Water Hyacinth Population Dynamics

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Abstract

Neochetina eichhorniae and *N. bruchi* have in some locations been very successful in controlling water hyacinth infestations. Understanding the conditions under which the weevils are not successful is a key area of research. We have used simple analytical tractable models to investigate this problem. We argue that biomass density and percentage coverage are the two most useful parameters to measure in a monitoring program. We modelled water hyacinth as a population of biomass. Under stable conditions, the logistic growth model accurately describes water hyacinth growth. Understanding how abiotic conditions alter the parameters of the model is essential for accurate prediction of water hyacinth growth. There appear to be five main factors limiting infestations of water hyacinth: salinity, temperature, nutrients, disturbance and natural enemies. The models are modified to include the effect of weevil damage. Simple deterministic models are developed that incorporate developmental delays and population stage structure. For realistic parameter values, the models predict eradication of water hyacinth. We discuss how this prediction is altered in a dynamic environment. The factors that may limit the weevil population under stable conditions, and so prevent eradication, are explored. In order to test these ideas, information on areas where control has and has not been successful needs to be collated.

THE current status of water hyacinth control has been well reviewed in these proceedings and elsewhere (Julien et al. 1996, 1999). Models have been used to investigate the effect of different management strategies (Ewel et al. 1975; Mitsch 1976; Lorber et al. 1984; Musil and Breen 1985b) drawing on the wealth of information from many studies conducted worldwide. However, there has been only one published model investigating the effect of biological control agents (Akbay et al. 1991). Models used to understand when an insect biological control agent will control a weed have produced insights into how control can be achieved (Lonsdale et al. 1995; Rees and Paynter 1997). Furthermore, the Lotka–Volterra model has been successfully used to simulate the growth of another aquatic weed (*Salvinia molesta*) before and during control by *Cyrtobagous salvinae* (Room 1990). This approach can be useful in drawing together existing knowledge, as well as to identify areas where research needs to be concentrated.

The aim of the current research is to develop a predictive model for the control of water hyacinth addressing the following questions:

- what causes variability in water hyacinth infestations?
- how does the introduction of *Neochetina eichhorniae* affect the size of the infestation?
- what can be done to improve control?

In this paper we will outline some preliminary results of modelling work and the hypotheses generated from this work.

Modelling Water Hyacinth Biomass

When building a model, an appropriate state variable, which describes the state of the system at any moment in time, must be selected. With animal populations, the state variable chosen is usually the number of individuals. When modelling diseases, the number infected,

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ACIAR Proceedings 102
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infectious, immune and susceptible can be used to characterise the host population. With plant populations, the choice of state variable is often less clear. In this section, we explain why we have chosen biomass as the state variable.

The current model will be most useful if the state variable reflects the magnitude of the problem. Water hyacinth infestations have negative impacts on health, food production, navigation, hydroelectric schemes, irrigation schemes and recreation (see e.g. Gopal 1987). These problems are caused by the sheer bulk of vegetation and the fact that the vegetation covers great areas. As the scale of the problem depends on the bulk of the weed, biomass would be an appropriate state variable.

Most studies have been conducted using biomass or individual density. The density of individuals is more easily determined than biomass, but the point at which an offshoot becomes a separate plant is not always clear. The main disadvantage of using individuals is the great variability in the size of an individual. Madsen (1993), using experimental data, proposed a humped relationship between biomass density and individual plant density. We have plotted these results and some from another study in Florida (Center and Spencer 1981) in Figure 1. Similar patterns are shown in several unpublished data sets (M. Purcell, unpublished data; T. D. Center, unpublished data). Plants grown at low density have relatively constant biomass. However, at densities above about 500 g (dry weight) per square metre there is no clear relationship between individual density and biomass. This suggests that biomass provides a better description of the scale of the problem than individual plant density.

