



Ministry for the
Environment
Manatū Mō Te Taiao

LAKE MANAGERS' HANDBOOK

Fish in New Zealand Lakes



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Introduction

Overview

The *Lake Managers' Handbook: Fish in New Zealand lakes* updates and expands the earlier review of the fish stocks and fisheries of New Zealand lakes and reservoirs produced by Rowe (1987) in the *Lake Managers' Handbook* (Vant 1987). The 1987 review described ways of characterising the fish stocks and fishery values for a given lake, summarised the main problems that can arise with fish stocks in lakes, and outlined the various ways of addressing these. However, over the past decade there has been a large increase in knowledge about the fish in New Zealand lakes, particularly native fish species. Old problems (such as the effects of eutrophication on fish) have been further refined, and new ones (such as turbidity, lake-level fluctuations and exotic fish introductions) have emerged. Life history and distributional information on fish has expanded, as has the range of technical approaches and solutions to fishery problems. There is therefore a need to collate and summarise this new information in a form accessible to lake managers.

The increase in knowledge has been driven mainly by the need for resource consents under the Resource Management Act 1991 (RMA). Because of the commercial nature of this process, much of this information is reported in restricted-distribution client reports (the 'grey literature') rather than in the scientific literature or publicly accessible documents. The information is also often fragmented, and lake managers cannot easily access it, nor appreciate the advances made in certain areas.

This review therefore attempts to draw together the old and new information in such a way that lake managers and developers can better appreciate the advances made, the new techniques for resolving problems with fish in lakes, and some of the emerging issues. In this sense it is intended primarily for lake managers. However, fishery managers have an important advocacy role in ensuring that lake developments do not reduce fish resources, and they will also find the information useful.

In the 1987 review emphasis was placed on salmonids, mainly because (apart from a few exceptions) little was known about other fish in New Zealand lakes at the time, and the main fisheries in lakes were based on rainbow and brown trout. Collectively, trout fisheries are still the major freshwater fisheries resource in New Zealand lakes. However, a number of large, shallow, coastal lakes support important commercial fisheries for eels, and the eel fishery is now being expanded through the stocking of hydroelectric reservoirs. Demand for coarse-fish fisheries is increasing, and there is also a growing interest in the conservation of native fish populations. These are valued for their contribution to biodiversity, and in many cases are now reduced or threatened.

Structure

Good accounts of the biology for most of the fish species found in lakes are already provided by McDowall (1990). However, the biology and ecology of lacustrine fish stocks often differs markedly from those of riverine fish. Information specific to fish in lakes rather than to riverine stocks is needed, and much of this has been gained over the past decade. Part I of this guide contains descriptions of the fish species, their communities, histories, habitats and migrations. The factors affecting fish are discussed in Part II, including food webs, water quality, fish introductions and water manipulations. Part III contains a discussion of monitoring, measurement and management. The guide concludes with a case study of Lake Rotoaira.

This guide covers both native and exotic fish populations in substantial lakes and reservoirs (surface areas over 20 ha), as listed by Irwin (1975) and categorised according to location and geological origin by Green and Lowe (1987). It does not cover fish restricted to ponds, swamps, wetlands and estuaries, as these ecosystems function somewhat differently to lakes. Nor does it include information on avian fish predators, fish diseases or the management of sports fish in lakes. Although some of the issues related to the impacts and control of exotic fish species in lakes are touched on, the control of such species is dealt with in more detail in the review of plant and fish pest species in New Zealand lakes by Clayton et al. (2002).

PART I: Description of fish in lakes

Identifying the fish species present in lakes

Lake managers need to be able to assess the effects that changes in water flow and water quality have on fish in the lakes and tributary streams they manage. This requires knowing which species are present, and their contribution to fisheries or lake ecosystems. In this section we provide information on the fish species present in New Zealand lakes. These are listed in Table 1.¹

Most of the fish species known to be present in New Zealand lakes were listed by Livingston et al. (1986a; 1986b). Many of the larger lakes in New Zealand have been surveyed at some time, so there is good knowledge of which fish species are present. However, many small lakes (surface area less than 0.5 km²) have not been surveyed, so information – particularly for the native species – may be deficient. In all lakes, however, fish populations are not static. In particular, some records of exotic fish may be out of date because species stocked into lakes may not have bred and may have since died out (for example, some rudd, tench and koi carp populations). Other species (such as trout) may no longer be stocked into a lake, and some fish that were once present (smelt, dwarf inanga) may now be extinct. Some exotic species (for example, koi carp, catfish, mosquitofish) are still being spread to new locations, and eels are being periodically stocked into reservoirs, impoundments and lakes (those they cannot access naturally) to provide a commercial harvest. Generally, if a species is known to breed in a particular lake, it can be assumed that it will still be present there. However, the status of stocked fish in lakes will always need to be updated.

The most comprehensive national record of the fish species present in individual New Zealand lakes is provided by the Freshwater Fish Database, which can be directly accessed through the National Institute of Water & Atmospheric Research Ltd (NIWA) web site (see box on the page 9). This database holds records for the fish species sampled in New Zealand lakes (and their inlet streams) over the past two decades, and is being continually updated as new information comes to hand. The database allows all records of the fish for each lake to be inspected on-line. NIWA, the Department of Conservation (DOC), fish and game councils, as well as some regional councils also maintain local databases, which record information on fish abundance, size, diet and growth rate from certain lakes.

¹ Information on determining the values of the fish stocks in New Zealand lakes was provided by Rowe (1987) in the *Lake Managers' Handbook*. Good descriptions, photographs, distribution maps and keys to each species are provided in McDowall (1990), and a shortened version of this information is provided in the *Freshwater Fish Atlas* on the NIWA web site: www.niwa.cri.nz.

Table 1: Species of fish found in New Zealand lakes

SPECIES	COMMON NAME
Native species	
<i>Anguilla dieffenbachii</i>	Longfin eel
<i>Anguilla australis</i>	Shortfin eel
<i>Galaxias brevipinnis</i>	Koaro
<i>Galaxias fasciatus</i>	Banded kokopu
<i>Galaxias maculatus</i>	Inanga
<i>Galaxias argenteus</i>	Giant kokopu
<i>Galaxias gracilis</i>	Dwarf inanga
<i>Galaxias rekohua</i>	Chatham galaxies
<i>Retropinna retropinna</i>	Common smelt
<i>Gobiomorphus cotidianus</i>	Common bully
<i>Gobiomorphus breviceps</i>	Upland bully
<i>Gobiomorphus basalis</i>	Cran's bully
<i>Gobiomorphus alpinus</i>	Tarndale bully
<i>Rhombosolea retiaria</i>	Black flounder
<i>Mugil cephalus</i>	Grey mullet
Salmonids	
<i>Oncorhynchus mykiss</i>	Rainbow trout
<i>Oncorhynchus tshawytscha</i>	Chinook salmon
<i>Oncorhynchus nerka</i>	Sockeye salmon
<i>Salmo trutta</i>	Brown trout
<i>Salmo salar</i>	Atlantic salmon
<i>Salvelinus fontinalis</i>	Brook trout
<i>Salvelinus namaycush</i>	Lake trout
Coarse fish species	
<i>Perca fluviatilis</i>	Perch
<i>Scardinius erythrophthalmus</i>	Rudd
<i>Tinca tinca</i>	Tench
<i>Carassius auratus</i>	Goldfish
<i>Cyprinus carpio</i>	Koi carp
<i>Ameiurus nebulosus</i>	Brown bullhead catfish
<i>Leuciscus idus</i>	Orfe
<i>Gambusia affinis</i>	Mosquitofish
<i>Ctenopharyngodon idellus</i>	Grass carp*
<i>Hypophthalmichthys molitrix</i>	Silver carp*

* Do not breed naturally in New Zealand

NIWA web site address: www.niwa.cri.nz

Clickable links to the Freshwater Fish Atlas can be found at the NIWA web site in the page on Freshwater, and in the section on Publications and Articles. Information on the Freshwater Fish Database and how to access it is also provided in the page on Freshwater, but under Online Services and Data.

The different fish communities in lakes

The composition of the fish fauna in a given lake differs mainly according to the lake's size, location, type of outlet to the sea (determining access by native fish species) and stocking history. Variations to the general patterns do occur, however, and the actual species present need to be checked before the fish fauna of a specific lake can be correctly characterised.

A broad classification of lakes based on both their altitude (also reflecting distance inland) and size is provided in Figure 1, which identifies five main types of fish community. Not all lakes will fit these categories, and the less common fish species may or may not be present in all lakes within a category. Nevertheless, the dominant fish species in each community provides a useful way of categorising both a lake and its community. The main lake categories are: salmonid, eel (small lake), eel (large lake), galaxiid, and coarse fish.

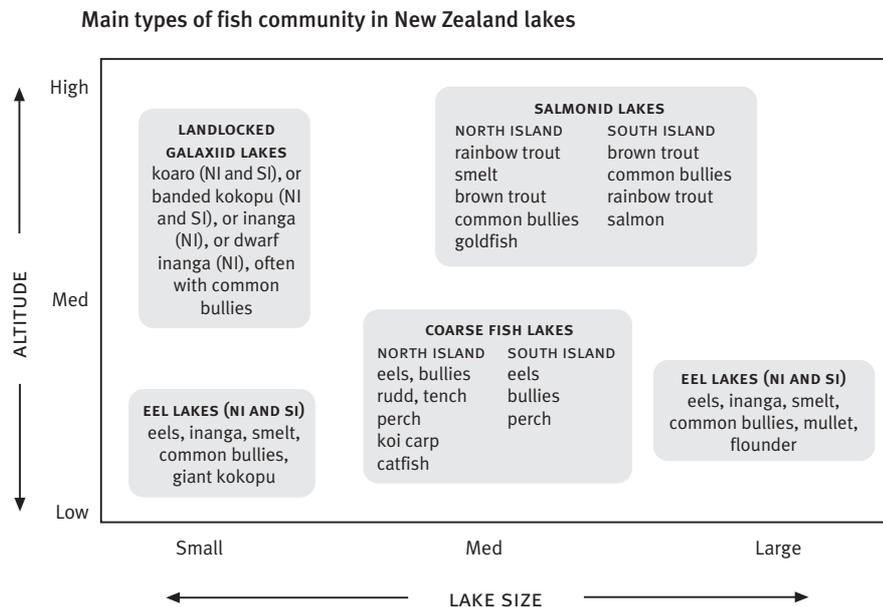


Figure 1: The main types of fish community in New Zealand lakes, classified by lake size and altitude

Note: The main fish species present within each class of lake are listed for both the North Island (NI) and South Island (SI).

