Coarse fish: the demise of plants and malaise of lakes?

Mary de Winton, Tony Dugdale, John Clayton

National Institute of Water and Atmospheric Research Limited, P.O. Box 11-115, Hamilton, New Zealand. m.dewinton@niwa.co.nz

ABSTRACT

‘Coarse fish’ were introduced to New Zealand for angling and ornamental purposes, but their presence may have far-reaching consequences within our water bodies. Through their deleterious impacts on water quality and direct disturbance of submerged plants, large populations of these alien fish have the potential to cause substantial and undesirable changes to lake and river ecosystems. Moreover, the continued influence of coarse fish may prevent the recovery or restoration of such water bodies. In this paper, we review international findings on the incompatibility of coarse fish and submerged vegetation resources that raised an alarm for the New Zealand situation. We also present recent results from NIWA’s research programme. Experiments on feeding preference confirm that herbivorous rudd (*Scardinius erythropthalmus*) present a particular risk to native submerged plants and may facilitate invasion by less palatable alien weeds. Rudd consumption rates were found to be seasonal and we confirmed a grazing preference for native plants over weed species. Fish exclusion from areas of a shallow eutrophic lake (Hamilton Lake, or Lake Rotoroa) that supports an abundant coarse fishery, was found to substantially increase the early establishment and survival of submerged plants. The complexities of plant–fish relationships and their outcome for vegetation development and persistence are considered using a simple, illustrative model. Some management issues are considered in the light of research results and NIWA’s past experiences with aquatic plant pests. Finally, some future research priorities are suggested.

Keywords: coarse fish, macrophytes, herbivory, fish/macrophyte interactions, rudd

1. INTRODUCTION

‘Coarse fishing’ was an English term coined to describe angling for freshwater fish that were not considered ‘gamefish’ (i.e. salmonids). A number of ‘coarse’ species were originally introduced to New Zealand to establish angling in habitats that were unsuitable for trout, or for ornamental ponds (Table 1). Their introduction and subsequent spread has been most often by intentional means, both legal and illegal, as well as accidental.

TABLE 1. COARSE FISH SPECIES PRESENT IN NEW ZEALAND WATERS.

COMMON NAME	SPECIES NAME	FIRST RECORDED IN NZ
Goldfish	*Carassius auratus*	Late 1800s
Brown bullhead catfish	*Ameiurus nebulosus*	1877
Perch	*Perca fluviatilis*	1860s
Rudd	*Scardinius erythrophthalmus*	1960s
Tench	*Tinca tinca*	1860s
Koi carp	*Cyprinus carpio carpio*	1960s
Golden orfe	*Leuciscus idus*	1980s

This paper considers the possibility that coarse fish have far-reaching and deleterious impacts within New Zealand's aquatic environments. The focus is on the fish's effects on submerged vegetation and the pivotal role of plants within waterways. Recent research by NIWA is outlined together with an overview of relevant international findings. A conceptual model is presented to help assess impacts of fish on submerged vegetation and the actions necessary to minimise further impacts by coarse fish are considered.

1.1 The beneficial role of submerged plants in lakes

The value and role of submerged plants within lake ecosystems is now generally recognised by lake managers. Plants contribute to biodiversity and habitat complexity, they provide a source of food and shelter for biota, and vegetation ties up excess nutrients and may moderate phytoplankton abundance. Plants also influence many physical processes within the littoral zone. Submerged vegetation buffers wave disturbance of bottom sediments and promotes the settlement of suspended particles from the water column.

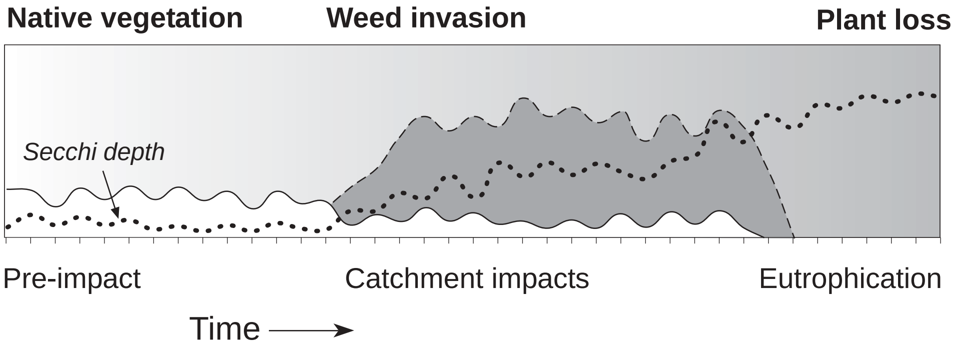
Nowhere is the influence of submerged plants more apparent than within shallow lake ecosystems that have a proportionally large area suitable for plant growth. However, these lakes are also the most vulnerable to eutrophication, deterioration in water quality and loss of ecological value. In this regard, vegetation presence has been found to have a pivotal role in determining lake condition.

