem. *Limnol. Oceanogr.*, 29: 472-486.
- VAN DONK, E., R.D. GULATI, and M.P. GRIMM, 1989. Food web manipulation in Lake Zwemlust: positive and negative effects during the first two years. *Hydrobiol. Bull.*, 23: 19-34.
- WILLEMSEN, J., 1980. Fishery aspects of eutrophication. *Hydrobiol. Bull.*, 14: 12-21.
- WRIGHT, R., 1987. The pike population of the A.R.C. Wildfowl reserve. In: *The Game conservancy, Annual review 1986*, p. 139-141 Fordingbridge.

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