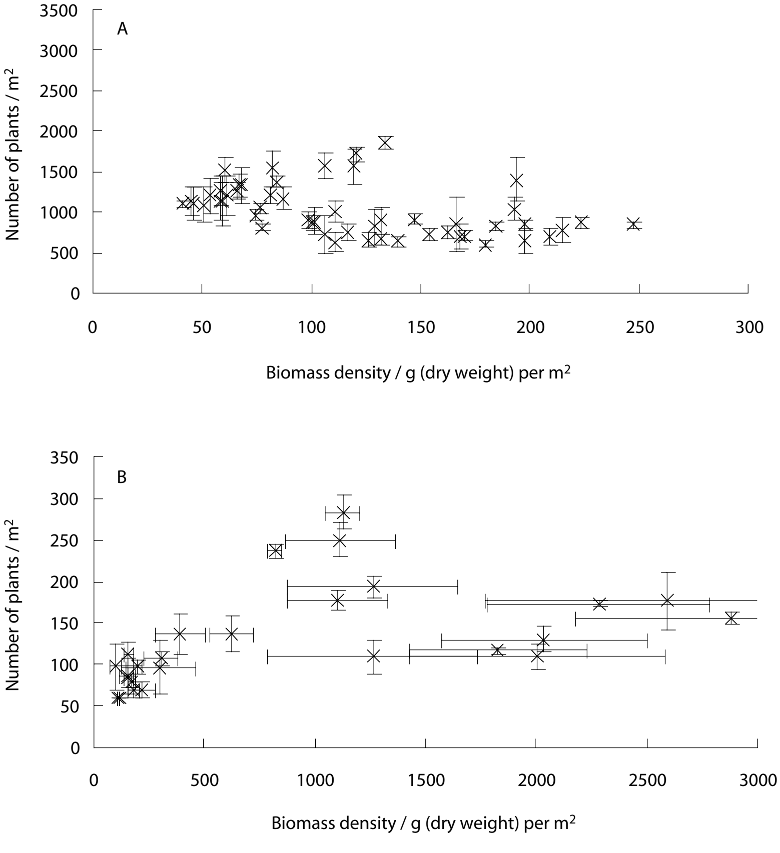

Figure 1. Biomass density plotted against individual density: A (Center and Spencer 1981); B (Madsen 1993)

Importantly, studies have shown little variation in plant water content (average of 94–95%), although there is some variation between studies and between the different plant parts (Penfound and Earle 1948; Sahai and Sinha 1970; Debusk et al. 1981). Therefore, it is straightforward to convert between dry and fresh weight.

It is possible that other units, e.g. petiole length, can also be converted to biomass, and if these units are easier to measure they might be a more appropriate unit for study. Center and Spencer (1981) found that plant weight in a lake in Florida was closely related to the mean number of leaves per plant and the mean maximum leaf length (including the petiole). It remains to be confirmed whether this relationship holds when weevils are present. Moreover, at different nutrient levels, the ratio of biomass in the roots and shoots is different, and so the proposed relationship may be different. However, finding a reliable surrogate would allow easier monitoring and allow the models to be tested using existing data-sets that do not contain information on biomass.

One of the assumptions of the modelling work is that populations of water hyacinth around the world are not genetically different with respect to growth. Clonal differences have been investigated (Watson and Cook 1987) and currently the genetic variation between populations of water hyacinth worldwide is being assessed as part of the IMPECCA project (Bateman, these proceedings). These studies suggest there is some variation, especially with flowering, but a simple growth model based on biomass should be generally applicable.

Logistic Model of Water Hyacinth

Here we discuss a simple model and how to parameterise this model using data. Understanding how environmental conditions affect the parameters of the model will be useful in predicting the size of water hyacinth infestations. We have modelled the growth of water hyacinth using a logistic model, equation 1 (also see Gutiérrez et al. 2001).

$$\frac{dP}{dt} = r.P.\left(1 - \frac{P}{K}\right) \qquad (1)$$

The biomass density of plant material is P (g (dry weight)/m^2) and dP/dt is the rate of change of the population. This model has two parameters: the intrinsic growth rate, r, and the carrying capacity, K. At low densities the population will increase at its intrinsic rate of growth, r. As the density of plants approaches the carrying capacity, K, the rate of increase in the population, dP/dt, tends linearly to zero. Furthermore, if the plant density is above the carrying capacity, then the population will fall to K. With constant parameters, this model has a stable point equilibrium at K and an unstable point equilibrium at zero, providing $r > 0$ (May 1981).

Both r and K are estimated from field and laboratory studies. Changes in biomass with time, r, have been measured in many different situations. We have also estimated the carrying capacity using the highest levels seen in nature and in long-term experiments. In both cases, we have expanded on the review of the water hyacinth growth parameters reported by Gopal (1987). Of these studies, those that have been carried out at several plant densities have been used to estimate both parameters. One of the assumptions of the logistic model is a negative linear relationship between plant density and intrinsic rate of growth. For most situations this gives a reasonable fit (Fig. 2). However, there is some curvature (Fig. 2C) which would imply an under-estimation of K. Within a site and season this model shows a good fit with experimental data. However, between studies and between seasons (Fig. 2C) there is variation in both the maximum intrinsic rate of growth r and the carrying capacity K. This variation reflects the variation in water hyacinth infestations and indirectly how water hyacinth is affected by the environmental conditions.