1.2 Transition of lakes and vegetation change

Shallow eutrophic lakes may switch suddenly from a condition of submerged plant presence and relatively high water quality to one of plant absence and degraded water quality as a result of nuisance phytoplankton blooms or inorganic turbidity. These changes take place with little alteration in lake nutrient levels. Instead the change is attributed largely to a loss of the influence of submerged vegetation.

A typical sequence of events leading to vegetation decline and change in lake condition can be seen for the shallow, Lower Waikato lakes (Fig. 1). Initially, these lakes would have maintained a high diversity of native submerged plants. In the mid 1900s, alien hydrocharitacean weeds became established in many Waikato water bodies, replacing native vegetation and occupying much of the water column. Concurrently, changing land use within the catchment

Figure 1. Generalised sequence of events leading to vegetation decline and a turbid condition in lakes of the Lower Waikato Region. Stylised Secchi Disc depth is shown as a dotted line.



contributed a higher run-off of nutrients and inorganic particles entering the lakes. Despite such enormous catchment impacts and increasing nutrient enrichment, the water quality of lakes was initially buffered by plant presence. It was only when submerged vegetation was lost that severe symptoms of eutrophication such as phytoplankton blooms became apparent.

The immediate causes of vegetation decline are not usually apparent, but are likely to include several additive or synergistic factors. First, the plants were likely to be under ongoing *stress* in the form of low light availability. Episodic inputs of catchment run-off would reduce light penetration through the water column and nutrient availability promoted the growth of phytoplankton and epiphytic algae. Such stress was exacerbated by the need for large alien weed beds to sustain respiratory tissues (lower stems and roots) from the small amount of photosynthetic tissue situated in the shallow photic zone. Secondly, vegetation would have experienced *disturbance* (removal of plant tissue) that would affect a plants ability to survive stress. Sources of disturbance might have included physical factors (storm events, large lake level fluctuation) or biotic factors (disease, grazing or uprooting by lake biota).

The factors preventing vegetation recovery within a degraded lake may be the same or different to those causing decline.

Another important and potentially influential component of shallow lake ecosystems are their fisheries. Shallow lakes can have an exceptionally high density of fish as they are productive systems with an abundance of benthic food sources and, moreover, the fish are more concentrated within the shallow water column compared with deeper lakes (Meijer et al. 1990; Jeppesen et al. 1997). Recently, coarse fish have been implicated in the deterioration of aquatic habitats, the loss of vegetation and in preventing plant recovery in shallow lakes. The evidence to suggest this role is outlined briefly below.

1.3 Why are coarse fish implicated in vegetation loss?

Evidence for negative relationships between fish and plants

A direct, negative relationship between submerged vegetation biomass and common carp (*Cyprinus carpio)* density was documented within enclosures in a marsh (Crivelli 1983). Similarly, Lougheed et al. (1998) found that a significant reduction in the species diversity of submerged vegetation in North American marshes was linked to carp presence. Even more dramatic evidence for fish impacts has come from ‘biomanipulation’ trials—the deliberate reduction of coarse fish stocks in lakes. In some instances spectacular plant recoveries have taken place following manipulations of fish abundance (Van Dijk & Van Donk 1991; Wright & Phillips 1992; Hanson & Butler 1994; Perrow et al. 1997; Lundholm & Simser 1999), however failures are also noted (Perrow et al. 1997).

