Aquatic macrophytes: restore, eradicate or is there a compromise?

Egbert H. van Nes [a,*], Marten Scheffer [a],
Marcel. S. van den Berg [b], Hugo Coops [b]

[a] *Aquatic Ecology and Water Quality Management Group, Wageningen Agricultural University,
P.O. Box 8080, 6700 DD Wageningen, The Netherlands*
[b] *RIZA, P.O. Box 17, 8200 AA Lelystad, The Netherlands*

Abstract

Promoting indigenous submerged macrophytes is considered an important measure to restore shallow lakes. On the other hand, dense stands of aquatic vegetation often cause nuisance for boating, swimming and by obstruction of water flow. Consequently, the interests of recreational users may conflict with nature conservation. At first sight, aiming lake management at intermediate vegetation biomass seems a good solution for this controversy. However, as can be shown with a simple economical model, such a compromise may not always be an optimal solution in terms of total welfare across all users of a lake. Here, we show that a management strategy aimed at moderate plant biomass can also be unfeasible for ecological reasons. This is shown by applying two very different models: a minimal logistic model of plant growth which is easy to understand, and the relatively complex and realistic simulation model Charisma which, among other things, includes the seasonal cycle and a detailed description of the dynamics of light availability for macrophytes. The qualitative results of both models were remarkably similar. If the ecosystem has no alternative stable states, it is possible to set vegetation to any desired sustainable level using an appropriate harvesting strategy. However, if an intermediate vegetation biomass is to be realized the costs of harvesting are high, because the yield is predicted to be maximal in that case. If the ecosystem has alternative stable states, harvesting becomes risky because the vegetation may collapse entirely below a certain, in practice unknown, biomass. Also, even moderate harvesting may reduce the resilience of the vegetated state, making the ecosystem more vulnerable to adverse conditions such as unfavorable weather conditions or bird grazing. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Aquatic weeds; Logistical growth equation; Functional response; Harvesting; Model; Charophytes

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* Corresponding author. Tel.: +31-317-482733; fax: +31-317-484411.
E-mail address: egbert.vannes@aqec.wkao.wau.nl (E.H. van Nes).

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1. Introduction

The interests of different groups of lake users often conflict. This is especially true with respect to the proliferation of aquatic macrophytes, for which nature conservationists and recreationists often have opposing interests (Clayton and Tanner, 1988; van Nes et al., 1999).

In general, a dense macrophyte vegetation is desirable from a conservationist's point-of-view. Both bird abundance and biodiversity are higher in vegetated lakes than in lakes without vegetation (Scheffer, 1998). Furthermore, vegetation reduces the turbidity of shallow lakes (e.g. Hasler and Jones, 1949; Timms and Moss, 1984; Van den Berg et al., 1998). Therefore, promotion of vegetation should be an important tool for lake restoration (Moss, 1990). van Nes et al. (1999) argue that the conservation benefits of most types of indigenous macrophytes can probably be represented by a sigmoidally increasing function of vegetation biomass. Possibly, the function has an optimum, above which dense macrophyte beds have a negative effect on biodiversity. The critical biomass at which macrophytes become beneficial for nature conservation, will vary considerably for different lakes and depends on the growth forms of the predominant plant species.

In contrast, recreational users (including boaters, surfers and swimmers) are often hindered by dense vegetation (Clayton and Tanner, 1988). Nuisance to recreational users may generally increase with macrophyte biomass (van Nes et al., 1999). Although the exact nature of the nuisance is unknown, it may be reasonable to assume a similar sigmoidal curve with vegetation biomass. Below a certain biomass level, boating and swimming are not hindered at all. If the vegetation stands exceed a critical density, in particular when the plants cover the water surface, vegetation becomes a nuisance. As for conservation, the growth form of the vegetation is highly relevant for recreation.

Although it is hard to compare the interests of the two very different groups, a possible way to deal with this is to use the approach of environmental economists to account for all interests in the common currency of 'welfare' or 'benefit' (Hanley and Spash, 1993; Perman et al., 1996; Varian, 1996). The overall welfare of the society is composed by the contribution of each group weighed with the political impact of the group. The optimal strategy from a 'rational social planner's' point-of-view is to aim at the biomass where the total welfare function is at an optimum.

van Nes et al. (1999) explored welfare functions for some distinct groups of macrophytes. They showed that the shape of the overall welfare function, describing vegetation of different growth forms, would be very different. For vegetation with a low growth form that does not reach the water surface, such as many *Chara* species, the conservation benefit is relatively high (Crawford, 1979; Clayton and Tanner, 1988; Coops and Doef, 1996), whereas the nuisance obviously is relatively low (Fig. 1). The result is a situation where a simple compromise between the two interest groups coincides with an optimum in overall welfare obtained from the lake. Aiming at an intermediate biomass seems the optimal policy in such case.