How the Environment Affects the Parameters of the Logistic Model

The conclusions from the parameterisation of the logistic model appear qualitatively similar to previous reviews. There appear to be five main factors limiting the growth rate and carrying capacity of water hyacinth: salinity, temperature, nutrients, disturbance and natural enemies (in the host range of water hyacinth).

- Salinity—water hyacinth is killed in waters that are more than about 0.2% saline (Haller et al. 1974: Nwankwo and Akinsoji 1988). This is important in estuarine areas e.g. the coastal lagoons of West Africa.
- Low temperature—stops the weed establishing in temperate areas and prevents it from reaching high levels in the sub-tropics e.g. California (Bock 1966). From their experimental study, Knipling et al. (1970) proposed a parabolic relationship between temperature and growth rate, with growth

Biological and Integrated Control of Water Hyacinth, *Eichhornia crassipes*,
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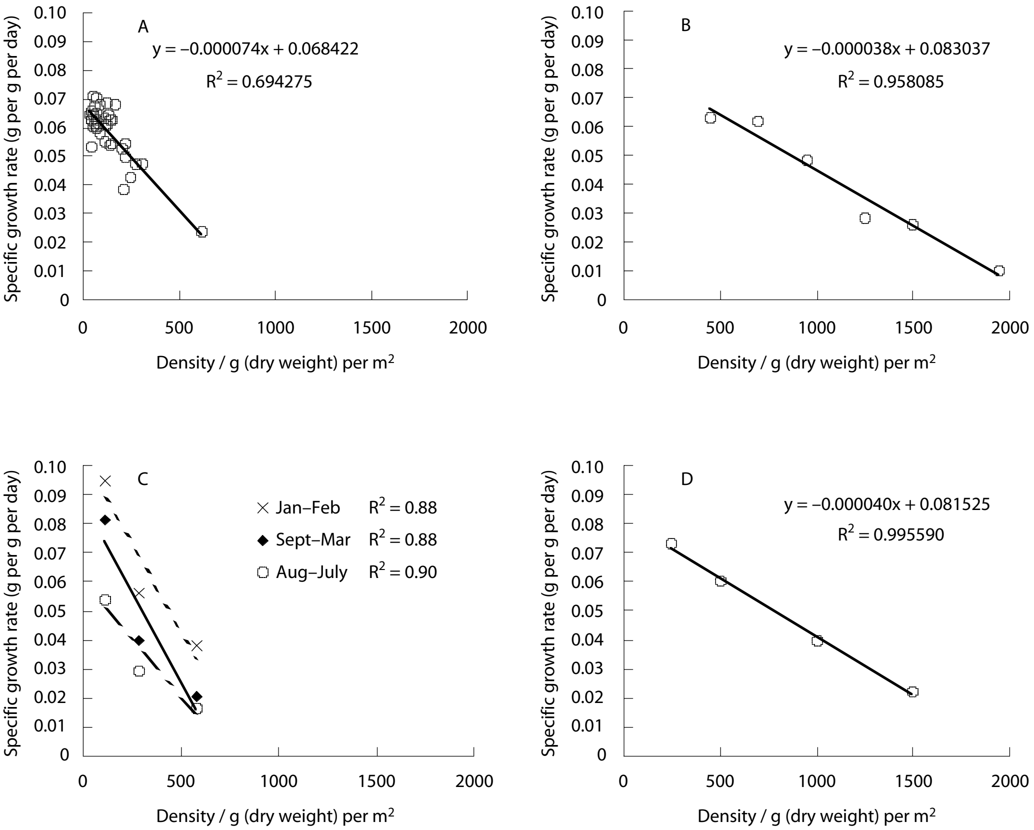

Figure 2. *r* against *K* measured experimentally in: A, Japan (Imaoka 1988); B, Florida, USA (Reddy 1984); C, Argentina (Fitzsimons 1986); and D, Florida, USA (Debusk 1981)

tailing off quickly after the optimum of 30°C. Imaoka and Teranishi (1988) proposed that *r* increases exponentially with ambient temperatures in the range 14 to 29°C. Both models predict that water hyacinth growth stops below 13°C. However, field populations of water hyacinth may be more limited by frost damage, as this increases the loss of biomass.