In the larger, inland hydro lakes of the South Island (for example, lakes of the Waiau, Clutha, Waitaki and Rakaia Rivers) the fish community is dominated by salmonids. Brown trout and rainbow trout are the most common species, with brown trout usually more prevalent than rainbow trout. Other salmonids such as

sockeye salmon, Atlantic salmon, chinook salmon, lake trout and brook trout are also present in some lakes (Table 2). Common bullies are the most abundant native fish species, although eels and koaro are also present in some of these lakes. Koaro are rare in most lakes and are confined mainly to inlet streams. They only remain common in lakes Pukaki, Tekapo and Alexandrina, and readily colonised Lake Mahinerangi after its formation.

Table 2: South Island lakes containing land-locked salmon stocks, and their current status

CHINOOK SALMON		SOCKEYE SALMON		ATLANTIC SALMON		LAKE TROUT	
LAKE	STATUS	LAKE	STATUS	LAKE	STATUS	LAKE	STATUS
Heron	U	Ohau	R	Te Anau	R	Pearson	R
Sumner	U	Benmore	R	Manapouri	R		
Coleridge	A	Aviemore	R				
Wakatipu	A	Waitaki	R				
Hawea	A						
Wanaka	C						
Dunstan	C						
Kaniere	R						
Paringa	C						
Moeraki	R						
Mapourika	C						
Okarito	C						
Ellery	R						

Notes: A = abundant; C = common; R = rare; U = unknown.

In the large, inland North Island lakes and reservoirs, near Taupo, Rotorua and Gisborne, the fish communities are also dominated by salmonids, but rainbow trout are more prevalent than brown trout, and there are no salmon. Common bullies are also the main native fish here, but land-locked populations of smelt are numerous in many of the North Island lakes and reservoirs containing trout. Some of these lakes also contain remnant populations of koaro. Koaro are no longer as abundant as they once were in the North Island lakes containing trout (Rowe 1990), and are scarce in Lake Taupo and all the Rotorua lakes, except in certain tributary streams where remnant populations persist. However, they are still reasonably common in a few large trout lakes such as Rotoaira and Waikare-iti. These, like the South Island lakes where koaro are still common, have either few trout or a mainly rainbow trout population.

In both islands the fish communities of the large, shallow, coastal lakes tend to differ from those of the larger, deeper, inland lakes. Trout are often absent or scarce, and native fish such as eels generally predominate. For example, eels are the dominant fish in lakes Ellesmere (Christchurch), Wairarapa (Wellington), Horowhenua (Levin), Waikare (Hamilton), Whangape (Hamilton) and Omapere (Kaikohe). Eels predominate because these lakes are close to the coast and so are easily accessible to migrants from the sea. Also, being lowland and coastal lakes, most have inadequate spawning streams for trout.

Where fish access to the sea via the outlet stream is completely unimpeded, poor swimmers can readily access the lake and so its fish community may comprise a wide range of species that migrate between fresh and marine waters to complete their life cycle (for example, common bullies, inanga, smelt and, in some lakes, giant kokopu, flounder and grey mullet). However, where access to the lakes is blocked (such as by a weir or dam), poor swimmers are excluded, and the species present are restricted to eels, along with a land-locked population of bullies.

Small lakes dominated by galaxiids are the fourth category of lake containing distinct fish communities. In small, inland lakes of the South Island such as Lakes Christabel and Chalice, and lakes close to Waikare-iti near Gisborne, the koaro is the main galaxiid species (Johnson et al. 1976; Meredyth-Young and Pullan 1977). Koaro also inhabited Lake Rotopounamu near Turangi, but are now thought to be extinct there (Rowe 1993a). Land-locked populations of banded kokopu often occur in west coast dune lakes and water supply reservoirs, but they are seldom abundant. Populations of banded kokopu occur in the Kaihoka Lakes near Nelson, in several west coast North Island dune lakes, and in most of Auckland's Waitakere and Hunua water reservoirs. In a very few such coastal lakes (for example, Lake Pounui near Wellington) giant kokopu rather than banded kokopu are the dominant galaxiid. In contrast, land-locked stocks of either inanga or dwarf inanga occur in a number of west coast dune lakes in the top half of the North Island. There are land-locked stocks of inanga in lakes Rotokawau, Waiparera and Ngatu (near Kaitaia), and dwarf inanga now occur in two lakes near Dargaville, eight on the North Kaipara Head, and one on the south Kaipara Head (Rowe and Chisnall 1997a). Different species of galaxiids therefore characterise the fish communities of many of the smaller lakes not dominated by eels or trout.

Coarse fish now characterise the fish community of many small lakes, particularly where there is no access to the sea, or where access is intermittent and the lake has been stocked with such fish. In the South Island, perch are common in many small lakes around Dunedin, and in the North Island lake-bound populations of perch are clustered around Wellington, Wanganui, Napier and Auckland. In the top half of the North Island coarse fish species such as goldfish, catfish, rudd or tench now occur in many of the smaller (under 50 ha) lakes and reservoirs, along with a sparse fauna of native fish and some trout. Some of these coarse fish species now also occur in some South Island lakes.

Rare and threatened species

The dwarf inanga, Tarnsdale bully and Chatham galaxias are the only native fish that can be described as rare in New Zealand lakes. Of these, the dwarf inanga currently has status with the IUCN (International Union for the Conservation of Nature) as a threatened species. Although other native fish may only occur in very few lakes (for example, banded kokopu) or are now greatly reduced in most lakes (koaro), diadromous stocks are present in many New Zealand rivers, so these species are not considered rare. Nevertheless, many land-locked populations of such native fish can be expected to have evolved within lakes to a point where they are now genetically distinct from the diadromous stocks (Ling et al. 2001). They therefore constitute evolutionarily significant units (ESUs), and these populations require some protection if biodiversity is to be maintained. Genetic studies have identified ESUs for dwarf inanga and inanga (Ling et al. 2001), and it

is likely that ESUs will be identified for many other native species in lakes, particularly koaro, common bullies, Cran's bullies, and possibly smelt.

Many of the exotic species listed in Table 2 are also rare in New Zealand lakes, either because their populations have been reduced, or because they have a restricted distribution. For example, Atlantic salmon, lake trout and orfe only occur in one or two lakes because of restricted distributions. A number of brook trout and sockeye salmon populations have been lost through either environmental change or interactions with other salmonids. Their populations can therefore be described as 'threatened', although this conservation status is generally reserved for native fish species.

Such a stance recognises that many exotic fish species have reduced native fish, and it derives from the precautionary corollary that all exotic fish pose a potential risk to endemic biodiversity. However, this stance ignores the potentially valuable genetic base that such stocks of exotic fish now provide. Current legislation and international agreements mean that these species could not be introduced again, so the extinction of the existing stocks of these fish may represent a significant loss. It is clear that the potential for environmental damage by these fish (should they be spread more widely) needs to be weighed against the potential value of maintaining their stocks before the status of these fish can be determined.

Fish life histories and habitats

In this section, we summarise and update information on New Zealand's lacustrine fish stocks. Fish species with similar life histories and biology are grouped together to form the following categories:

- salmonids
- eels
- galaxiids
- smelt
- bullies
- other native species
- non-salmonid exotic fish.

For each group we first provide information on the species comprising the group, then the biology of the main representatives of each group. This covers spawning behaviour, times and habitats, and, where available, information on age at maturation, longevity, growth, spatial distribution, adult habitats and food. If known, differences between individual species within a group are noted, as are the likely role(s) and the conservation status of the fish species in lake ecosystems.

Life history patterns for fish species in New Zealand lakes can be categorised into four main types based on the patterns for riverine fish.

- *Catadromous species* grow to adulthood in freshwater environments, but spawn at sea (for example, eels, black flounder and mullet). Catadromous species occur in most lowland lakes.
- *Anadromous species* grow to adulthood in the sea but return to freshwater to spawn. No anadromous species occur in lakes, but land-locked stocks of these species use the lake as an ecological equivalent to the sea (for example, salmon and trout).
- *Amphidromous species* have a juvenile phase at sea but mostly grow to adulthood and spawn in freshwater (for example, koaro, banded kokopu, inanga, common bullies, smelt). Amphidromous stocks of inanga and smelt occur in a number of small coastal lakes. For land-locked stocks of these species, lakes serve as the ecological equivalent of the sea. Their larval and juvenile phases occur in the lake, whereas adults mostly grow and spawn in the streams. However, it is apparent that the adults for many of these species are also able to remain and develop in lakes (for example, koaro, banded kokopu, inanga and smelt).
- *True lacustrine species* spend their entire life cycle in freshwater. Some native species, such as dwarf inanga and common bullies, carry out their entire life cycle in the lake and do not need streams for spawning. Most of the non-salmonid exotic fish fall into this category.

Salmonids

General

The salmonids include what are commonly called the trouts (brown, rainbow, lake and brook) and salmon (chinook, sockeye and Atlantic) present in New Zealand. Brown and/or rainbow trout now occur in most North and South Island lakes, with brown trout generally predominating in the South Island and rainbow trout in the North. However, populations of chinook, sockeye and Atlantic salmon, lake trout, and brook trout also occur in some lakes inhabited by brown or rainbow trout. These rarer salmonids are mainly restricted to the South Island and are scarce (see Table 2). Sockeye salmon, Atlantic salmon and lake trout can now be regarded as rare and endangered within New Zealand. The New Zealand stocks of sockeye salmon may in fact be close to extinction, largely as a consequence of the Upper Waitaki Power Development Scheme (Graynoth 1995; Quinn et al. 1998).

Brook trout occur in both the North and South Islands. A lacustrine population occurs in Lake Emily, but populations in the North Island are restricted (mainly by competition from rainbow trout) to lake inlet streams. Small, self-sustaining populations persist in several small inlet streams draining into lakes Rotorua, Taupo and Moawhango. There is a small lacustrine population in the Hinemaiaia Reservoir in the catchment of Lake Taupo, but this is probably because other trout species are absent.

The life history, biology and habitats of the two main trout species (brown and rainbow trout) in New Zealand lakes are relatively well known, but those for the rarer salmonid species are not. They can only be inferred from overseas studies, and specific details of their habitats and life history in New Zealand lakes are mostly lacking. The exception is the sockeye salmon, which has been studied for many years in the Waitaki River system (Graynoth 1987; 1995; Graynoth et al. 1986).

Spawning

All the salmonids – apart from the lake trout – require a gravel bed in flowing water to incubate their eggs, so they spawn mainly in the inlet streams of lakes where there are suitable gravels and water depths. Lake trout spawn on gravel beds in the deeper waters of North American lakes, and can be expected to use a similar habitat in Lake Pearson. However, rainbow trout can spawn on the gravel beds of outlet as well as inlet streams (Rowe, Konui et al. 2000), and on the gravels present in the littoral² margins of lakes whose streams provide limited spawning habitat (Penlington 1983). Mature trout migrate from lakes into spawning streams each year – brown trout mainly in winter and rainbow trout in spring (see section 3).