Canopy-forming or floating vegetation causes nuisance for boating and swimming at relatively low densities and such vegetation is of low benefit in lake restoration (Fig. 2). As a result, the total welfare may often be minimal at an intermediate biomass. Seeking a compromise between both groups by realizing an intermediate plant biomass is obviously the worst policy in this case (van Nes et al., 1999).
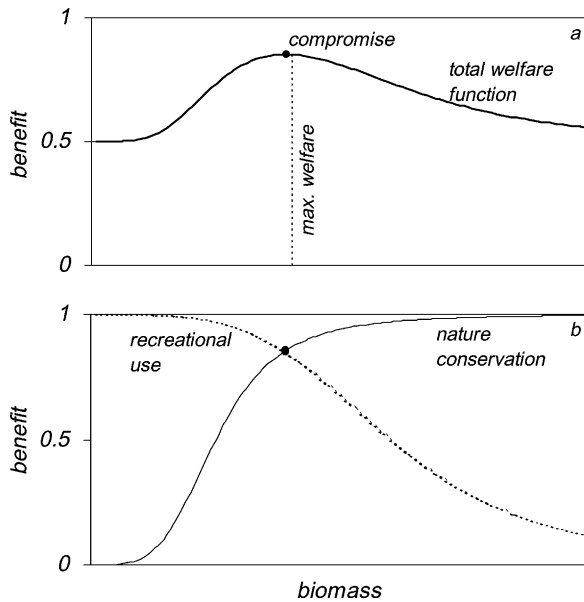
Fig. 1. Benefit obtained from a lake by recreational users and nature conservationists assuming aquatic vegetation with a low growth form such as charophytes (see text). The total benefit (panel a) is the mean of the benefit functions of the separate user groups (panel b). The point with a compromise between both groups (closed circle) coincides with the maximum total benefit (van Nes et al., 1999).

In this paper we analyze the response of an aquatic plant population, subject to harvesting by means of a simple generic model and a more complex and realistic model describing the growth of *Chara aspera* Deth. ex Willd. The results indicate that even if the intermediate biomass is desirable from an economic point-of-view, it would in some cases be impossible or at least very costly to keep the vegetation biomass at such level.

2. A minimal model of harvesting vegetation

The simple model is similar to those used to analyze the dynamics of grazing systems in terrestrial ecology (Noy-Meir, 1975; van de Koppel et al., 1997). The main difference here is that the vegetation is not grazed by herbivorous animals, but instead harvested by humans.

We describe the change of vegetation biomass (V) by a logistic equation with a carrying capacity K:

$$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right) \tag{1}$$

This classical model assumes that intraspecific competition causes a linear decrease of the relative growth rate ($dV/dt/V$) with increasing vegetation biomass. At carrying capacity (K),
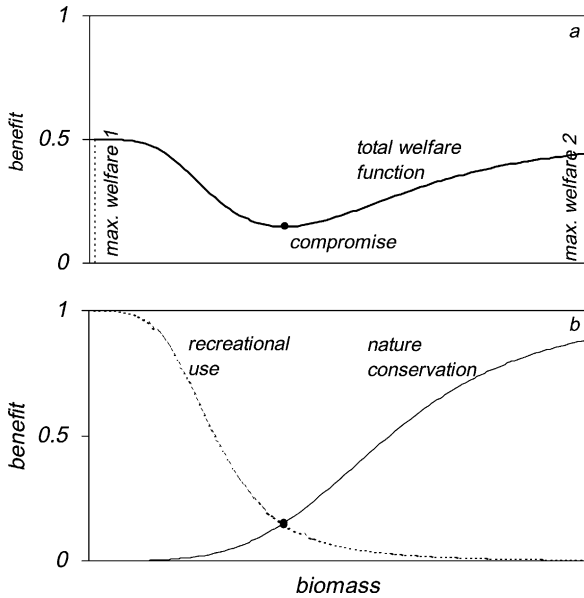
Fig. 2. As in Fig. 1, but for canopy-forming or floating vegetation that causes nuisance to recreationists even at low biomass while having relatively little benefit from a nature conservationist point-of-view. The point with a compromise between both groups (closed circle) coincides with the minimum total benefit (van Nes et al., 1999).

the net relative growth rate is zero. At a very low biomass, the maximum relative growth rate (*r*) is approached.

We describe harvesting (*H*) as a Holling type I functional response, viz. a harvesting rate increasing linearly with vegetation biomass (Holling, 1959):

$$\frac{\mathrm{d}H}{\mathrm{d}t} = hV \tag{2}$$

This type of functional response implies there is no limitation of the harvest due to handling time. This functional response implies that at each time step a fixed proportion (*h*) of the vegetation is removed, independent on standing crop (for example, a mowing boat cuts the vegetation in 10% of the lake area daily). Fig. 3a shows the production of the vegetation and the losses due to such type I harvesting with several harvesting rates (*h*). At the intersections of the production and the harvesting lines, consumption equals production and the vegetation is in equilibrium. With increasing harvesting effort (steeper lines), the equilibrium vegetation biomass decreases. The resulting relationship between the harvesting rate and the equilibrium vegetation biomass (obtained by equaling Eqs. (1) and (2)) is linear (Fig. 3b). This means that in this case it is easy to set the vegetation biomass to any desired level by manipulating the harvest effort. Note that the realized harvest is maximal at the intermediate vegetation biomass, because for the logistic growth model, population growth is highest when biomass is half the carrying capacity (Fig. 3a).
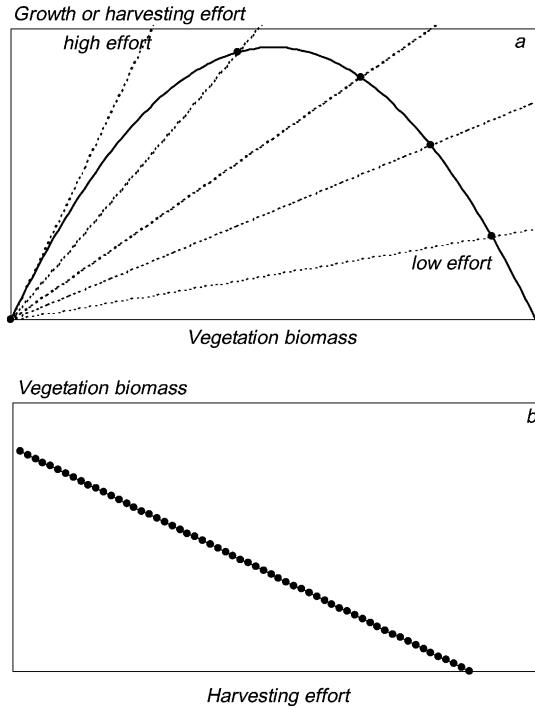
Fig. 3. (a) The growth ($g\,m^{-2}$ per day) (solid lines) and harvest yield ($g\,m^{-2}$ per day) (hatched lines) of logistically growing vegetation at different harvesting rates as function of vegetation biomass. Harvesting is implemented as a type I functional response. The closed circles at the intersections of the growth lines and the harvest lines show the equilibrium biomass with harvesting, (b) the relation between daily harvesting effort and biomass of the vegetation.