- Nutrients—the levels of available nitrogen and phosphorus have been often cited as the most important factors in limiting water hyacinth growth (Carignan and Neiff 1994; Heard and Winterton 2000; Musil and Breen 1985a; Reddy et al. 1989, 1990, 1991). The half-saturation co-efficients for water hyacinth grown under constant conditions have been found to be from 0.05 to 1 mg/mL for total nitrogen and from 0.02 to 0.1 mg/mL for phosphates. Water hyacinth growth quickly tails off below the lower limits. The effect of other mineral deficiencies has also been studied (Newman and Haller 1988).
- Disturbance—flooding can break up large mats of water hyacinth and leave plants stranded on land. Similarly, currents flush water hyacinth downstream. However, water hyacinth can still build up on sheltered edges and at blockages. Wave action may itself limit growth by directly damaging plants and by forcing the weed to maintain aerenchymous tissue.
- Natural enemies—in its native range in South America, water hyacinth is controlled by a suite of natural enemies. It can be the dominant floating aquatic weed but not always and not everywhere (H. Evans, pers. comm.).

Modelling Water Hyacinth and *N. eichhorniae*

We now modify the model to investigate the introduction of a weevil biological control agent, *Neochetina eichhorniae*, to water hyacinth in its exotic range. The weevils do not have discrete generations, although winter or a severe event may synchronise a population. Moreover, plant biomass production is a continual process. Therefore, a continuous time model was used. Caughley and Lawton (1981) presented a range of plant/herbivore models e.g. equation 2.

$$\frac{dP}{dt} = r.P.\left(1 - \frac{P}{K}\right) - c_1.A.\left(1 - e^{-d_1.P}\right) \qquad (2)$$

$$\frac{dA}{dt} = A.\left(-a + c_2.\left(1 - e^{-d_2.P}\right)\right)$$

The equation for the plant population is the logistic growth model with a loss term due to weevil feeding: $c_1.A.(1 - e^{-d1.P})$. The weevil population, A, increases at the maximum rate $-a + c_2$ when there are many plants (i.e. $e^{-d2.P}$ is approximately zero), and declines at the maximum rate of a when there are few plants. Using parameters from the literature (Center and Durden 1986; Jayanth and Visalakshy 1990; Heard and Winterton 2000), this model predicts that water hyacinth will very quickly be eradicated (Fig. 3A).

This model assumes all weevils have the same effect on the plant. However, late larval stages are the most damaging. To mimic this we have added a time delay to the growth of the weevil population. Under these conditions, the weevil no longer drives water hyacinth to extinction, but instead the system undergoes large amplitude cycles. Water hyacinth is driven to extremely low densities during these cycles, which

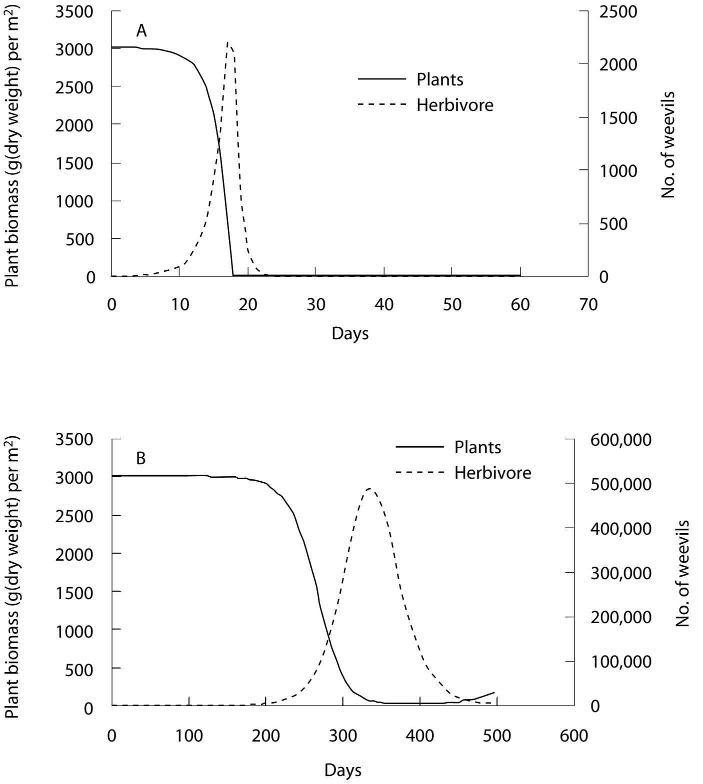

Figure 3. Model outputs for models with A, no time delay, and B, with a time delay

would effectively result in extinction. This simple model assumes the weevil population can be characterised by the number of larvae. To improve the realism of the model we have added stage structure. The weevil population is approximated by '… a sequence of developmental stages within each of which all individuals can sensibly be regarded as functionally identical (that is all having the same per capita vital rates)' (Gurney et al. 1983). This makes the models more difficult to analyse, but again the weevils appear to eradicate the plant.