Although the locations of inlet and outlet tributary streams used by salmonids for spawning are generally known by fish and game councils, the locations of specific reaches used for egg laying may not have been identified for all tributaries, or all species. Also, the relative importance of tributaries for the recruitment³ of brown versus rainbow trout stocks in lakes where both species occur is not well understood (Graynoth 1999b). As a result, decisions on resource consents

² Shallow benthic zone from edge of lake down to depth where plants no longer grow.

³ Supply of juvenile fish to the fishable stock.

affecting such streams are more difficult. In many North Island lakes (for example, most Rotorua lakes and lakes further north), trout spawning habitat is limited and/or absent, and annual stocking of hatchery-reared fish is needed to maintain the stocks.

Trout generally mature at an age of two to three years and can spawn once a year for up to four to five years (Smith 1959; Rowe, Konui et al. 2000), but brown trout can live for a few years longer than rainbow trout (Dedual et al. 1997). The post-spawning mortality rate for trout is higher for males than for females, so the older age classes become progressively dominated by females (Dedual et al. 1997; Rowe, Konui et al. 2000).

Growth

Growth rates are strongly influenced by water temperatures, and in particular by the seasonal duration of water temperatures for optimal growth. Growth rates of trout have now been recorded for many lakes (see, for example, Fish 1966; 1968; Penlington 1985; Graynoth 1996; Dedual et al. 1997; Rowe, Konui et al. 2000) and growth is generally slower in the colder, South Island lakes than in the warmer North Island lakes. Food supply is also important, and growth is fastest in central North Island lakes which combine optimal thermal habitat and abundant smelt. Fast growth (especially during spring) leads to an early age at first maturation in trout (at two-plus years, instead of three-plus or older), and maturation curtails further growth in most salmonids (Rowe and Thorpe 1990a; Rowe, Konui et al. 2000). Fast growth therefore results in a stock of relatively young, moderate-sized, mature trout (although some can be late maturing and large), whereas slower growth may result in a stock of generally older, larger trout which are prized as trophy fish. Because anglers prefer larger trout, stocked fish are now generally from later-maturing strains.

Distribution

Adult rainbow trout can usually be found throughout the water column of lakes down to depths of 150 m (Cryer 1991). However, in two Rotorua lakes most trout occurred in midwater, at depths of 10–40 m, where water temperatures were optimal for growth (Rowe and Chisnall 1995). There are no data on the depth distribution of brown trout, but they can be expected to have a more littoral distribution than rainbow trout. Trout move throughout a lake, covering perhaps several kilometres over several days (James and Kelso 1995), so their spatial distribution can be expected to vary widely.

Feeding

Adult trout are opportunistic carnivores, feeding on whatever suitable prey is most abundant. In many lakes their main prey are snails, aquatic and terrestrial insect larvae, small forage fish, and crayfish, with brown trout being generally more piscivorous than rainbows (Graynoth et al. 1986; McCarter 1986). They will feed on any small fish, including native species such as galaxiids, bullies and smelt. In South Island lakes bullies are the main forage fish species, whereas in North Island lakes smelt are often the main prey (Rowe 1984a). Smelt are usually consumed by the smaller (20–30 cm long) yearling trout, and large prey such as crayfish are consumed by the larger (over 40 cm long) fish. Odonata (dragonfly) larvae are an important prey for adult brown and rainbow trout in several North Island lakes during spring, with terrestrial insects (for example, green beetle and

cicadas) predominating in summer. Winter foods include snails, forage fish and, in some lakes, *Daphnia*. In Lake Lyndon large rainbow trout were found to be cannibalistic, and this may have accounted for some of the annual variation in adult trout abundance (Percival and Burnet 1963).

In comparison with adults, the distribution and foods of juvenile trout in lakes are not well understood (Graynoth 1999b). Stream rearing is likely to be more important than lake rearing for juvenile trout (Roseneau 1991; Hayes 1995), but in some lakes most wild trout are derived from lake-shore spawning (Penlington 1983). As juvenile trout in lakes are likely to be more vulnerable to changes than adults, and as their mortality rates have a large influence on the stocks of adult fish entering fisheries, this constitutes an important gap.

Recreational and ecological roles

Although trout provide important recreational fisheries in many lakes, they may also have an important ecological role as top predators. Recently salmonid predation has been shown to regulate the abundance of planktivorous fish in some North American lakes, and so plays a role in the top-down regulation of water quality (Scavia et al. 1986).

Eels

General

Longfin and shortfin eels inhabit lakes throughout New Zealand. They are good climbers and can be found in nearly all lakes, although some species differences are apparent. Longfin eels (particularly females) tend to be more prevalent in the larger, deeper, inland lakes (Jellyman 1995; Beentjes et al. 1997), whereas shortfin eels predominate in shallow coastal lakes (Jellyman 1989; Chisnall 1996; Jellyman and Chisnall 1999). Eels are probably the most studied of all the freshwater fish in New Zealand lakes. For example, lakes such as Waikare, Waahi, Pounui and Ellesmere have all been sites for long-term research investigations (Jellyman 1989; Chisnall and Hayes 1991; Hayes et al. 1992; Jellyman et al. 1995; 1996; Chisnall 1996; Jellyman and Chisnall 1999).

Spawning

Spawning occurs at sea, and lakes are populated by the annual influx of elvers migrating upstream from the sea. Elvers are good climbers, capable of ascending wet, vertical faces, and can penetrate well inland. Adult eels are also adept at moving overland through wet grass and vegetation. As a consequence, lowland lakes with no apparent access to the sea are often populated with eels. Upstream migration is only halted by large rapids (such as Hunua falls), artificial dams and perched culverts. Mature adults move towards lake outlets during autumn, before moving downstream to the sea where they undertake a return migration to oceanic spawning grounds.

Distribution

The predominance of shortfin eels in lowland coastal lakes and longfin eels in inland, higher-altitude lakes probably reflects habitat preferences. Longfin and shortfin eels are both caught in the shallow and deep waters of lakes (Jellyman et al. 1996), but most are found near the lake edge, particularly where marginal habitat containing raupo is present (Chisnall 1996; Jellyman and Chisnall 1999).

A degree of size segregation occurs, with most large eels (over 400 mm) found further offshore than smaller ones (Chisnall 1996; Jellyman and Chisnall 1999). Eels exhibit territorial behaviour in lakes (D. Jellyman, personal communication) and prefer softer, silt-based substrates to hard, sand-based ones (Jellyman and Chisnall 1999).

Feeding

Eels are nocturnal, benthic predators feeding mostly on invertebrates when small (under 400 mm long) and more on crayfish and small fish such as bullies as they grow (Jellyman 1989; 1996). However, during floods they move into the inundated lake margins to utilise earthworms and other terrestrial foods (Chisnall 1990; Jellyman 1989).

Commercial role

Eels are regularly harvested in many lakes as part of a commercial fishery. They are now also stocked into a number of lakes and reservoirs where access has been blocked by dams, or where they have no natural access (Beentjes et al. 1997; Chisnall et al. 1998). However, where there is no outlet and little harvesting occurs, eels become land-locked and can eventually become quite large (over 1.0 m long). Because they become increasingly piscivorous over about 40 cm long, land-locked eels may eventually impact on native fish populations before they die out. Both common bullies and dwarf inanga show a reduced abundance in lakes with eels present (Rowe 1999a; Rowe and Chisnall 1997b). They may also reduce crayfish populations in such lakes. Upstream passage of juvenile eels over dams, and of adults back downstream, are now major issues associated with resource consents for dams (see section 8).

Galaxiids

General

Before the introduction of trout to New Zealand, most lakes contained populations of native galaxiid fish. Amphidromous populations of inanga still occur in a number of shallow, coastal lakes (for example, Lakes Ellesmere and Wairarapa), where there is ready access to and from the sea. However, a number of amphidromous galaxiid species, including inanga, are capable of forming land-locked populations. In general, the koaro was the most widespread of these species, inhabiting many inland lakes not accessible to other species. However, adult banded kokopu are also good climbers and land-locked populations occur in a number of coastal lakes, including the Kaihoka lakes near Nelson, several North Island west coast dune lakes (for example, Lake Ototoa), and in a number of small reservoirs (such as the Waitakere and Hunua reservoirs near Auckland). Land-locked populations of inanga are more restricted and occur in only a handful of Northland dune lakes (for example, Ngatu and Waiparera).

The giant kokopu is probably the most restricted – albeit most widespread – of these land-locked galaxiids, occurring in a few Southland lakes and in Lake Pounui. The dwarf inanga is a distinct species of galaxiid (McDowall 1967), which has recently evolved from land-locked populations of inanga (Gleeson et al. 1999; Ling et al. 2001). It is now confined to 12 North Island west coast dune lakes (Rowe and Chisnall 1997a). It has no riverine or amphidromous equivalent, and in this sense has become the only true lacustrine species of native fish. There is

abundant information on riverine stocks of galaxiids, but data on lacustrine stocks are limited, except for koaro and dwarf inanga.

Koaro

Spawning

Lacustrine koaro spawn mainly over summer (Rowe, Konui et al. 2002) and eggs have been found at this time in Taupo streams (Kusabs 1989), suggesting that spawning occurs in the inlet streams of lakes. The large summer migrations of adult koaro that once occurred into submerged springs in Lake Rotoaira (Fletcher 1919; Phillipps 1924) are likely to have been primarily for spawning. A reduction in the abundance of adults in this lake between September and April, together with a marked decline in the proportion of mature versus spent fish, is consistent with summer spawning in inlet streams/springs (Rowe, Konui et al. 2002). However, as koaro occur in some small South Island tarns without permanent inlet streams, some spawning may occur within these lakes. Riverine stocks spawn over the cobbly margins of small streams, probably during flood events, and lacustrine stocks are likely to duplicate this. Most eggs remain in the moist/wet interstices between the cobbles until the water levels increase again, and the eggs then hatch. Permanent streams may therefore not be needed for koaro spawning.

Growth

In Lake Rotoaira koaro matured at a relatively small size (about 60 mm). The males matured at a smaller size than females, and they probably spawn each year after they mature. Most adult koaro are 80–120 mm long, but they can grow up to 270 mm in lakes (Rowe 1999b). Growth rates in Taupo streams (Kusabs 1989) suggest they can live for up to 10 years.

After eggs hatch the long, thin transparent larvae are washed into the lake, where they rear through to the whitebait stage. In Lake Coleridge the larvae occur in deep water (20–40 m) during November–December but move into shallower waters in January and February (Taylor et al. 2000). In Lake Rotoaira larvae are more prevalent in surface waters at night than during the day (Rowe, Konui et al. 2002). Once they become ‘whitebait’, at a size of about 30 mm, the juveniles aggregate in schools close to the surface and probably feed mainly on zooplankton. In this respect they are similar to smelt, and would be highly vulnerable to trout predation. After they reach 40–50 mm long juveniles (akin to whitebait) either migrate into inlet streams, where they grow to adulthood, or stay in the lake and become benthic. In Lake Taupo such migrations occur mainly in November and December (Kusabs 1989). Populations of adults in the inlet streams of lakes are usually confined to reaches where there are few or no trout (Rowe, Konui et al. 2002).