There is strong evidence of a positive feedback for vegetation growth in shallow lakes (Scheffer, 1998), which is ignored in the above analysis. Vegetation enhances its own growth conditions by clearing the water and by reducing erosion. Due to this effect, growth of plants within a dense bed may occur under conditions where growth of few isolated plants would be impossible (negative) due to, for instance, inadequate under water light conditions. To represent such a situation in a very simple way, we add a term to Eq. (1) allowing growth to become negative at low vegetation biomasses, while raising it to positive values once vegetation biomass is larger than a critical value (H_g):

$$\frac{dV}{dt} = \left(\frac{2V^p}{V^p + H_g^p} - 1 \right) rV \left(1 - \frac{V}{K} \right) \tag{3}$$

The added term $(2V^P/(V^p + H_g^p) - 1)$ is a Hill function that rises from -1 to 1 with increasing vegetation V. The power (p) determines the steepness of this sigmoidal 'clearing effect'.

Growth or harvesting effort
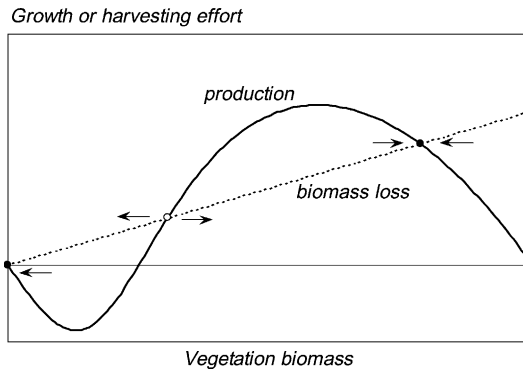

Vegetation biomass

Fig. 4. The growth rate of the vegetation in a situation with a positive feedback of vegetation on its own growth and a Holling type I harvest line. The harvest line can intersect at three points. These intersection points are equilibria. If the production curve exceeds the biomass loss, there is a net increase of the biomass (indicated with arrows). From these arrows can be concluded that two of the equilibria are stable (closed circles), and the other equilibrium is unstable (open circle).

The consequence of this extension is that even with a linear functional response the harvest line can now intersect at two points (plus the origin) with the production curve, hence there can be three equilibrium biomass values (Fig. 4). It can be seen easily that the middle intersection point (open dot) represents an unstable equilibrium. At the left-hand side of this unstable equilibrium the biomass loss is higher than the plant production, therefore the vegetation biomass will decrease. At the right-hand side, the production is higher than the losses, so the biomass will increase, moving away from the equilibrium. If the system is in such an unstable situation, only a tiny disturbance is needed to invoke the system to move away towards one of the stable equilibria. In practice, the system will never stay in an unstable equilibrium. Thus, the origin and the right-hand intersection point represent the two alternative stable states of the model.

An important consequence of this situation is that the relationship between the harvesting rate and the equilibrium vegetation biomass is not linear anymore (Fig. 5). As in Fig. 3, the response to increasing harvesting rates can be shown by plotting equilibrium vegetation biomass (the intersection points in panel 5a) as a function of harvesting rate (panel 5b). The resulting graph has a stable and an unstable (dashed) branch, which meet in a point generally referred to as a 'fold' or 'saddle-node' bifurcation (Strogatz, 1994). If the harvesting rate in a vegetated lake is increased, vegetation biomass decreases until the bifurcation point is reached. Beyond this point, the vegetation biomass collapses, and settles to a stable state with zero biomass. This implies that it is not possible to set the vegetation biomass to any desired level, since only relatively high biomass or no biomass at all can be achieved. Note that the maximum realized harvest occurs just before the collapse of the vegetation (Fig. 5a).