Fish mechanisms acting on plants

Coarse fish populations are suspected to maintain de-vegetated conditions in shallow lakes via several proposed mechanisms. Sustained substrate disturbance by benthic feeding fish is suggested to prevent germination and colonisation by submerged vegetation (Ten Winkel & Meulemans 1984), and uprooting and 'vegetation destruction' resulted from carp feeding activity (Crivelli 1983). Nest building by fish is an important source of vegetation disturbance in Northern Hemisphere temperate lakes (Carpenter & McCreary 1985). Other mechanisms involve indirect effects via the light climate for plant growth. A positive relationship was proven between densities of benthivorous/ planktivorous fish and turbidity promoted by sediment re-suspension (Meijer et al. 1990; Breukelaar et al. 1994), while fish predation on zooplankton could further increase phytoplankton abundance (Hanson & Butler 1994). There are also suggestions that abundant benthivorous fish (e.g. tench) may reduce snail numbers, hence releasing attached algae from grazing pressure and leading to smothering epiphytic growths (Brönmark & Weisner 1992). Finally, direct grazing by herbivorous rudd contributed to changes in plant species composition and the loss of vegetation elements in a Dutch lake (Van Donk & Otte 1996).

While New Zealand lacks bream (*Abramis brama*) and roach (*Rutilus rutilus*), the fish species most often implicated in plant loss overseas, introduced benthivorous, planktivorous and herbivorous coarse fish may have a similar role here. The presence of koi carp, the ornamental variety of common carp, is of particular concern as its impacts on plants are likely to be the same as documented for the wild strain.

Several observations made in New Zealand lakes raised the possibility of coarse fish impacts here. Prior to a major vegetation decline in Lake Rotoroa (Hamilton), the rudd population was known to be abundant, with plant material forming the majority of their diet. This circumstantial evidence suggested rudd contributed to the plant loss (Clayton & de Winton 1994). Within Lower Waikato lakes that have lost their submerged vegetation (Lakes Waahi, Rotoroa and Rotomanuka) it is common to observe benthic depressions that are characteristic of fish disturbance of substrates. A similar disturbance of lake sediments has been observed at Tokaanu, Lake Taupo, in association with large schools of catfish. Fish disturbance was also suspected within Lake Hayes, Otago, where overturn of *Elodea canadensis* weed beds was associated with a high perch population.

1.4 NIWA research

Rudd grazing trials

Recent studies by NIWA and the University of Waikato indicate that rudd selectively feed on certain species of submerged plants. A range of native and alien plant species were presented to rudd, both in captivity and in a water body (Lake Karapiro) where rudd are known to be abundant. The order that

TABLE 2. THE CONSUMPTION ORDER (RANKED 1–6) OF A RANGE OF NATIVE AND ALIEN AQUATIC PLANTS WHEN PRESENTED TO CAPTIVE RUDD (201–246 mm FL (FORK LENGTH)). Trials were carried out in outdoor troughs at Ruakura, Hamilton, at ambient temperatures in summer, autumn, winter and spring.

SPECIES	COMMON NAME	NATIVE/ALIEN	RANK
Nitella hookeri	Nitella	Native	1
Potamogeton ochreatus	Pondweed	Native	2
Elodea canadensis	Elodea	Alien	3
Chara globularis	Chara	Native	4=
Chara fibrosa	Chara	Native	4=
Egeria densa	Egeria	Alien	5=
Lagarosiphon major	Lagarosiphon	Alien	5=
Ceratophyllum demersum	Hornwort	Alien	6

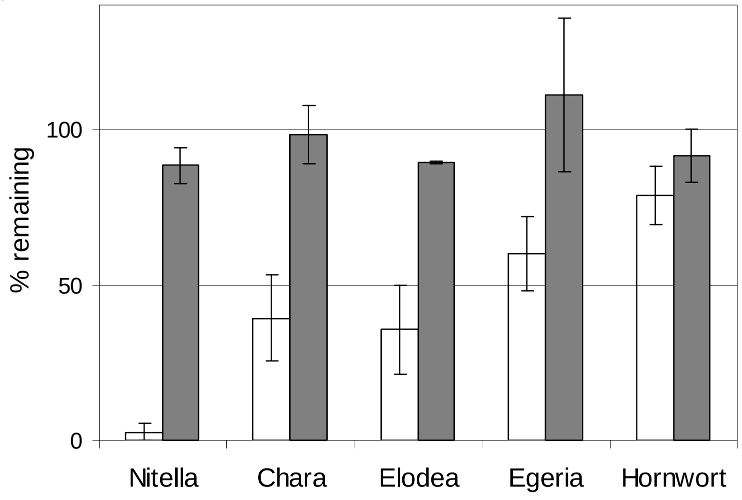


Figure 2. Percentage (± 1 standard error) of original biomass remaining of 70 g wet weight bunches of five aquatic plant species after fish grazing (light bars) and protection from fish grazing (dark bars) in Lake Karapiro for three days. The trial was repeated on four occasions between February and June 1999.