Feeding

Adults are found throughout the littoral and benthic zones of lakes down to at least 100 m (Fletcher 1919; Rowe 1993b). They feed on a wide range of invertebrates, including mayfly, stonefly, caddisfly and chironomid larvae (Graynoth et al. 1993; Rowe, Konui et al. 2002). Purse caddis larvae, which are attached to plants or rock surfaces, are a major prey for koaro in Lake Rotoaira, indicating that these fish are essentially benthic grazers (Rowe, Konui et al. 2002). However, they also eat fish eggs (Kusabs 1989), and the largest (over 90 mm) can

feed on snails and bullies (Rowe, Konui et al. 2002). Surprisingly, large numbers of adults were reported to be washed up on the shores of Lakes Taupo and Rotoaira by wave action during storms (Fletcher 1919; Rowe, Konui et al. 2002).

Distribution

Koaro were once the most abundant fish in many inland lakes and were harvested by Maori (Fletcher 1919). The introduction of trout greatly reduced their abundance (McDowall 1990), but the schooling juveniles (mostly under 50 mm long) remained abundant enough to be an important prey species for both trout and land-locked chinook salmon in some lakes (Rowe 1990; E. Graynoth, personal observation). It is apparent that smelt can displace koaro in lakes, and that the introduction of smelt to many central North Island lakes in the 1930s resulted in a further decline of koaro over and above that produced by trout predation (Rowe 1990). In Lake Rotopounamu, where trout are absent and koaro were once abundant, the introduction of smelt resulted in their extinction (Rowe 1993a).

Today, lacustrine populations of koaro are rare and are restricted to lakes with no trout (Challice, for example), with just rainbow trout and no smelt (Alexandrina, Rotoaira, Waikare-iti), and turbid lakes with few trout (Pukaki and Tekapo). Remnant populations occur in other lakes but are largely restricted to the inlet streams (for example, Coleridge, Wanaka, and Hawea in the South Island, and Tarawera, Rotoiti and Taupo in the North Island)

Other galaxiid species

Banded kokopu

The biology and life history of land-locked banded kokopu has had very little attention. Adults feed on a range of aquatic invertebrates in lakes (Moore et al. undated), and were observed to spawn in an inlet stream of the Waihi Beach water reservoir during a June flood (Mitchell and Penlington 1982). These observations suggest that spawning may occur in the streams rather than in lake habitats, and that the life history and biology of banded kokopu in lakes will be similar to that for koaro.

Giant kokopu

The giant kokopu is New Zealand's largest galaxiid. It commonly reaches sizes of 300–400 mm in length and grows up to 580 mm long (McDowall 1990). In Lake Pounui adults ranged in size from 180 to 330 mm and preferred raupo swamp habitat to the shallow, rush-covered margins, or open water habitat (Jellyman 1979). They feed on both terrestrial and aquatic invertebrates, but large fish are partly piscivorous and can be expected to ambush small forage fish from the cover of the raupo stands. Nothing is known of their spawning in lakes.

Inanga

Little is known of the biology of inanga. Amphidromous inanga prefer the sheltered western shores of Lake Ellesmere to the more exposed eastern shores (Glova and Sager 2000). Foods are likely to be similar to those for smelt in shallow lakes, ranging from plankton, to small aquatic and terrestrial invertebrates for adults. Spawning grounds for amphidromous stocks in lakes are unknown, but could occur in lakes as well as streams. Land-locked inanga differ from amphidromous stocks in that they have fewer vertebrae, are smaller, and have

more gill rakers (McDowall 1972; Rowe and Chisnall 1997a). Such evolutionary changes in morphology suggest a more planktivorous life style. As with amphidromous stocks, little is known of the biology and life history of land-locked inanga.

Dwarf inanga

More is known about dwarf inanga, mainly because of its status as a threatened species (McDowall and Rowe 1996) and its classification as vulnerable in the IUCN red data book. It can be assumed that its spawning occurs within lakes as these fish are found in a number of dune lakes with no inlet streams. However, the seasonal timing and location of spawning grounds is unknown. Dwarf inanga mature at a small size (30 mm), but they probably only live for one to two years, with the largest fish being about 80 mm long. The larvae are planktonic, and juveniles start forming schools in the pelagic zone (i.e., the open-water regions of the lake, away from the littoral or benthic zone) at about 25 mm (Rowe and Chisnall 1996a). Fish over about 40 mm move to the littoral zone, where they feed on invertebrates during the day, but larger adults (50–80 mm) are absent from the littoral zone during the day and school in the deeper waters near the middle of lake (Rowe and Chisnall 1996a), returning to the littoral zone to feed at night. Dwarf inanga therefore depend on a range of lake habitats during their life cycle and could be vulnerable to changes in these. They are a major prey for trout in some lakes (Rowe and Chisnall 1997a), and were successfully introduced to Lake Ototoa (south Kaipara Head) in 1986 to provide a forage species for trout (Thompson 1989).

Smelt

General

The only species of smelt found in New Zealand lakes is the common smelt. Smelt in lakes are generally lacustrine (carry out their entire life cycle within the lake). However, amphidromous stocks of common smelt (migrating between marine and freshwater habitats, but not for the purpose of spawning) occur in some shallow coastal lakes with unimpeded access to the sea (for example, Lakes Ellesmere, Wairarapa and Waahi). The land-locked, lacustrine populations in North Island trout lakes have mostly been established by stocking. Apart from two exceptions (Lakes Camp and Poerua), attempts to establish lacustrine stocks in South Island alpine lakes have been unsuccessful (McDowall 1990). Both lacustrine and amphidromous stocks co-existed in Lake Waahi until the lacustrine stock declined (Northcote and Ward 1985).

Spawning

During spring and summer smelt scatter their eggs over clean sand substrates in the shallow, sandy margins of lakes (for example, 0.5–2.5 m in Lake Taupo), or in inlet rivers and streams (Jolly 1967; Stephens 1984). The eggs hatch relatively quickly (in about 10 days) and the 8–10 mm long transparent larvae quickly become planktonic.

Distribution

Both juveniles and adults are schooling fish, inhabiting the littoral zone as well as open waters. However, depth distributions vary between lakes, with shallower distributions occurring in more turbid lakes (Rowe and Taumoepeau, submitted).

In lakes deeper than about 10 m, smelt form schools within discrete depth layers by day (Rowe 1993b). Juveniles (30–50 mm long) school near the lake surface (0–5 m), whereas the larger fish (over 50 mm) prefer deeper waters. At night all these schools disband as fish disperse and move to the lake surface (Rowe 1994).

Although the daytime depth of fish is relatively constant in deep lakes such as Rotoiti, Okataina and Rotoma, densities often vary greatly from one side – or end – of the lake to the other (Rowe 1994). Such variation in areal distribution is often associated with strong winds, which create a circular water current in the epilimnion (the lake region above the thermocline, which prevents the mixing of waters below). When such winds prevail for several days, surface waters move towards the exposed shoreline and plunge down to create a counter-current near the bottom of the epilimnion. Fish then become concentrated in sheltered, backwater areas such as leeward shores, and behind submerged reefs or promontories that provide protection from the subsurface currents. In Lake Ellesmere smelt prefer the more sheltered western shores over the exposed eastern ones (Glova and Sagar 2000).

Feeding

The larvae feed on phytoplankton as well as micro-zooplankton (Cryer 1988), and although the juveniles and adults are mainly planktivorous in large, inland lakes (Jolly 1967; Stephens 1983), in small, shallow lakes they feed mainly on chironomid larvae (Forsyth and James 1988; Boubée and Ward 1997; Northcote and Chapman 1999). The largest smelt also feed on larval fish (Jolly 1967; Stephens 1983; Forsyth and James 1988).

Ecological and recreational roles

Like bullies, common smelt are a major prey species for rainbow trout in North Island lakes and underpin these fisheries, particularly in Lake Taupo. They are also harvested for food in a small way by Maori in Lake Taupo (Rowe 1997). Smelt are the main planktivore in New Zealand lakes, and as such may influence the composition and seasonal abundance of zooplankton populations. Amphidromous stocks in lakes are now probably rare, and lacustrine stocks appear to decline as lakes become more productive. Reasons for this are still speculative, but siltation of spawning substrates is thought to play a role in this.

Bullies

General

Only four of the seven species of bully in New Zealand are known to land-lock and form self-sustaining populations in lakes and reservoirs. The common bully is the most widespread, and there are few lakes where it is not present. The upland bully is found in a number of South Island lakes and has been well studied in the Spectacles Lakes (Staples 1975a; 1975b). The Tarndale bully is the most restricted species and is only known to occur in three small lakes in the upper regions of the Clarence River catchment. Cran's bully is found only in North Island lakes, such as the Mangatawhiri and Mangatangi Reservoirs near Auckland. Both common and Cran's bullies have been reported in these reservoirs, so the two species may co-exist. However, most lakes contain only one species of bully and competitive interactions between the species have not been studied. The life history and biology of bullies in lakes appears to be very similar, and although there are undoubtedly species differences they are not yet documented.

Spawning

Bullies deposit eggs in nests on hard substrates such as rocks, wood, old weed stalks and mussel shells, mainly in the littoral zones of lakes. These nests are fanned and guarded by males. Spawning occurs mainly in spring and summer, and although most nests are found in shallow waters (less than 5 m), bullies will breed on hard objects (such as moorings) in much deeper water (up to 10 m). Most bullies mature first at age two and a few live for up to five years.

Growth and development

After hatching the 3–4 mm-long larvae become planktivorous and by day congregate in a discrete depth layer some 5–20 m below the lake surface (Rowe 1993b). At night they migrate to surface waters (Rowe and Chisnall 1996b). The duration of the larval phase varies, and measurement of it is complicated by the fact that in some lakes spawning and hence recruitment of larvae may occur over a long period during spring and summer (Stephens 1982). At about 15–18 mm long the larvae settle on the lake bottom, usually in spring, and become benthic. Adult bullies are generally 30–60 mm long in lakes, but some older and hence larger fish (up to 100 mm long) are sometimes present.

Feeding

Larval bullies feed mainly on zooplankton (Rowe and Chisnall 1996b), whereas adults feed primarily on benthic invertebrates such as chironomid larvae, mayfly nymphs and snails (Forsyth and James 1988). In the deeper waters of oligotrophic lakes adults feed mainly on benthic crustacea (Rowe, Nichols et al. 2001). During winter few adults are seen in the shallows of lakes (0–2 m), but in summer they are abundant, presumably because of the warmer waters and increased food supply. The abundance of both adults and larvae increases as lakes become more productive, with the highest populations occurring in shallow, eutrophic lakes (Rowe 1999a).