2.1. Other harvesting strategies

The condition that there is no limitation in the daily harvest is probably not realistic, especially when mechanically harvesting large areas with removing of the plant material
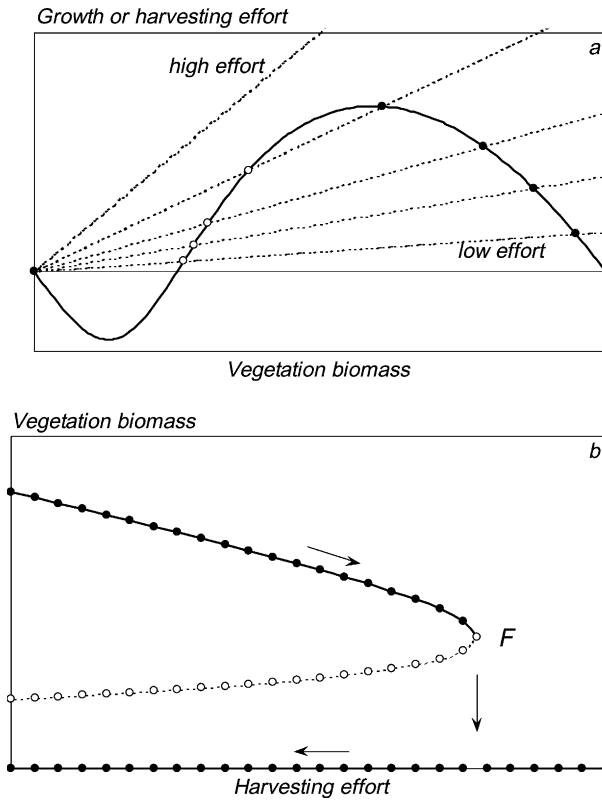
Fig. 5. (a) Growth rate of vegetation in a situation with alternative equilibria and harvesting with several intensities. Harvesting is represented by a type I functional response. Closed circles show the equilibrium biomass with harvesting; open circles are unstable equilibria, (b) relationship between harvesting effort and biomass of the vegetation. F is a fold bifurcation. If the harvesting rate exceeds this critical value, the alternative equilibria disappear and the vegetation is lost.

from the water body. In those cases, the removing of the biomass is time consuming and often the limiting factor (Wade, 1990). Then, at higher vegetation biomasses, the efficiency of the harvesters will become relatively lower. In such situations, the functional response should level off at high vegetation biomass rather than increase linearly. The consequences can be illustrated using the Holling type II functional response (Holling, 1959), which is a commonly used relationship to describe predation and grazing:

$$\frac{\mathrm{d}H}{\mathrm{d}t} = h_{\max}\frac{V}{V + H_V} \tag{4}$$

The half saturation H_V (g m^{-2}) is the vegetation biomass where the harvest is half the maximum harvesting rate $h_{\max}$ (g m^{-2} per day) which is achieved at very high vegetation biomass. For certain values of H_V and $h_{\max}$, Eq. (4) intersects with the logistic production curve at two points (plus the origin), hence three equilibria exist (Fig. 6a). Analogous
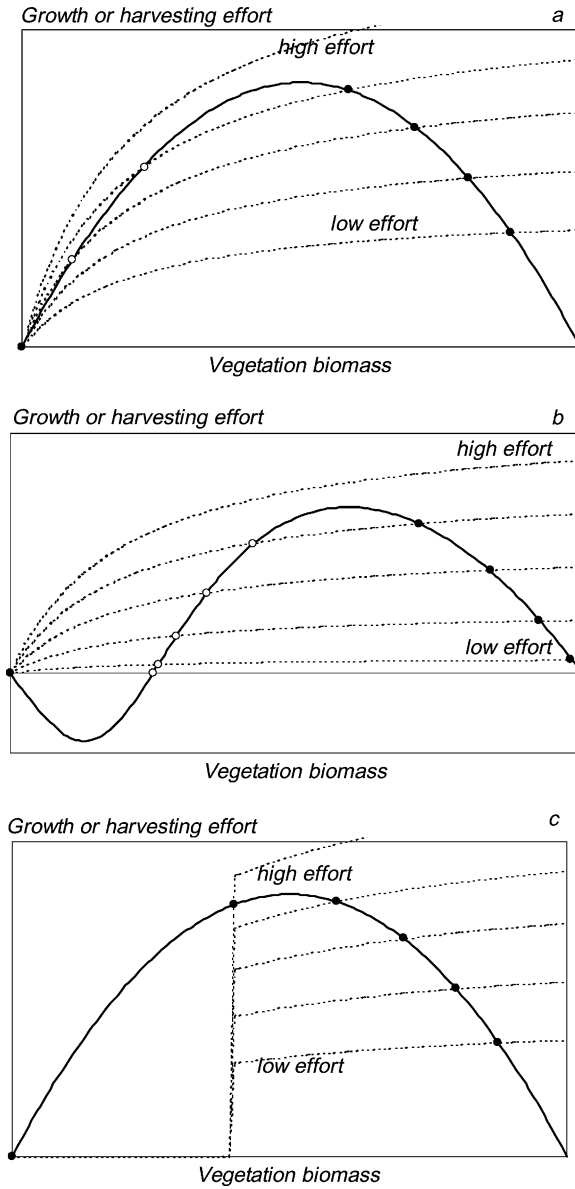
Fig. 6. The effect of harvesting with a type II functional response with several intensities on the logistic growth model with or without positive feedback. The intersections between the harvesting lines (hatched) and the production line (solid) are equilibria that can either be stable (closed circles) or unstable (open circles). (a) Type II functional response with logistic growth model; (b) type II functional response when there are alternative equilibria due to positive feedbacks; (c) and (d) the stabilizing effect of a stopping rule added to the type II functional response, (e) as (d) but with a slightly different positive feedback.
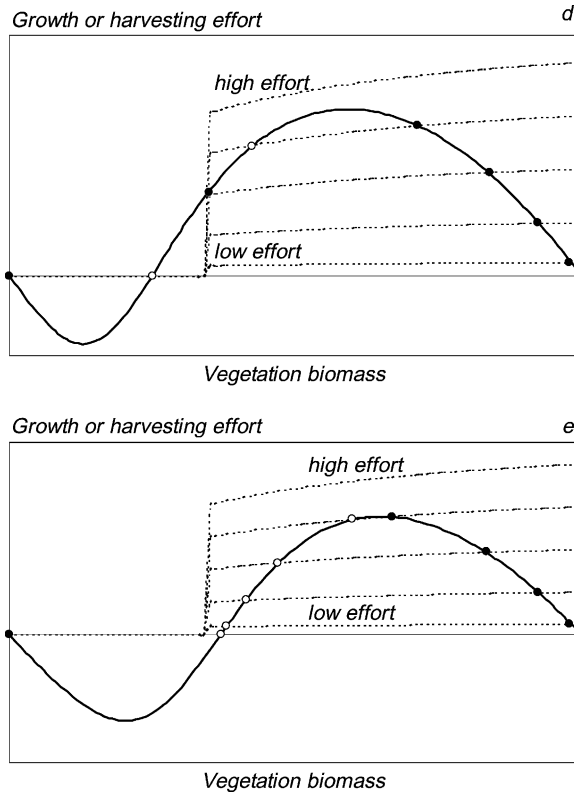
Fig. 6. (*Continued*).