rudd consumed plants in captivity is given in Table 2. This order was confirmed for five of these species exposed to grazing at a site in Lake Karapiro (Fig. 2).

The data show that rudd eat some species of native plants before alien species. This feeding behaviour is likely to be having a detrimental effect on native plant communities, particularly where they are threatened by invasion by alien weeds.

Grazing rates of captive rudd in summer and winter have also been investigated for a range of aquatic plants (Table 3). Nitella was always grazed at a greater intensity than both chara and elodea (*post hoc* Bonferroni $P \leq 0.001$). The difference between chara and elodea was not significant (*post hoc* Bonferroni $P = 0.233$). In winter, grazing rates were 65–93% less than in summer for all three plants (ANOVA $P \leq 0.002$).

NIWA is currently investigating the mechanism of impact of coarse fish on aquatic plants. Initial studies have focused on gaining video footage of captive rudd, perch and catfish. Preliminary results show that rudd actively pluck native charophytes from the sediment while catfish, at least during daylight hours,

TABLE 3. MEAN CONSUMPTION RATES BY CAPTIVE RUDD (209–227 mm FL) IN SUMMER (FEBRUARY) AND WINTER (JUNE). Means represent four trials using three fish per tank for each species in each season. FW = fresh weight, DW = dry weight. Standard errors are given in parenthesis.

PLANT SPECIES	% FISH BODY WEIGHT DAY^{-1} SUMMER	% FISH BODY WEIGHT DAY^{-1} WINTER	mg PLANT DW g FISH FW^{-1} DAY^{-1} SUMMER	mg PLANT DW g FISH FW^{-1} DAY^{-1} WINTER
Nitella hookeri	21.7 (1.8)	5.8 (0.7)	12.1 (1.0)	4.3 (0.5)
Elodea canadensis	3.5 (0.6)	0.4 (0.2)	3.9 (0.7)	0.3 (0.2)
Chara globularis	4.4 (0.6)	1.1 (0.2)	5.9 (0.8)	1.2 (0.2)

tend to hide under the plants, sometimes burrowing into the sediment. Observations on perch have been hampered by low survival rates in captivity.

Fish exclusion trials

NIWA recently investigated the impact of a coarse-fish population on early establishment of submerged plants (charophytes) in Lake Rotoroa, Hamilton (de Winton et al. 2002). Replicated mesh exclosures (7 mm mesh size) were used to exclude large fish at three sites within the lake and charophyte 'seed' and plants were introduced both inside and outside the exclosures.

Germling response (number and biomass), and transplant persistence were consistently higher within the exclosures. Results for *Chara corallina*, the most common plant in Lake Rotoroa, are summarised in Fig. 3, while another charophyte species had a similar pattern of germling response. At all sites, *C. corallina* establishment and transplant persistence in exclosures were significantly greater (ANOVA, $P < 0.05$) than outside, with the exception of germling number at one site only.