Distribution

Although bullies are most abundant in the littoral zone of lakes at depths of around 10–12 m, demersal⁴ populations occur from 30 m to at least 80 m (Rowe, Macaulay et al. 2001). An inshore/offshore movement of fish occurs in very shallow waters (0–5 m) between dusk and dawn (Rowe 1993a), but this does not appear to happen in demersal populations.

Cran's and upland bullies are found in some inland lakes and reservoirs not containing common bullies. Cran's bully is restricted to the North Island (for example, Hunua reservoirs) and upland bullies occur mainly, but not exclusively, in small inland lakes and tarns in the South Island. They have a similar life history to common bullies. Staples (1975a; 1975b) has provided a comprehensive account of the biology of upland bullies in two small tarns. Tarndale bullies occur in several small inland lakes west of Kaikoura (McDowall 1990), but nothing is known of their biology. Other bully species present in New Zealand waters (giant, redfin and bluegill bullies) require migration to and from the sea to complete their life cycle, and are not known to form lacustrine stocks.

⁴ Demersal fish inhabit the benthic zone near the lake bed and below the littoral zone.

Ecological roles

In many lakes bullies are a major prey species for sports fish such as trout and salmon, as well as for piscivorous (over 400 mm-long) eels. Bullies may also play a role in lake ecology because their larvae are planktivorous and may therefore influence zooplankton community structure (Rowe 1994; Jeppesen et al. 1997). When they become benthic (at about 15–18 mm) most settle in the littoral zone, so there is a transfer of carbon production from the pelagic to the littoral zone, as well as an increase in predation pressure on littoral invertebrates.

Bullies are probably essential for the recruitment of mussels to lake littoral zones. They are the main host for the glochidia larvae of mussels, and are probably used by mussels to transport their larvae from deeper waters into the shallows. Recently, common bullies have been found to occupy the demersal zone of lakes down to at least 80 m, and they probably occur on the bottom at even greater depths (Rowe, Nichols et al. 2001). The ecological role of these demersal populations is yet to be determined.

Mullet and flounder

The other native fish found in New Zealand lakes include the grey mullet and black flounder. Both spawn in marine environments, but many juveniles and adults migrate into shallow coastal lakes to feed (for example, Lakes Ellesmere, Wairarapa and Taharoa). They are not strong swimmers so are only found in lakes where there is a low-gradient outlet stream connecting the lake to the sea. Adult grey mullet (250–350 mm long) are mainly detritivores (Wells 1984). Adult black flounder are usually 200–250 mm long, but they can reach 450 mm (McDowall 1990). Little is known about their biology or ecology in lakes. Grey mullet form important traditional fisheries in some lakes (for example, Lake Taharoa west of Otorohanga), and loss of these fisheries through the creation of weirs is a concern.

Non-salmonid exotic species

These species include perch, goldfish, rudd, tench, catfish, mosquitofish, koi carp and orfe. The other non-salmonid exotic fish present in New Zealand are either restricted to geothermal waters (for example, mollies and guppies), or do not breed naturally in the wild (grass carp and silver carp). There have been few published studies on these exotic fish populations in New Zealand lakes, so life history and habitat requirements are generally inferred from overseas studies. However, adaptation can be expected to have occurred to differences in climate, lake habitats and interactions with native fish in New Zealand lakes. In general, coarse fish prefer warmer waters than salmonids and therefore most are found in the North Island.

Perch

Perch populations are widespread throughout both the North and South Islands (McDowall 1990) and are one of the most studied of the non-salmonid exotic fish in New Zealand. They spawn during spring. Eggs are encased in a long, gelatinous sheath, which sinks and sticks to plants, sticks and logs. This sheath is believed to deter predators (Newsome and Tompkins 1985). Perch can grow to a large size (600 mm), but this is rare and the largest fish are generally 200–350 mm long (McDowall 1990). In Lake Pounui they were observed to mature first at a young age (mostly one year for males and two for females), and the largest fish were eight – 12 years old (Jellyman 1980).

In lakes they congregate in size-segregated schools, and juveniles feed mainly on plankton, shifting to invertebrates and fish as they grow larger. In Lake Okaihu small fish up to 200 mm long feed mostly on chironomid larvae, while the larger fish are piscivorous (Schipper 1980). However, in Lake Mahinerangi they feed on a wide range of invertebrates, and fish are not an important part of their diet (Duncan 1967). They are a prized eating fish in Europe, and in New Zealand there are recreational sport fisheries in a number of small lakes in the South Island, and around Auckland. Attempts to increase perch fishing in Lake Rotoroa near Hamilton in the 1980s were largely unsuccessful, indicating there is not a large demand for perch fisheries there.

Catfish

Brown bullhead catfish are widely distributed in the North Island, but in the South Island they have only been reported in Lake Mahinapua near Hokitika and the Kaituna Lagoon near Lake Ellesmere. Whether breeding populations now occur in these waters is unknown. Breeding occurs during summer in small, guarded depressions in shallow waters. Catfish commonly grow to 200–250 mm and are essentially a benthic species. However, recent observations in Lake Taupo indicate that as the population there has expanded they have increased foraging habitats to encompass the entire water column, from the surface to depths of 10 m (M. Dedual, personal communication). In Lake Taupo adults feed mainly on benthic invertebrates, with crayfish becoming an increasingly important prey as fish size increases (Barnes 1996). However, the diet of juveniles in lakes is still unknown.

The catfish is a prized species for eating in parts of the US, but attempts at establishing an export or local market in New Zealand have not been successful. It is not known what effects catfish have on other species, but reports from fishermen suggest there may be some interaction with eels (McDowall 1987) and possibly goldfish. Their future spread seems inevitable as they are an extremely hardy species, capable of surviving out of water for prolonged periods, and may be transported from lake to lake via eel nets and/or trailers.

Goldfish

Most North Island lakes contain feral populations of goldfish, but they have been reported from only a few South Island lakes (including Lakes Ellesmere and Brunner). Spawning requirements and times are likely to be similar to those for rudd and tench – see below). Goldfish are rarely abundant in New Zealand lakes, although thousands, ranging from 70–120 mm in length, occur in a warm, shallow, weedy arm of Lake Rotoehu near Rotorua (D. K. Rowe, unpublished data). There are no known studies of their feeding habits in New Zealand. Most of those examined have contained detritus in their gut, indicating that while mainly herbivorous, adults may also feed on detritus. Juveniles can be expected to be omnivorous.

Rudd

Rudd are a European species illegally introduced to New Zealand in 1967. They are now widespread, but most populations are in the top half of the North Island and there are few reports of their occurrence in the South Island. Their biology (in Europe) and likely impact in New Zealand waters was extensively reviewed by Cadwallader (1977). Knowledge of their biology in New Zealand lakes comes from a three-year study in Parkinson's Lake (near Pukekohe). It seems likely that most

fish spawn several times a year (in spring, summer and autumn), producing three distinct size groups in each year class. If so, this may account for the large population of rudd and the consequent stunting of their growth. Plants are the preferred spawning substrate, but it seems likely that rudd will deposit eggs on wood, shells and rocks when plant material is scarce. They continued to breed in Parkinson's Lake even after macrophytes were completely removed (Rowe and Champion 1994).

Most rudd mature first at age two to three (depending on sex) and sized about 100 mm. They can live for at least six years, by which time they are about 270 mm long. Rudd larvae occur in the littoral zone, hiding in the shallow fringing vegetation, but both juveniles and adults school in the littoral zone, with the larger fish occurring in deeper waters just outside the weed beds. In Parkinson's Lake juvenile rudd (15–90 mm long) were omnivorous, feeding mostly on planktonic crustacea and insect larvae, whereas adults (over 110 mm) were essentially herbivorous, feeding on filamentous algae and the macrophyte *Egeria* (D. K. Rowe, unpublished data). Later studies indicated that they prefer soft plants such as *Nitella* and *Elodea* to tougher species such as *Egeria* and hornwort (Lake et al. In press). The largest fish (over 200 mm) in Parkinson's Lake feed mainly on macrophytes, but common bullies occur in over 10% of these fish.

Rudd are easily seen in lakes because of their red coloration and schooling behaviour. This makes them vulnerable to shag predation (Rowe 1984b; Rowe and Champion 1994), and when cover provided by macrophytes is removed they quickly decline. They are not known to interfere directly with other fish, but do adversely affect trout fisheries because their populations increase quickly and the numerous small, stunted fish attack lures much more readily than do trout (Rowe and Champion 1994). They may also inhibit the re-growth of macrophytes in lakes where this has been reduced (Wells 1999).

Tench

Tench are a benthic species, rarely seen in lakes, and prefer shallow, warm, weedy ponds. Their spawning requirements are similar to those of goldfish and rudd in that they mainly spawn on vegetation. Feeding habits have not been reported in New Zealand, but they can be expected to feed mainly on benthic invertebrates. However, a number of large fish (20–30 cm long) from Parkinson's Lake were feeding solely on the zooplankton *Bosmina* (Rowe and Champion 1994). Tench do not appear to be common in lakes, although this may be due to their cryptic⁵ nature. A total fish census in Parkinson's Lake revealed that they were by far the most abundant fish present (Rowe and Champion 1994). Their effects on lake ecosystems and other species are unknown, but they are keenly sought after by coarse fish anglers.

Koi carp

Koi carp are an ornamental variety of common carp. They were thought to be confined to the North Island, but, like mosquitofish, some were recently found in ponds near Nelson and are being eradicated by the Department of Conservation. They are common in lakes in the lower Waikato River catchment, and also occur in a number of small lakes north of Auckland, which were illegally stocked. Spawning habits are not well known, but large aggregations occur at certain

⁵ Rarely seen because of a tendency to hide whenever the lake is disturbed.

locations prior to spawning in spring (for example, lagoons near the confluence of the Mangatawhiri and Waikato Rivers, and in Lake Waahi), and it is assumed that fish spawn on vegetation somewhere within these locations.

Hybridisation with goldfish has been recorded in New Zealand (Smith and Pullan 1987). Koi carp can grow to over 15 kg. They are essentially herbivorous, and prefer still, warm, weedy waters. They are prodigious spawners and very large populations can build up in optimal habitats. Because of their potential impact on water quality in lakes (see section 7), they are regarded as a pest species in New Zealand and are classified as noxious. They are also classified as an unwanted organism under the Biosecurity Act. However, they are sought after by some coarse fish anglers and by bow hunters because of their size.

Gambusia (mosquitofish)

Gambusia are a warm-water fish and are currently confined to the North Island, although a recent report indicates that they may now occur in Nelson. They were introduced to New Zealand to control mosquito larvae and are now found in many waters north of Taupo. They are live-bearers so there is no requirement for spawning habitat. Continuous spawning during summer produces very large populations in lakes, provided good habitat is present. They are most common during summer, when large aggregations occur in and among the rushes and shallow macrophytes of lake littoral zones. During winter they are thought to either decline or move into deeper waters, as they disappear from the shallow littoral zone.