to the analysis of the model with alternative stable states (Fig. 4), it can easily be seen that two of these equilibria are stable whereas the middle one is unstable (open dot). The origin represents the overexploited state, which means that all produced biomass is removed repeatedly by harvesting. In this state, the number of reproducing individuals is limiting the biomass. The right-hand intersection point represents the underexploited state, at which the interspecific competition limits the population growth. In case that the model has also a positive feedback without a harvester (Fig. 6b), the situation is similar to that with a Holling type I harvest strategy (Fig. 5). Over a wide range of parameters the model then has alternative stable states, only at very high harvesting rates there is only an overexploited state without vegetation.

   Like the strategies discussed earlier, this harvesting strategy is probably unrealistic for lake managers, because they may anticipate on the vegetation biomass and do not keep the vegetation in an overexploited state if the target biomass is intermediate. Adding a stopping rule to the harvest function, by harvesting only if the biomass exceeds a critical level, does achieve this (Fig. 6c, d). If the biomass exceeds the critical level, the manager will start harvesting with a type II functional response (Eq. (4)). This harvesting strategy is stabilizing

if an appropriate critical biomass is chosen. Without positive feedback (Fig. 6c), there is mostly only one underexploited equilibrium (unless a very small critical level is chosen). If the model has alternative equilibria, the situation is more complicated (Fig. 6d and e). If the critical level is chosen at the right-hand side of the intersection of the production line with the origin (Fig. 6d), harvesting is quite safe. If the harvesting rate is low, harvesting will lead to the underexploited equilibrium (right-most solid dots). At moderate harvesting rates, the critical vegetation biomass becomes a stable equilibrium. In this case, the system has three alternative equilibria: one at the origin, when there is not enough plants to keep the water clear, one at the critical vegetation biomass and one underexploited state (right-hand solid dot). If the harvesting rate is even higher, the underexploited state is not possible anymore. Thus, if the capacity of harvesting is large enough it is easy to set the vegetation to a certain biomass. However, the exact shape of the production curve is usually unknown. If the production curve has a slightly different shape (Fig. 6e), harvesting with a large capacity (upper lines) will always result in a collapse of the vegetation.

3. A more elaborate model of harvesting macrophytes

The above minimal models use an extremely simple description of vegetation growth. To investigate whether the results are not an artifact of simplifications, we did the same analysis with the macrophyte model Charisma (van Nes et al., 2001), an elaborate simulation model based on the model Megaplant (Scheffer et al., 1993). The base of this model is the seasonal cycle of individual plants. In autumn the vegetation dies off to survive the winter as underground structures. In spring, growth is initiated and the overwintering structures are transformed into vegetation. Photosynthesis depends on the biomass distribution of the growing plant over the vertical gradient of light in the water column. Population regulation results from self-shading and competition for inorganic carbon. A positive feedback of plants on their own growth is included by allowing vegetation to reduce turbidity of the water. Due to this effect, the model has alternative stable states over a certain range of vertical light attenuation coefficients (van Nes et al., 2001). We used parameter settings that were calibrated for *C. aspera* in Lake Veluwemeer (van Nes et al., 2001). While the model may run on a spatially explicit basis, we used a single grid cell with a water depth of 1 m for simplicity. A small import of overwintering structures ($0.1\,\mathrm{m}^{-2}$ per year) was used to prevent the vegetation from becoming completely extinct in the studied grid cell. For the current purpose we added a 'harvester' that can have different functional responses. For simplicity, the harvester was programmed to remove vegetation continuously during the whole growing season using the same strategy, though this is usually not a realistic harvesting regime.