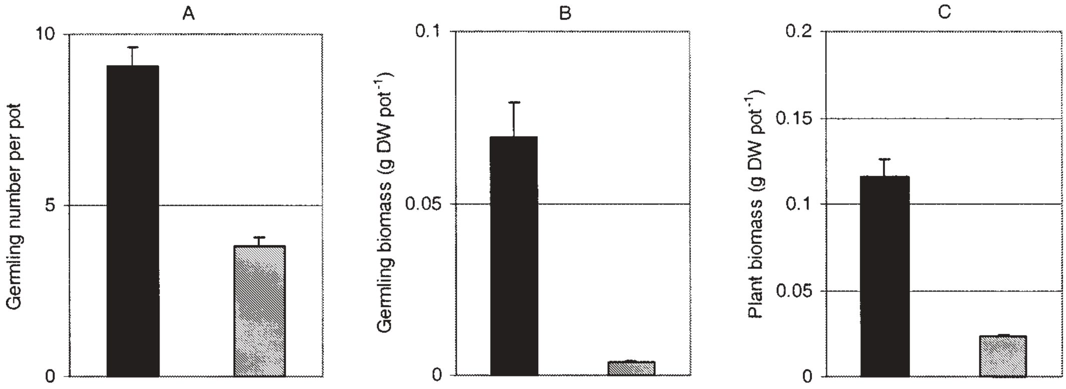


Figure 3. Performance of *Chara corallina* germlings (A and B) and transplants (C) from within fish exclosures (solid blocks) and outside of exclosures (hatched blocks) in Lake Rotoroa. Data is mean ± 1 standard error of the mean.

Water quality data showed the exclosures did not create a significantly better light climate for plant growth. Moreover, as increasing wave exposure across the three sites did not depress plant performance, it was unlikely that wave shelter was a significant factor for vegetation establishment in this lake.

It was concluded that fish access was the major factor responsible for the reduced plant response outside the exclosures and that the impacts resulted from a selection or combination of grazing, mechanical damage, uprooting and smothering by re-suspended substrates. Further, indirect effects of fish operating via water clarity would not have been detected in this trial.

A Waikato University survey of fish populations in Lake Rotoroa shortly after this trial confirmed the presence of perch, rudd, goldfish, catfish and tench, as well as eels, with catfish numbers being much higher than other species. Our trial did not identify which species were having an effect, but herbivory by rudd and disturbance by benthic feeders were implied by experimental results.

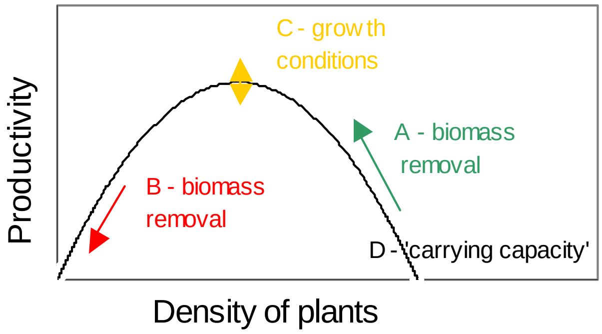
Conceptual model

Direct impacts of coarse fish on submerged plants and outcomes for vegetation persistence may be extremely complex. In this regard a conceptual model may be useful to consider interactions and to formulate research questions. We have investigated a simple model that has been used to analyse the risk of overgrazing in an agricultural setting (Noy-Meir 1975), and which has promise for the aquatic situation (Scheffer 1998). The model has two components: one describing plant production under certain conditions; the other describing fish removal of plant matter based on a scenario of fish abundance and feeding behaviour. Plant production and loss (by fish consumption or disturbance) may be plotted on the same graph and the difference between production and loss indicates if plants will show a net increase or decrease in abundance.

Plant production

Plant productivity (e.g. dry matter produced, per unit area, per unit time) is low when few plants are present and increases as plant density increases, up to a point (Fig. 4). Productivity is also low at the maximum possible plant density (D), as the individual growth of each plant is limited by competition for light and other resources. Maximum productivity occurs at some intermediate plant density.

Figure 4. Conceptual model of plant productivity at differing plant densities.

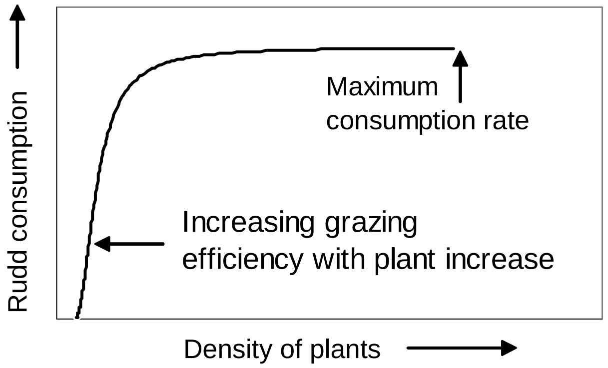


Theoretically, when a plant stand is close to its maximum density (D) and some plant matter is removed then productivity would temporarily increase (A). However, if the same perturbation occurs while plant density is low (B) the productivity is temporarily reduced. The maximum productivity (C) and maximum density of plants (D) is set by growth conditions for plants, such as the light climate.