Gambusia feed on a wide range of plankton and small invertebrates. An aggressive fish, they will attack larger fish, often immobilising them by damaging their tail, fins or eyes (Rowe 1998). Because of this they are now recognised as a potentially serious pest species and have been declared an unwanted organism under the Biosecurity Act. However, they may not be a problem in all lakes. Populations have existed in waters draining into several of the Rotorua lakes for many years. These gambusia have remained confined to weedy marginal waters or small inlet streams free of trout, and have not become established within the lakes, where they would be vulnerable to predation by trout. In Lake Waikare (Northland) removal of the stocked populations of rainbow trout was followed by a much larger increase in gambusia than that in an adjacent control lake (Rowe et al. 1999). Thus trout predation may exert some control over these fish.

Orfe

Orfe were illegally introduced into New Zealand and are confined to one lake near Auckland. They are similar to rudd, but nothing is known of their biology in New Zealand. McDowall (1990) reviewed their biology in European waters, which indicated that they feed mainly on invertebrates but can also feed on plants and fish, have a high fecundity, can tolerate slightly saline waters, and are relatively long-lived (up to 20 years).

Fish are highly mobile, and most species move between feeding and breeding grounds on a seasonal basis, and between feeding and resting areas on a daily basis. If such movements are restricted or changed, the spawning and growth of fish can be reduced. It is therefore important for lake managers and developers to know the type and timing of such movements so that disruptive activities in lakes or lake tributaries can be scheduled to minimise impacts, and so flow changes, barriers, or abstractions⁶ can be planned to avoid or minimise effects on fish.

Salmonids

Salmonids tend to migrate to inlet and (in some lakes) outlet streams to spawn. In lakes where suitable streams for spawning are in short supply, lake-shore spawning in shallow gravels can occur (Penlington 1983). Regional fish and game councils, DOC (for lakes Taupo and Otamangakau), and/or fisheries research providers (such as NIWA) will know which lake tributaries are utilised by salmonids for spawning. However, there are many lakes for which this knowledge is lacking, and the specific stream reaches used by salmonids are generally not well known and/or mapped.

The seasonal timing of salmonid spawning migrations varies between species, and can also vary between lakes for the same species, so spawning times for each species need to be determined for each lake. Once again, regional fish and game councils, DOC (for lakes Taupo and Otamangakau), and/or fisheries research providers (such as NIWA) can be approached for data on spawning times for trout for some of the major lakes and streams. However, data on the seasonal timing of salmonid migrations is generally sparse because of the time and expense involved in maintaining fish traps in streams.

Most brown trout spawn in winter and migrate into spawning tributaries as water temperatures decline (May to August). In contrast, most rainbow trout spawn in late winter and spring (July to October) as water temperatures are rising. In some lake inlet streams the spawning season is relatively short (four months), whereas in others it is much longer (eight months). In cold, spring-fed streams trout spawning migrations can occur throughout the year, although peak periods are much the same as in catchment-fed streams. Trout migrate into streams mainly – but not exclusively – at night. For example, runs during the night comprised 70% of the total in Lake Rotoaira (Rowe, Konui et al. 2000).

Light from the moon also influences migrations. Runs were generally lowest on bright, moonlit nights and greatest during dark moonless nights (Rowe, Konui et al. 2000). Lunar influences aside, day-to-day variation in trout numbers is related mainly to flows, with the largest runs occurring during periods of high flow.

Mortality for trout eggs increases as water temperatures exceed 11–12 °C (Rowe and Scott 1990), and increasing stream water temperatures during spring months probably govern the duration of the spawning season in each stream. Streams

⁶ Removals of water from the lake.

that are predominantly spring-fed have a low constant temperature (Mosely 1982), so spawning and egg incubation can occur year-round. In other streams, autumn and spring water temperatures may be too high for good egg survival, so the spawning season becomes restricted to winter. The presence of riparian cover reduces maximum water temperatures in salmonid streams (Barton and Taylor 1981), and a dense canopy of riparian bush may increase the amount of spawning habitat and the duration of the trout-spawning season, particularly in warm northern waters where spring water temperatures quickly approach lethal limits for egg survival.

Other important seasonal migrations, or movements, for salmonids include the downstream nocturnal emigration of many small (25–30 mm) fry that occurs soon after hatching. Those that remain in streams rear through to the parr stage (ranging in length from 40 to 120 mm). These fish eventually migrate into lakes, mainly during summer months, although some will remain in the streams and grow to adulthood (Graynoth 1999b).

Eels

Eels need to migrate to the sea to spawn, and during late summer/autumn many that are over about 40 cm long (size varies with species and location (Todd 1980)) move towards lake outlets prior to their downstream migration to the sea (Hobbs 1947). Males usually migrate before females and shortfins before longfins (McDowall 1990). Migrations mainly occur at night and their intensity is related to lunar phase as well as to the weather, with runs being greatest when there is little light and an increase in river flow. Little is known about how they navigate through lakes to find the outlets to the sea, but they are probably capable of sensing outlet flows and recent tagging studies suggest they are capable of exploratory behaviour around lake margins and at dam faces.

Juvenile elvers migrate into rivers from the sea during August–November (McDowall 1990), but the timing of entry into lakes or reservoirs further upstream may (not surprisingly) vary with distance from the sea. For example, in the Rangitaiki River, elvers arrived at Matahina (which is less than 30 km from the river mouth) between January and March; at Aniwhenua (a further 20 km upriver) they arrived between June and July.

Elvers are adept at climbing vertical rock faces and high falls, so they can penetrate far inland and colonise high-altitude lakes. However, their upstream migration can also be prevented, or reduced, by falls or rapids that are too fast for swimming and do not provide a wet surface for climbing. Adult eels also undertake limited overland migrations between water bodies, mainly on wet nights. They can therefore colonise some lakes and ponds with no surface flow to the sea, but these are generally close to the streams from which the eels come. Little is known about the ability of eels to move overland and therefore which lakes and ponds are susceptible to migrations, or what factors may influence this.

Galaxiids

Riverine koaro and banded kokopu spawn in streams (McDowall 1990), while lacustrine stocks are thought to spawn mainly, if not exclusively, in the inlet streams of lakes (see section 2). This suggests that lake residents must migrate to and from the inlet streams to spawn. However, some koaro and banded kokopu

populations occur in small lakes with no permanent inflows (for example, koaro in Lake Marymere in the Waimakariri Basin). The adults in these lakes may spawn in the lake itself (Stokell 1955), but there is no evidence for this, and spawning could occur in temporary streams during floods. One spawning of banded kokopu in an inlet stream of a small lake was related to a flood event (Mitchell and Penlington 1982). It seems likely that during heavy rain the adults moved from the lake to a suitable spawning site in the stream, where they spawned on the flooded margins while the high flows were maintained. When the water level in the stream dropped, the eggs would have been left exposed (albeit in a moist environment) until the next flood. Egg hatching would then occur, with the larvae being washed downstream to the lake.

Return migrations of many juvenile (whitebait-stage) koaro occurs into the inlet streams of Lake Taupo, mainly in November and December (Kusabs 1989). However, some juveniles remain in lakes, or return to them, where they grow to adulthood. In Lake Rotoaira there were large migrations of adult koaro from the lake into underground springs and back again over summer (November–February), and this coincided with spawning (Rowe, Konui et al. 2000). Such migrations are therefore thought to be for spawning, with most lacustrine fish spawning in the lake tributaries.

Other movements by galaxiids in lakes are not so much migrations as life-history changes cued by changes in development or fish size. For example, koaro move from the pelagic to the benthic zone (littoral as well as demersal) when they become adults (Rowe, Konui et al. 2002). Similarly, dwarf inanga juveniles occupy the pelagic zone, but at about 40 mm long they move to the littoral zone to feed (Rowe and Chisnall 1996a). At about 50 mm long they move to the deeper hypolimnetic waters near the middle of lakes by day (probably to avoid predation by shags), returning to the littoral zone to feed at night (Rowe and Chisnall 1996a).

Smelt

Migrations and movements by smelt in lakes are complex. In some lakes and reservoirs smelt move to and aggregate around spawning sites on beaches during spring and summer. They also spawn in the inlet streams and rivers of lakes, and migrate into these during the spawning season. Sub-adult fish aggregate in many streams during summer, perhaps attracted by the generally warmer waters and lack of predators. During winter all smelt (spawners as well as sub-adults) move back into the lake. Mass one-way movements between lakes also occur, notably the movement of smelt schools through the Ohau Channel, between lakes Rotorua and Rotoiti in the North Island, and presumably a passive movement of larvae and juveniles from Lake Taupo down the Waikato River and into and between each of the hydroelectric reservoirs.

Other movements by smelt are principally to gain access to either food or warm water for growth. For example, adult smelt undertake vertical movements of 30–40 m towards the lake surface at night and move back to these depths at dawn (Rowe 1994; Rowe and Chisnall 1996b).

Bullies

Common bullies, particularly the larger fish, move inshore to the shallow littoral zone of lakes at night (Forsyth and James 1988; Rowe 1993a), presumably for foraging. Similarly, larval bullies undertake 5–20 m vertical movements towards the lake surface at night and return to these depths at dawn (Rowe 1994; Rowe and Chisnall 1996b). This, too, may be a feeding migration, but it may also expose larvae to the warm surface waters of lakes at times when predation is reduced and so enhance growth (Rowe 1999a). A major seasonal shift in bully distribution within lakes occurs mainly in spring, when many larval bullies move out of the limnetic zone and settle on the lake bottom (Rowe 1994). Most congregate in the littoral zone, suggesting a movement from the demersal to the littoral, although demersal bullies occur at depths of at least 80 m, indicating that some remain in deep water (Rowe, Nichols et al. 2001).

Mullet and flounder

Grey mullet juveniles migrate into lakes in summer (Taylor and Graynoth 1996). In some lakes diadromous populations of black flounder may also occur, implying a migration of juveniles into these lakes at certain times of the year. The seasonal timing of these species movements has not been well recorded and will no doubt depend on the distance of each lake from the sea. For example, migrations to inland lakes can be expected to take longer than to coastal ones so the arrival of juveniles to the lake will be later.

Non-salmonid exotic fish

Coarse fish are not generally known to migrate to spawning grounds or feeding areas in lakes. However, koi carp, perch and other species can be expected to move to and aggregate at favoured sites for spawning during spring. For example, large populations of koi carp regularly build up in late spring and summer in the lower reaches of the Mangatawhiri River (a tributary of the Waikato River), where there is a large lagoon, which presumably provides optimal conditions for spawning. Similarly, other coarse fish species can be expected to move to shallow, densely vegetated areas of lakes to spawn during summer.