To analyze the effect of different harvesting intensities on the equilibrium vegetation biomass we used the following numerical procedure. We started with a fixed initial biomass of overwintering structures (default $10\,\mathrm{g\,m}^{-2}$) in a state where vegetation can develop (low harvesting rate). During the simulations, the harvesting intensity was increased in small steps until disappearance of the vegetation. To check for hysteresis, we then took the same number of steps backwards (decreasing harvest intensity) to allow the vegetation to re-establish itself.
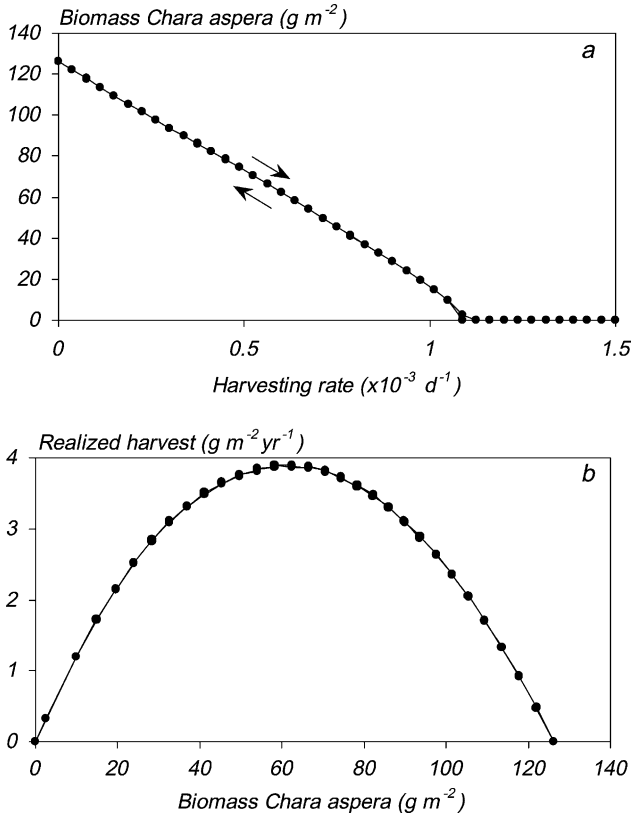
Fig. 7. Effect of harvesting on *Chara* vegetation evaluated with the more realistic model Charisma, using a Holling type I functional response of harvesting at a vertical light attenuation of $2\,m^{-1}$. (a) The effect of different harvesting rates on the equilibrium summer biomass of *Chara* (day 183). The arrows indicate the direction of changing the harvesting rate, showing that there are no alternative equilibria, (b) the realized harvest per year and the realized equilibrium summer biomass. These combinations were generated by varying the harvesting rate.

At each step in this procedure, a 200 year vegetation development was simulated to allow the biomass to reach a stable level; subsequently, the biomass at day 183 (1 July) for 5 successive years was plotted. Thereafter, in the next step, the final state of the previous step was used as a starting point.

The first analysis was done assuming relatively clear water (vertical light attenuation coefficient (K_D) of $2\,m^{-1}$ outside the vegetation beds). Under this regime, the system has no multiple equilibria (van Nes et al., 2001). For the first analysis we used a harvester with a type I functional response (Fig. 7). The equilibrium summer biomass decreases almost linearly with increasing harvesting rate (Fig. 7a), which is remarkably well in line with the logistic growth model (Fig. 3b). We can also reconstruct Fig. 3a with the complex model, but only in an indirect way by plotting the realized harvest per year against the realized summer biomass with different harvesting rates (Fig. 7b). Also this figure closely resembles
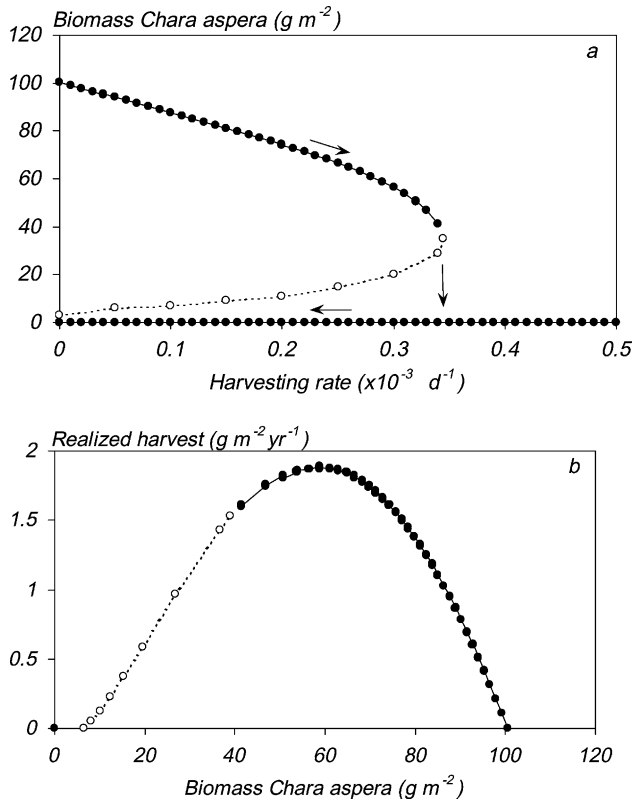
Fig. 8. Effect of harvesting on *Chara* vegetation evaluated with the more realistic model Charisma, using a Holling type I functional response of harvesting at a vertical light attenuation of $4.5\,\mathrm{m}^{-1}$. (a) The effect of different harvesting rates on the equilibrium summer biomass of *Chara* (day 183) (closed circles). The arrows indicate the direction of changing the harvesting rate, showing that there are two alternative equilibria. Open circles are estimates of the unstable equilibria generated by varying the initial biomass, (b) the produced harvest per year and the realized equilibrium summer biomass. These combinations were generated by varying the harvesting rate. The open circles are also estimates of the unstable equilibria.

the yield curve from the logistic growth model (Fig. 3a). The conclusions are thus identical to those from the logistic model: under these conditions and parameter settings, vegetation can be set to any desired level and the maximum biomass yield occurs with an intermediate vegetation biomass, which is, therefore, probably the most costly situation to maintain.