These models predict that, given stable conditions, water hyacinth will always be controlled. However, from field sites this is known not to be the case (T. Center, pers. comm.). Therefore, the models appear to overemphasise the effect of the weevils and so in some way fail to capture an important aspect of the water hyacinth/weevil interaction.

What Limits the Weevils?

In this section, we investigate why control is not always as predicted. We first discuss how a fluctuating environment can, within the framework of the existing models, prevent water hyacinth from being eradicated. Then we move onto what happens in stable situations where the models do not give the correct qualitative conclusion.

Under certain dynamic scenarios, the weevils may have little impact on the water hyacinth population. Frost kills leaves, which in turn kills weevil eggs and young larvae. However, late larvae, pre-pupae and pupae may survive around the rootstock. When plants begin to regrow in the spring, the weevils need to finish maturing, mate, oviposit, and develop before the next late larval stages can cause major damage to the plants. This developmental delay in the weevil population may allow the plant to outgrow weevil damage, providing the plant has not been too heavily damaged by the frost. Factors that speed the water hyacinth regrowth, e.g. high nutrients, may exacerbate this. Alternatively, water hyacinth grows at temperatures lower than the weevils and so the weed is freed from herbivore pressure early in the growing season. The effect of cold on the weevil populations is currently under investigation (M. Hill, pers. comm.). Herbicidal or mechanical control may cause similar problems by removing the age structure in the weevil population and, for a short time, freeing the weed from herbivore pressure. Extreme natural conditions may also have an adverse effect on control. Flooding can bring new plants from upstream or remove weevil-infested plants from a population. Drought may dramatically reduce the population of plants and weevils. After drought, water hyacinth seeds will germinate with rising water levels and these new weevil-free plants can re-establish the problem before the weevil population can respond (Guillarmod and Allanson 1978). Furthermore, an infestation may persist despite a high weevil population if new plants continually arrive from upstream.

The lack of control under stable conditions, however, suggests there is something limiting the weevils. Here we explore where density dependence may be acting in the weevil population—at the egg, the larval, the pupal or the adult stage. Oviposition sites are probably not limiting and at very high egg densities the fertility of the eggs does not appear to change. Furthermore, there are few records of egg parasitism or predation, and so it is unlikely to occur at the egg stage. Larval cannibalism has been used as a possible explanation (DeLoach and Cordo 1976), but the few accounts of this suggest it is a rare, accidental phenomenon caused by larger larvae accidentally tunneling through smaller larvae (T. Center and M. Julien, pers. comm.). Larval competition for food may directly increase larval mortality; indirectly increase mortality by prolonging larval duration; or reduce the size of larvae at pupation and thereby increase pupal mortality or decrease adult fecundity (Gurney and Nisbet (1985) presented some models illustrating these). Larval damage can result in the flooding and shedding of a petiole, which would kill any larvae remaining in it (Center 1987). This sort of asymmetrical competition would occur only at high damaging densities, but should result in a few of a given age group developing. In order to elucidate this, we have undertaken an experiment to measure the effect of egg density on larval development at two different water nutrient levels.

Pupae, or pre-pupae, may be the limiting stage because, even accounting for the shorter stage duration, pupal cocoons in the field are often less common than larvae (M. Julien, pers. comm.). Pupal mortality may be higher in silted water or where the plant roots used by the pre-pupae are buried in the sediment. Muddy edges to a water-body appear to be correlated with unsuccessful control (Visalakshy and Jayanth 1996; O. Ajounu, pers. comm.). Experimentally, larvae have been shown to develop and cause damage to rooted plants (Forno 1981). Pupae have also been found on rooted plants in the field (M. Hill, pers. comm.). However, Visalakshy and Jayanth (1996) found that larvae on plants with silted roots were a third as likely to survive to adults as larvae on free floating plants, although once pupae had formed a cocoon there was no difference in survival. They proposed that, in silted conditions, there was either a shortage of pupation sites or the pre-pupae have a much lower success in forming cocoons on silted roots.