Main fish migrations and movements in lakes

SPECIES	FROM	TO	SEASON	PEAK TIME
TO SPAWNING HABITATS				
Rainbow trout	lake	streams	winter/spring	July - October
Brown trout	lake	streams	winter	May - August
Koaro	lake	streams	summer	November - March
Eels	lake	sea	summer/autumn	December - April
Smelt	lake	streams and beaches	spring/summer	October - March
Mullet	lake	sea		
TO FEEDING HABITATS				
Juvenile trout	stream	lake	summer	December - March
Juvenile koaro	lake	streams	spring/summer	November - December
Juvenile eels	sea	lake	summer/autumn	January - April
Juvenile mullet	sea	lakes		
Juvenile bullies	pelagic	benthic	summer	December - March

PART II: Factors affecting lake fish

Feeding, food webs and trophic interactions

Analysing the food webs and food chains of a lake allows us to identify the productive bases underpinning its fisheries, as well as the main prey and predator species whose habitats may be affected by changes to the lake. Such analysis is also useful for assessing the relative importance of littoral versus pelagic zones, and also the potential for biomagnification of pesticides or heavy metals in fish flesh (and hence the health risks to the public). More recently, trophic interactions have been intensively studied because of the realisation that 'top-down' effects by fish predators on planktivorous fish can influence the water quality of some lakes. In future, knowledge of trophic interactions may well lead to methods for controlling pest fish species.

A food chain is essentially a single predator/prey pathway leading from the source of primary production to a top predator (for example, phytoplankton → zooplankton → planktivorous fish → carnivorous fish). A food web comprises all the main food chains (of which there may be several) leading to the top predator. For example, in Lake Taupo the food web leading to rainbow trout is relatively simple. Phytoplankton (species unknown) are the main prey for zooplankton, principally *Bosmina*, in this food web. This is the main food for smelt, which are in turn the main prey for trout, constituting more than 80% of the food for most trout throughout the year (Stephens 1984; Cryer 1991). The largest trout (over 50 cm) also feed on crayfish and bullies, but this is not common. The Lake Taupo food web is therefore based mainly on a single food chain (phytoplankton → *Bosmina* → smelt → rainbow trout). As a result, changes in the annual and seasonal abundance of any one 'link' in this chain could have major effects on trout production. In contrast, the food web in other lakes, such as Rotoaira, is much more complex, comprising a number of chains (see Figure 2). Such complex food webs are probably more resilient to environmental changes.

Seasonal changes in prey species also need to be considered. In Lake Rotoaira trout feed mainly on snails throughout the year. However, insect larvae and goldfish are major prey during summer, switching to *Daphnia* and koaro during winter. Thus, summer production is based mainly on the littoral food chain, whereas winter production depends more on the limnetic chain (Rowe, Cudby et al. 2000).

In a typical limnetic food chain (as outlined above) there are usually four main trophic levels, although some food chains may have only three, and others five. The number of levels can determine the extent of heavy metal or pesticide biomagnification by top predators, as concentrations often increase or 'magnify' at each level (Rasmussen et al. 1990). Thus, a top predator in a four-level food chain will generally contain higher concentrations of heavy metals or pesticides than one in a three-level chain. Food webs can therefore potentially be used to model the accumulation of metals or pesticides in aquatic ecosystems.

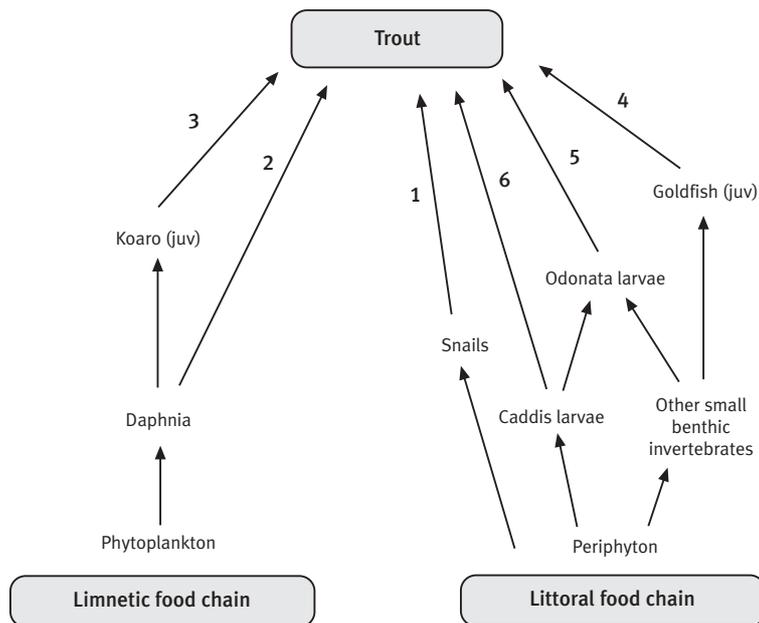


Figure 2: Food web for trout in Lake Rotoaira in 1974

Note: numbers beside arrows indicate the relative importance of prey groups to trout.

Where food chains are essentially structural (do not indicate the magnitude of energy or carbon flow between a predator and its prey, as in Figure 2), they are limited to defining the main production pathways important for fish species. However, interaction webs (which do indicate the magnitude of interaction) can be used to determine changes in predator-prey relationships and therefore before-and-after effects of lake changes on fish populations. They can indicate the effect of changes in the abundance of one or more prey species in the food web on top predators, so can be used to model the potential impacts of species interactions.

For example, food web analysis has been recently combined with elements of the Wisconsin bioenergetics model (see section 9) to model food web interactions in a lake. This enables prediction of the effects of stocking activities on predator-prey interactions, and hence the abundance of target fish species (Beauchamp et al. 1995). It is likely that these approaches to fishery management in lakes will become more popular, although such modelling must be underpinned by good biological data and experience of fish predator-prey interactions – which are often lacking. The use of isotopic analyses (see section 9) to identify predator-prey interactions is increasing and can provide useful insights into food web structure, but it is no substitute for good diet studies based on the inspection of the gut contents of large numbers of fish.

There are numerous contaminants known to affect fish, but the main ones in New Zealand lakes are likely to be:

- mercury and arsenic (from geothermal sources)
- contaminants in the wastes from galvanising and wood-treatment plants, which enter lakes via tributary streams
- agricultural chemicals
- suspended solids.

Specific data on the toxic and sub-lethal levels of such contaminants and their effects on fish behaviour are included in many studies and books. This section is therefore designed to provide an introduction to the contaminants most relevant to New Zealand lakes, and to illustrate some of the main biological processes by which certain types of contaminant can cause problems that lake managers need to consider.⁷

Mercury and arsenic from geothermal sources

Mercury from geothermal sources is the main heavy metal contaminant of fish in New Zealand lakes. Large rainbow trout in a number of the central North Island lakes (Weissberg and Zobel 1973; Brooks et al. 1976; Kim 1995; Robinson et al. 1995), and in reservoirs immediately below the Wairakei geothermal field south of Taupo (Mills 1995) can contain relatively high levels. Mercury is bioaccumulated up the food chain, and concentrations in some large trout from North Island lakes (for example, Rotorua, Rotoiti, Rotomahana, Ohakuri and Maraetai) have been found to exceed the food standard of 0.5 mg/kg. Large trout in some of the Rotorua and Waikato hydro lakes contain mercury levels high enough to be of concern if people consumed them on a regular basis. Other lakes likely to be affected include those with geothermal inputs (either surface or sub-surface).

Other fish species may also be affected. Eels in the Waitangi River below the Ngawha springs were found to contain mercury due to contamination of riverine food webs below the springs (Chisnall and Rowe 1997). Some of these eels had apparently moved to adjacent uncontaminated tributaries, and others will have moved upstream into Lake Ngatu. Thus heavy metal contamination can be spread by migratory fish.

Arsenic can also be associated with geothermal waters and is present in some fish. Where the main geothermal discharge is steam, mercury contamination can be expected. If the discharge is in the water phase, arsenic is likely to be present (M Timperley, personal communication). Arsenic levels in trout from the Waikato hydro lakes were elevated (Aggett and Aspell 1980; Robinson et al. 1995), but not high enough to be of concern. However, arsenic levels in macrophytic plants are high enough to be toxic to cattle (Lancaster et al. 1971) and are likely to be high in herbivorous fish such as goldfish and rudd, or detritivores such as catfish.

⁷ Nutrients are not considered contaminants in this context as they affect lake trophic status and water quality and don't affect fish directly.

Agricultural, industrial and metropolitan wastes

In the past many wastes from galvanising and wood-treatment plants were dumped in landfills within lake catchments. These wastes contained toxic chemicals and heavy metals, and ground-water leakage from older sites can be expected eventually to transport the toxic substances into lakes. For example, polychlorinated biphenyls (PCBs) have been found in Lake Rotorua (Gifford et al. 1993). In addition, residues of pesticides used in agriculture and horticulture, and lead contamination from road runoff and paint leaching, can all be expected to enter lakes and find their way into aquatic food chains.

Many New Zealand lakes close to urban centres historically received raw or partially treated sewage, which contained wastes including heavy metals and chemical residues, some of which may now be in the lake sediments. The role of lake bed sediments in sealing and treating such wastes and preventing their incorporation into the food chain is unknown. However, the potential danger of these toxic substances in lakes remains, and disturbance of lake beds, or hypolimnetic deoxygenation, could re-introduce some of them into lake food webs.

The main concern with such toxic metals and chemicals is their potential for bioaccumulation into, and biomagnification up, the food chain into top predators such as fish, birdlife and humans. This has been well documented for organochlorines such as DDT, which can reduce populations of avian predators that prey on fish. Biomagnification of PCBs was related to the length of the food chain in many Ontario salmonid lakes (Rasmussen et al. 1990), but not in Swedish lakes (Berglund et al. 2000). The extent of biomagnification up food chains can therefore be expected to vary between lakes, and this probably depends on the structure of the food web and the concentrations in the various prey species. For example, toxaphene levels were not biomagnified up the food chain to lake trout in a North American lake because they are concentrated in lipids (Campbell et al. 2000). They were highest in copepods (because of their high lipid content) and therefore only higher in lake trout that had been feeding in the pelagic zone (where copepods are abundant) rather than the littoral zone. The fate and levels of toxic substances in fish can therefore depend on a number of factors other than food chain length.

Apart from the issues of bioaccumulation and biomagnification, some fish species are extremely sensitive to small concentrations of heavy metals such as zinc, manganese and cadmium, and to certain pesticides. They may be affected by small quantities of these and other toxic chemicals present in discharges. Identification of toxic levels and dilution ratios for fish is often problematic because lethal levels for New Zealand species have not been measured. However, a number of sensitive fish species (such as rainbow trout) have been tested, and provide some guide to the levels that may affect New Zealand fish. These are described by Alabaster and Lloyd (1984), and the water quality standards promulgated for European freshwater fish (EIFAC 1987). Useful summaries of water-quality standards for many metals and organic substances can be found in the Canadian water-quality guidelines (CCREM 1987, and updates), and the United States Environmental Protection Agency criteria (US EPA 1977). A review of the latter was carried out by the American Fisheries Society, with comments made on many of the limitations of these criteria when applied to fish (Thurston et al. 1979).