Fish grazing or disturbance

We can consider various simple scenarios of how coarse fish may impact upon plants, resulting from their feeding behaviour and abundance. One important assumption made by this model is that the fish population size is essentially independent of plant abundance. This is likely to be the case in the short term. For example, populations of most benthivorous fish are not reliant on plants as food and even rudd, although primarily herbivorous, can undergo a dietary change to invertebrate prey that can sustain a population when plants are unavailable.

Figure 5. A theoretical pattern of plant biomass removal by rudd grazing for differing plant densities.



In Fig. 5 we consider the possible consumption pattern for rudd. The likely pattern of consumption for herbivores is an initial increase in feeding efficiency with increasing plant density, followed by a plateau as individuals become satiated at higher plant availability. If fish are efficient feeders, the consumption curve is initially steep. The height of the consumption curve is set by the size of the herbivore population (individual consumption pattern × population density).

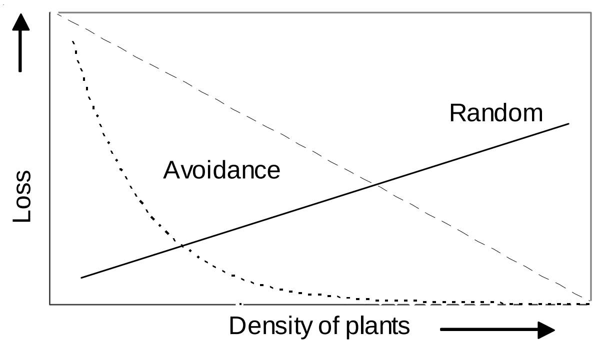


Figure 6. Theoretical patterns of plant biomass removal by benthivorous fish disturbance for differing plant densities.

In Fig. 6 we consider possible patterns of plant biomass removal by fish disturbance while foraging for benthic prey. If disturbance is a random event linked to fish activity then we might expect the level of biomass removal to be proportional to plant density. If fish actively avoid densely planted areas because of reduced access to benthic prey, then biomass removal may decline with increasing plant density. Again the height of the loss curves would be set by the size of the fish population.

Production minus loss

Figure 7 shows a plant production-density curve superimposed on a loss curve based on rudd grazing. Where loss exceeds production the density of plants decreases, and where production exceeds loss the density of plants increases. The points where plant production and loss curves intercept are termed equilibria points.

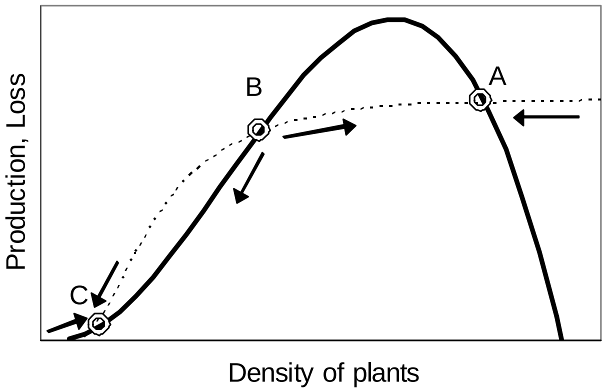


Figure 7. Scenarios of plant production and loss to fish activities, showing the position of equilibria points and the direction of plant development with differing plant density.

The position of equilibria is important. Some equilibria (A) may represent just a small decrease in the maximum attainable plant biomass. On the other hand, unstable equilibria (B) represent breakpoints or thresholds for plant density, below which fish would tend to suppress vegetation development. Still other equlibria may hold the system in a low plant biomass state (C).

If the plant production curve is set lower because of light stress, or the loss curve is higher because of a large fish population, then the presence and position of the equilibria move accordingly.

If a number of equilibria points and the direction of the system are plotted on axes of fish density and plant density, predictions can be made about the sustainability of submerged vegetation for a given level of fish abundance. The model could identify a target fish population size that would be compatible with either protection or recovery of submerged vegetation. For example, colonising plants are likely to require a lower fish presence than that compatible with the persistence of established vegetation.