Finally, the limitation may occur at the adult stage through either emigration or mortality. Adults have been observed to develop flight muscles at the expense of egg production (Buckingham and Passoa 1985). It is possible that, at relatively high densities or when food quality is low, the female weevils switch to a dispersive mode (Center and Durden 1986). Losses to natural enemies may be less important, as few parasitoids attack the weevils outside their native range (T. Center, pers. comm.) and, although birds have been seen to eat adults, adult weevils are generally not available to predators, hiding in the base of the petioles. However, the relatively quick success of biological control agents in western Mexico (T.D. Center, pers. comm.), is thought to be due to eliminating a microsporidian infection which reduces the efficacy of the agents.

The most likely candidates for limiting the weevils in stable conditions appear to be some form of larval competition linked to plant nutritional status; prepupal mortality in silted areas; adult migration again linked to low plant quality or parasitic burden i.e. microsporidians.

Other Modelling Approaches

The models described are designed to be general, and as such have simplifying assumptions; for example, that water hyacinth can be modelled as a population of biomass. However, to answer specific questions the models may need more detail. Plant physiological models, based on the metabolic pool concept (Gutiérrez 1996), are being developed as part of the IMPECCA mycoherbicide project. These models investigate how different application strategies affect water hyacinth population dynamics under different environmental conditions. These questions necessitate a more detailed modelling approach, in particular one that includes leaf dynamics. However, both approaches address the causes of variability in water hyacinth infestations. If the models concur, the conclusions should be independent of the modelling technique used. The latest version of the model is available free at <http://www.agrsci.dk/plb/nho/hyacinth.htm>.

Discussion and Conclusions

In this section we draw the conclusions from the work on modelling water hyacinth, discuss how the addition of the weevils to the models affects the outcomes and why the models may not reflect the real situation.

Monitoring of water hyacinth should be carried out using biomass and surface area covered, as these give the best measure of the problem. Leaf length and number of leaves can be used as a surrogate, but the exact relationship may be very site specific. A simple logistic model gives a good description of water hyacinth growth. The parameterisation of the logistic model has highlighted several conclusions from other studies. Water hyacinth cannot survive at salinities above about 0.2%. Water hyacinth can grow in water temperatures of between 13 and 40°C and grows optimally at 30°C. High temperatures increase water hyacinth mortality, but mortality does not increase at low temperatures without frost. Frost kills leaves and after several days or a hard frost the meristem can be damaged and the plant killed. Under constant conditions, water hyacinth shows a hyperbolic relationship between water nutrient concentration and growth rate, with half-saturation co-efficients of between 0.05 and 1 mg/mL for total nitrogen and between 0.02 and 0.1 mg/mL for phosphates. However, complications mean that the plant nutrient content is a more accurate guide with a linear relationship between the percentage nitrogen in the leaves and the growth rate (Aoyama and Nishizaki 1993). Water hyacinth growth rate is also reduced by wave action, and in such environments it may persist only in sheltered regions or as part of a mat. Natural enemies also limit water hyacinth growth. To test the model predictions, information needs to be collated on where water hyacinth has and has not caused problems and how infestations develop. This would require historical data-sets possibly including remote sensing.

When the models are adapted to include weevils, the prediction is for water hyacinth to be effectively eradicated in all stable conditions. This qualitative prediction does not appear to be affected by refinements to make the model more biologically realistic e.g. introducing time delays corresponding to developmental delays or the introduction of stage structure. However, these predictions are altered in a dynamic situation e.g. frost and flooding. In order to test and refine the model, information again needs to be collated on where control has and importantly where it has not been successful. One important aspect not included in the models is spatial heterogeniety of attack. The adult weevils are able to swim and are mobile, but in general they are sedentary and some plants may temporally escape attack. It would be expected, therefore, that in larger water bodies the reduction would be relatively less than on a similar smaller water body. The modelling work has thrown up a number of potentially important questions, the answers to which could be very important in directing future control measures.

Under what conditions does water hyacinth remain at low levels? What limits the size of the weevil populations? Under what conditions are they limited below a level that causes significant reductions in the water hyacinth population? Do shallow or muddy banks provide refuge for water hyacinth plants by preventing *N. eichhorniae* from pupating? Does adult weevil migration prevent damaged water hyacinth from being eradicated? How does the interaction between water nutrient level, plant nutrient level and weevil damage affect the level of water hyacinth and weevils seen? How do the larvae compete when at high densities? How are the weevils dispersed, and can this account for failure in control? Why doesn't *N. eichhorniae* work everywhere? These questions will be addressed by refining the models, experimentation and more detailed investigation of field data.

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