The model Charisma produces alternative equilibria, if the vertical light attenuation co-efficient is between 3.9 and $6.4\,\mathrm{m}^{-1}$, with the parameter settings of *C. aspera* in Lake Veluwemeer (van Nes et al., 2001). If in this range of vertical light attenuations (for in-stance $K_D = 5\,\mathrm{m}^{-1}$) the harvesting rate is increased stepwise, the vegetation suddenly collapses at a certain critical harvesting rate (Fig. 8a). The biological explanation is that at this point vegetation biomass becomes too modest to improve transparency enough to allow sufficient plant growth. If harvesting is stopped after such a vegetation collapse, the

vegetation is not able to recolonize the lake, because the system has switched to an alternative stable state without vegetation and with a high turbidity. The unstable equilibria (open dots) between the alternative stable states could not be found exactly, but their location was estimated numerically by finding the minimum initial summer biomass from which the vegetation can develop. Like in the case of clear water, the graph is qualitatively the same as the one produced by the simple model (Fig. 5b). The reconstructed yield function (Fig. 8b) shows a remarkable similarity with the production line of the minimal model (Fig. 5a) as well. (The unstable equilibria in Fig. 8b are estimated by setting the initial biomass on the estimated unstable equilibria and calculating the summer biomass and the realized harvest in the subsequent simulated year. The negative part could, for obvious reasons, not be reproduced).
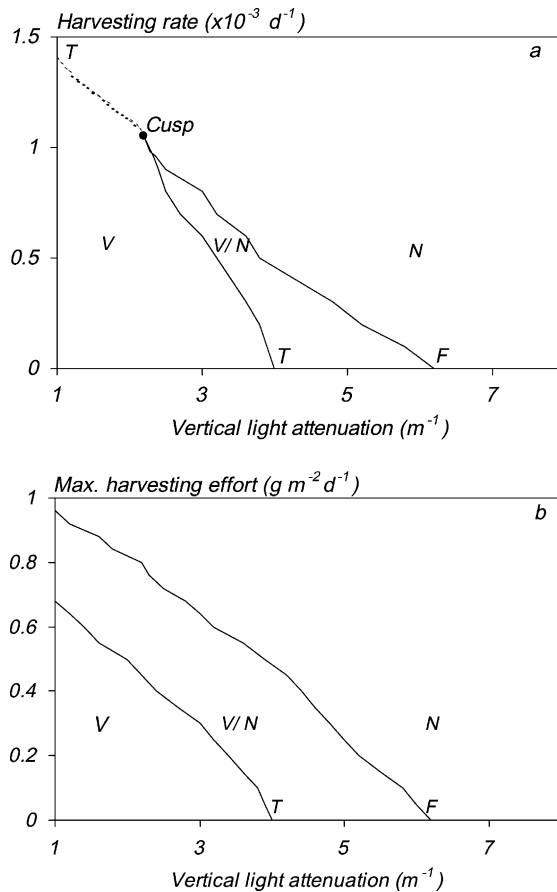

Fig. 9. Bifurcation plot of the harvesting rate and the vertical light attenuation coefficient (a) and of the maximum harvesting rate with a functional response type II with the vertical light attenuation coefficient (b). V: vegetated state; V/N: either vegetated or no vegetation as alternative equilibria; N: no vegetation; dashed line: non-catastrophic bifurcation, solid line: a catastrophic bifurcation; T: transcritical bifurcation, F: fold bifurcation; Cusp: cusp point. See explanation in the text.

A more complete image of the effect of harvesting and turbidity on the stable states of the system is obtained by constructing a 'bifurcation plot' (Fig. 9a). This plot is constructed by repeating the above analysis for several different light attenuation coefficients. By plotting only the points where the vegetation will recover ('transcritical bifurcations') and the points were vegetation collapses ('fold bifurcations'), a map of the zone with two alternative stable states in the parameter space (Fig. 9a) is produced. With increasing harvesting rates the zone where alternative equilibria occur, becomes smaller, shifts to lower attenuation coefficients and vanishes at a certain point ($K_D = 2.2$). This special point where the fold bifurcation collides with the transcritical bifurcation is called a 'cusp point' in non-linear dynamical systems theory (Strogatz, 1994). Beyond this point, the transcritical bifurcation becomes non-catastrophic, which means that this bifurcation is a gradual transition, in our case, moving from a vegetated state to a state without plants.

We also constructed a bifurcation plot using a harvester with a Holling type II functional response (see Eq. (3) in the Section 2). In this case there is no cusp point (Fig. 9b). The alternative states remain present even in clear water (vertical light attenuation of 1). Under these conditions, the clearing effect of macrophytes can not be responsible for the alternative stable states, since the plants can not reduce the turbidity below $1 \, \mathrm{m}^{-1}$ in the model. Under these conditions it is possible to reproduce Fig. 6 for the complex model (not shown), therefore, it is very likely that the same mechanism is responsible for the presence of alternative stable states. If the biomass is below a critical value, the harvester can overexploit the vegetation and the biomass decreases to zero. Above this critical value, harvesting becomes too inefficient to keep the vegetation low. Consequently, the vegetation can increase and establish a higher equilibrium. Thus, the alternative stable states shown in Fig. 9b are caused by both the overexploitation feedback and the positive feedback by the clearing effect of macrophytes.