2. FUTURE RESEARCH

2.1 Which coarse fish hold the most risk for New Zealand's aquatic ecosystems?

A 'Species Risk Assessment' should be undertaken for both naturalised fish, those present in the aquarium trade and possible future introductions, similar to that recently completed for aquatic plant pests in New Zealand (Champion & Clayton 2000). Coarse fish species need to be ranked in order to distinguish those of intolerable risk from those likely to have negligible impacts in this country. A risk assessment should include a number of weighted criteria such as life-history traits (e.g. breeding potential, feeding habit) and habitat requirements (e.g. temperature tolerance). Although importation of coldwater fish species is not currently permitted this does not rule out illegal fish incursions. Therefore risk assessments may be an important way of prioritising actions.

2.2 How do different coarse fish species impact directly or indirectly on aquatic plant species and ecosystem health?

More experimental information is needed on the particular effects of fish species on submerged plants. Experiments should focus on direct feeding and indirect behavioural responses of fish to plants to identify mechanisms by which impacts take place. In this respect, NIWA is initiating trials using underwater video to observe the types of impacts on plants by rudd, catfish and perch. Later we will attempt to build up a picture of fish impacts over a range of plant abundance levels, with a view to testing simple models such as the one proposed above.

2.3 What can we learn from studying lakes already impacted by coarse fish?

A number of New Zealand waterways are already known or suspected to exhibit coarse fish impacts and field-based studies could help identify singular or multiple fish species impacts. For example, NIWA is currently investigating how fish removal and exclusion from a sector of Lake Rotoroa (Hamilton) influences the speed and extent of charophyte colonisation from ‘seed’ and transplants. Other de-vegetated lakes present similar opportunities to determine if coarse fish are a common barrier to plant re-establishment. The recent discovery of rudd in Serpentine North, a Waikato lake with abundant native vegetation, could provide a valuable site to test the effects of rudd on native vegetation in the field.

2.4 How can wild populations of coarse fish be effectively managed?

Methods need to be developed for manipulating or eradicating coarse fish populations on a whole-lake scale. Intensive or selective fishing techniques, rotenone-based control or eradication and enhancement of piscivores (e.g. shags, large eels or perch) are possible methods that require further testing and refinement before they can be used successfully in New Zealand.

Ultimately, the goal of future research is to predict the impact on an aquatic system by a coarse fish population, identify target levels of fish that are compatible with vegetation resources or water quality, and to be able to manage fisheries accordingly.

3. MANAGEMENT ISSUES

Until more is known about the impacts of coarse fish on New Zealand's environment, it is vital that no more problem fish be imported to this country. In this respect, the species risk assessments suggested above would provide useful guidelines for border control.

Secondly, we believe there should be a moratorium against further releases of coarse fish in New Zealand. The mechanisms by which coarse fish species are transferred from one water body to another need to be clearly identified and better managed. Legislation permitting transfers should be urgently reviewed. Unintentional (e.g. catfish in fishing nets) and illegal transfers (e.g. irresponsible release of rudd) need to be managed proactively through education and direct intervention. Educational campaigns need to be targeted directly at management agencies, recreational and commercial fishers and the public. At the beginning of the 20th century it was considered desirable to introduce and establish game mammals throughout New Zealand. The consequences of these actions are now imprinted permanently upon New Zealand's biodiversity and landscape, while parallel changes are now taking place within our unique aquatic ecosystems.

Finally, fragmented responsibilities for inland waters in this country cause significant problems and delays in managing pest aquatic weeds, with a similar scenario likely when dealing with pest freshwater fish. The various agencies and authorities managing ecological aspects of New Zealand's water bodies must cooperate closely so that conflicts of interest do not arise. Fiscal responsibilities also need to be identified.

4. CONCLUSION

There is now sufficient evidence that some coarse fish pose a significant risk to the health of New Zealand's waterways. It is imperative that agencies and authorities managing aspects of freshwater ecosystems in this country act together and with foresight, in order to minimise future impacts.

5. ACKNOWLEDGEMENTS

We thank co-researchers Michael Lake, Aleki Taumoepeau, Rohan Wells (NIWA) and Brendan Hicks (Waikato University). Neil Cox (AgResearch) assisted with statistical analyses. Funding for research activities was provided by the Foundation for Research, Science and Technology (contract number CO1X0221) and the Hamilton City Council.

6. REFERENCES

Breukelaar, A.W.; Lammens, E.H.R.R.; Klein Breueler, J.G.P.; Tátrai, I. 1994: Effects of benthivorous bream (*Abramis brama*) and carp (*Cyprinus carpio*) on sediment resuspension and concentrations of nutrients and chlorophyll *a*. *Freshwater Biology 32*: 113–121.

Brönmark, C.; Weisner, S.E.B. 1992: Indirect effects of fish community structure on submerged vegetation in shallow, eutrophic lakes: an alternative mechanism. *Hydrobiologia 243/244*: 293–301.

Carpenter, S.R.; McCreary, N.J. 1985: Effects of fish nests on pattern and zonation of submerged macrophytes in a softwater lake. *Aquatic Botany 22*: 21–32.

Champion, P.D.; Clayton, J.S. 2000: Border control for potential aquatic weeds; Stage 1. Weed risk model. *Science for Conservation 141*. Department of Conservation, Wellington. 48 p.

Clayton, J.S.; de Winton, M.D. 1994: Lake Rotoroa, a candidate for restoration or restraint? In: Collier, K.J. (ed) The restoration of aquatic habitats. Selected papers from the second day of the New Zealand Limnological Society 1993 annual conference. Department of Conservation, Wellington.

Crivelli, A.J. 1983: The destruction of aquatic vegetation by carp, a comparison between Southern France and the United States. *Hydrobiologia 106*: 37–41.

de Winton, M.D.; Taumoepeau, A.T.; Clayton, J.S. 2002: Fish effects on charophyte establishment in a shallow, eutrophic New Zealand lake. *New Zealand Journal of Marine and Freshwater Research 36*: 815–823.

Hanson, M.A.; Butler, M.G. 1994: Responses of plankton, turbidity and macrophytes to biomanipulation in a shallow prairie lake. *Canadian Journal of Fisheries and Aquatic Science. 51*: 1180–1188.

Jeppesen, E.; Jensen, J.P.; Sondergaard, M.; Lauridsen, T.; Pedersen, L.J.; Jensen, L. 1997: Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia 342/343*: 151–164.

Lougheed, V.L.; Crosbie, B.; Chow-Fraser, P. 1998: Predictions on the effect of common carp (*Cyprinus carpio*) exclusion on water quality, zooplankton, and submergent macrophytes in a Great Lakes wetland. *Canadian Journal of Fisheries and Aquatic Science 55*: 1189–1197.

Lundholm, J.T.; Simser, W.L. 1999: Regeneration of submerged macrophyte populations in a disturbed Lake Ontario coastal marsh. *Journal of Great Lakes Research 25*: 395–400.

Meijer, M.-L.; de Haan, M.W.; Breukelaar, A.W.; Buitveld, H. 1990: Is reduction of the benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? *Hydrobiologia 200 /201*: 303–315.

Noy-Meir, I. 1975: Stability of grazing systems: an application of predator prey graphs. *Journal of Ecology 63*: 459–482.

Perrow, M.R.; Meijer, M.-L.; Dawidowicz, P.; Coops, H. 1997: Biomanipulation in shallow lakes: state of the art. *Hydrobiologia 342/343*: 355–365.

Scheffer, M. 1998: Ecology of shallow lakes. Chapman & Hall, London. 357 p.

Ten Winkel, E.H.; Meulemans, J.T. 1984: Effects of fish on submerged vegetation. *Hydrobiologia Bulletin 18*: 157–158.

Van Dijk, G.M.; Van Donk, E. 1991: Perspectives for submerged macrophytes in shallow lake restoration projects in The Netherlands. *Hydrobiologia Bulletin 24*: 125–131.

Van Donk, E.; Otte, A. 1996: Effects of grazing by fish and waterfowl on the biomass and species composition of submerged macrophytes. *Hydrobiologia 340*: 285–290.

Wright, R.M.; Phillips, V.E. 1992: Changes in the aquatic vegetation of two gravel pit lakes after reducing the fish population density. *Aquatic Botany 43*: 43–49.