4. Discussion

Our model analyses suggest that it may be impossible to realize a substantial reduction of submerged plant biomass in shallow lakes by harvesting without risking the complete loss of submerged vegetation. Some harvesting strategies are intrinsically destabilizing the system, because they may result in a switch to an overexploited state, analogous to that obtained in overgrazed pasture systems (Noy-Meir, 1975). Even careful harvesting protocols may cause complete loss of vegetation in eutrophic lakes, as a result of a positive feedback of the increasing turbidity that results in a further decrease in vegetation growth. In those lakes, it will be difficult to know a priori what should be a safe vegetation biomass to avoid a switch to a turbid phytoplankton dominated state without plants. One problem, indicated by the models used, is that maintaining a plant population at an intermediate biomass is costly, as this should be done exactly at the point at which regrowth is maximal, and consequently the required harvest effort is the highest. These results suggest that it may often be a more efficient strategy to assign entire lakes for recreational use and others for nature conservation, though this is often not applicable.

This conclusion is supported by earlier analyses using a simple economic model (van Nes et al., 1999), showing that even if an intermediate vegetation biomass can be obtained by

harvesting, it may not always represent a situation which is desirable from the point-of-view of the benefit of community of lake users. In particular, if the vegetation is floating or canopy-forming so that even a low biomass causes considerable nuisance, aiming at an intermediate biomass is a bad strategy from an economic point-of-view (Fig. 2).

It should be stressed that in practice the political solution of a conflict of interests, does often not coincide with the optimum environmental economic solution, as presented here, due to various socio-economic mechanisms (Scheffer et al., 2000). For instance, there can be a bias due to differences in the organizational power of groups of lake users. Furthermore, there is often a tendency to choose a compromise, even if this is not the solution with the maximum overall welfare of the society (Scheffer et al., 2000).

Obviously, our simple analyses do present a rather black and white image of the problem of controlling vegetation nuisance. In specific cases, compromise solutions may be possible without aiming at intermediate biomass. It may be possible for instance to control vegetation in small restricted parts of a lake designated for swimming or boating, without affecting overall lake ecosystem dynamics too strongly. Also, if the vegetation consists of a mixture of canopy-forming plants and species with a low growth form, it may be effective to harvest selectively the canopy-forming species, by mowing at a certain height above the lower plant canopy. Charisma simulation runs have been made for the case with a mixed vegetation of *C. aspera* and *Potamogeton perfoliatus* L. in the shallow eutrophic Lake Veluwemeer (Coops and van Nes, unpublished). In the lake, canopy-forming *P. perfoliatus* caused extensive nuisance to recreational navigation, whereas *C. aspera* dominance would meet the interests of both navigation and conservation. Preliminary model simulations with the model Charisma suggest that one such mowing event may be sufficient to substantially reduce the biomass of the canopy-forming species for 2–4 years (Coops and van Nes, unpublished). The low speed of recovery of the canopy-forming species (*P. perfoliatus*) is caused by competition with the lower growing species (*C. aspera*). An analogous manipulation of the outcome of competition by selective harvesting has been shown elsewhere with a simple model (McClanahan, 1995). Likewise, a species shift has been observed after non-selective harvesting in ditches (Best, 1993). Though these results indicate that it should be possible to use selective harvesting successfully, it is still difficult to predict the outcome of such strategy. The model Charisma can be extremely sensitive to parameter settings when modeling the competition between two species (van Nes et al., unpublished). Furthermore, it is not yet clear how harvesting affects the biomass. The plants may regrow rapidly, even to a higher density than before harvesting (Kimbel and Carpenter, 1981; Engel, 1990), sometimes referred to as a "pruning effect" (Serafy et al., 1994). Even if biomass regrowth within one season is fast, there can still be a significant effect on the biomass in the next season (Kimbel and Carpenter, 1981).

The harvesting strategies we analyzed here are simple and not very realistic. The continuous cutting strategies have been selected for simplicity and used to illustrate basic principles. We did not analyze the effect of cutting of the vegetation in a few discrete annual events. The timing of such events is essential (van Vierssen et al., 1994). If cutting occurs just before the plants form overwintering structures, the effect on the next years' generation would be much larger (Engel, 1990; Dall'Armellina et al., 1996). Furthermore, a harvesting strategy that anticipates on the vegetation biomass reduces the risk of switching to the alternative turbid equilibrium, as was shown by the stabilizing effect of a stopping rule added to the

Holling type II strategy (Fig. 6c, d and e). Including prudent anticipation in management strategies, however, may appear impracticable. For a long-term effect the number of surviving overwintering structures will be crucial, but this amount is hard to predict from the vegetation biomass during the growing season.

Our analysis illustrates that combining different model approaches can be helpful for obtaining a better understanding of a problem. Our modeling approaches each have their own strengths and shortcomings (Scheffer, 1998). The minimal model is easier to understand, but may leave out many relevant aspects. The rather complex model Charisma is much more realistic, although, because of its complexity, it is often difficult to understand the reasons for obtaining certain results. By combining both approaches, we gained an understanding of the main mechanisms and obtained an impression of their realism and relative importance. The fact that we obtained the same results in both model approaches provides some credibility to the apparently oversimplified minimal model. The approach of simultaneously addressing macrophyte restoration issues with simple and elaborate models appears a promising way to solve also other and more complex questions regarding the functioning of ecosystems. It could help to bridge the gap between classical population ecology and the approach of individual based modeling, which too often appear incompatible (Fahse et al., 1998; Grimm, 1999).

Acknowledgements

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