Useful information on many pesticides, herbicides, agricultural chemicals and veterinary products, including details of toxicological studies on fish, is provided at the following internet web sites:

www.state.nj.us/health/eoh/rtkweb/rtkhsfs.html

ace.orst.edu/info/extoxnet/pips/ghindex.html.

www.epa.gov/ecotox

Suspended solids

Suspended solids and water turbidity have profound influences on lake ecosystems in New Zealand. A number of South and North Island lakes have experienced increases in suspended solids due to diversion of waters into the lakes for hydro-power (for example, Coleridge, Ruataniwha and Rotoaira). Suspended solids have increased in other lakes because of discharges of coal fines (for example, Lake Waihi). However, in many lakes the suspended solids load will have increased through changes in land use (for example, logging, or conversion of forest to pasture).

The very high levels of suspended solids needed to kill fish (over 1000 mg/l) rarely occur in lakes. Increased pollution by suspended solids is generally non-lethal and involves either increases in turbidity or changes to lake substrates from the settling of fines. Effects of turbidity on lake-water transparency and fish are dealt with in section 6. The direct effects of turbidity on fish in lakes are mainly limited to species that are highly dependent on visual feeding, such as trout and smelt, and changes in prey species (and hence in distribution) may occur for such species. However, the settlement of solids on plants and the lake bottom can be expected to produce indirect effects on fish populations through changes in the macroinvertebrate food supply and in benthic habitats for fish. Both smelt and common bully populations are lower in lakes that have high levels of siltation (D. K. Rowe, unpublished data), although the mechanisms for this (increased egg mortality from smothering or reduced prey species) are unknown. As these fish are major prey species for trout, trout production may also be reduced in silted lakes.

Water-quality limits for native fish and trout

This section covers the water-quality requirements of native fish and salmonids, because these species generally prefer higher water quality than the non-salmonid exotic fish and lake managers are generally more concerned with ensuring the populations of the more sensitive native and salmonid species are maintained. We also cover eutrophication here, because the main effects of eutrophication on fish are related to changes in water quality – particularly oxygen levels – and increases in turbidity from silt.

In 1991 the need to determine the water-quality preferences and tolerances of New Zealand native fish was raised because they were thought to play a major role in determining the habitat, and hence the distribution, of native fish (Rowe 1991). In particular, water-quality variables that vary with depth (such as temperature, oxygen and light) can influence the habitable depth range for lacustrine fish. They therefore have a major influence on fish depth distributions in lakes (Rowe 1994; Rowe and Chisnall 1995), and determine the total volume of 'habitable' water in lakes. This measure provides a much better way of assessing differences in abundance, or lake-carrying capacity, than total lake area. However, before such measures of total fish habitat in lakes can be developed and refined, the preferred and limiting water-quality variables need to be identified through laboratory experiment and their effects on fish distributions in lakes determined.

The temperature tolerances and preferences, pH preferences, and lethal ammonia and oxygen limits for common native fish have been determined in laboratory experiments (Richardson et al. 1994; Richardson 1997; West et al. 1997; Dean and Richardson 1999). The effects of increased turbidity on common native fish have been determined in both the laboratory and in the wild (Boubée et al. 1997; Rowe and Dean 1998; Rowe, Hicks et al. 2000; Richardson et al. 2001). Field data on the responses of rainbow trout and common bullies in lakes to temperature, oxygen, water transparency and turbidity have been recently recorded in New Zealand waters (Rowe and Boubée 1994; Rowe and Chisnall 1995; Rowe 1999a), and complement the extensive literature on laboratory studies. This data provides a much more comprehensive basis for assessing the optimal water-quality requirements for individual fish species in lakes, and therefore for determining the potential effects of changes in these variables on fish communities.

Water temperature

Preferred temperatures for native fish species were determined by Richardson et al. (1994) and were linearly related to lethal temperatures. The preferred temperatures ranged from 16 to 27°C, depending on the species. This variation reflects differences between genera rather than between species. For example, the *Galaxiidae* and *Retropinnidae* (smelts) are cool-water genera, and prefer lower temperatures than the *Gobiidae* (bullies), which prefer cooler waters than the *Anguillidae* (eel species). Within genera, differences between species were related to known habitat associations. For example, adult inanga are usually found in warmer waters than banded kokopu. Similarly, shortfin eels dominate in lowland coastal lakes whereas longfin eels dominate in the generally colder waters of higher-altitude inland lakes.

The effects of changes in water temperature on native fish distributions in lakes have not been determined. However, the depth distributions of bully larvae and smelt are tightly stratified (Rowe 1993b; 1994), and these fish no doubt select their preferred depth by using depth gradients in physical variables such as pressure, temperature, light and oxygen. If temperature is an important cue for depth selection, then changes in the temperature profile of lakes will alter the depth distributions of the native fish, and this could affect their exposure to prey species.

The temperature preferences and tolerances of 'juvenile' salmonids have been well studied (mainly in laboratory tanks) over the past three decades, but only recently have useful field data on adults become available. Field studies, plus reviews of the available information for trout, indicate that preferred temperatures can be increased by acclimation and exposure to temperatures up to about 25°C. Mortality occurs for both species when temperatures exceed 25–26°C for more than about seven days. However, this may depend on oxygen levels. Warmer waters contain lower oxygen levels at saturation, and any decrease in oxygen below the saturation level could compound the effects of warm water. Juvenile rainbow trout prefer warmer waters (17–19°C) than adults (12–13°C) (Rowe and Boubée 1994; Rowe and Chisnall 1995), and adults in the wild tend to avoid waters much over 17°C. When temperatures reach this level, trout tend to move to colder waters, and they are rarely found where temperatures exceed 19°C (brown trout) and 21°C (rainbows) (Rowe and Boubée 1994; Rowe and Chisnall 1995).

Acoustic studies of depth distributions in Lake Taupo and the Rotorua lakes have revealed that rainbow trout do not occupy the full water column in these deep lakes, and that their depth distribution changes with the seasons. Most trout are distributed in accordance with their water temperature preferences (Cryer 1991; Rowe and Chisnall 1995), which can increase during summer. However, trout will move into waters outside their preferred range to feed. In the Rotorua lakes trout tended to remain in the depth strata where water temperatures were optimal for growth, but some were present in shallower waters, where smelt occurred, indicating they make forays into warmer surface waters to feed. This no doubt leads to acclimation to warmer temperatures and results in a shallower depth distribution.

In summer, when water temperatures in some northern lakes become too hot for trout (over 21°C), they can move into deeper, colder waters. This is not possible in shallow lakes, where they tend to congregate around cold-water stream mouths. For example, when water temperatures exceed 20–21°C for periods of more than several days, large numbers of trout accumulate in the mouths of the spring-fed streams in Lake Rotorua, or around certain inlet streams that drain into the Waikato hydro lakes. In shallow lakes where there are no such cold-water refuges, trout feeding declines and their growth rate is reduced (Rowe 1984b).

Where changed inflows or outflows influence the temperature profile in lakes, the depth range for optimal thermal habitat for trout can be measured to see whether it is constricted over summer months. Similarly, the number of daylight hours during the season when water temperatures are suitable for trout growth has been calculated and used as a measure of the duration of the annual growing season. This can then be compared with pre-impact records to predict the effects of water temperature changes on the duration of the growing season for trout. Growth

models incorporating temperature and day length as the main factors have been used to assess effects of temperature changes on brown trout growth in rivers (J. Hayes, personal communication), and could be adapted to lakes.

Oxygen

In laboratory tanks most native fish can withstand oxygen concentrations as low as 1 mg/l for short periods (Dean and Richardson 1999). However, the time for death to occur at this level is likely to vary greatly between species. Smelt and juvenile common bullies can only tolerate such conditions for minutes, whereas banded kokopu can cope for six to seven hours, and inanga and adult bullies tolerated these conditions for over 40 hours (Dean and Richardson 1999). These data indicate that smelt and juvenile bullies are likely to be the native fish most sensitive to low oxygen levels in lakes.

There are few useful field data on the effect of oxygen levels on native fish in lakes. However, acoustic studies on fish distributions suggest that larval bullies may be more sensitive than either juvenile or adult smelt (Rowe 1994), and that smelt and rainbow trout avoid levels below 2.5–3 mg/l (Rowe 1994; Rowe and Chisnall 1995). Juvenile bullies are more sensitive than adults (Dean and Richardson 1999), suggesting a size relationship and supporting the possibility that larvae will be more sensitive than juveniles. If larval bullies prove to be the most sensitive, they may be affected by oxygen levels of only 3–4 mg/l.

Water transparency, light levels and turbidity

Vision is important to fish for navigation, feeding and predator avoidance, so reductions in water transparency or light levels caused by increases in turbidity can be expected to have a pervasive influence on their behaviour and distribution. Increased turbidity may be beneficial to some species (for example, by reducing predation risk), while reducing the foraging efficiency of species that are visual feeders.

Common bullies appear to be relatively insensitive to increases in turbidity and the accompanying reductions in water transparency and light penetration. Feeding rates were unaffected by turbidities up to 160 nephelometric turbidity units (NTUs) for juveniles (Rowe and Dean 1998) and 320 NTUs for adults (Rowe 1999a). In North Island lakes the abundance of both adults and larvae increased as turbidity-induced decline in water clarity occurred (Rowe 1999a).

Similar changes can be expected in South Island lakes. For example, bullies are highly abundant in the relatively turbid waters of Lake Ellesmere. There is no difference in the depth distributions of adults in the littoral zones of turbid and clear lakes, indicating that turbidity and water clarity have little effect on their depth selection (Rowe, Nichols et al. 2001). However, the depth distributions of pelagic larval bullies are shallower in turbid lakes than in clear ones (Rowe 1996). As larvae can feed in low light conditions (Rowe and Chisnall 1996b), such changes in distribution are unlikely to affect either growth or abundance. These results imply that increases in turbidity level, or reductions in light levels or visual clarity, result in a shallower distribution of larval bullies but do not reduce their abundance. If reduced water transparency reduces predation on bullies, it may in fact increase their abundance. However, evidence is now mounting that the abundance of adult bullies is reduced in lakes where suspended solids settle and

smother the benthos (D. K. Rowe, unpublished data), so increased turbidity may affect adult bullies by reducing their food supply and habitat.

Koaro also appear to be relatively insensitive to turbidity. Feeding rates for juveniles were not reduced by turbidities up to 320 NTU (Rowe and Dean 1998) and adult abundance was relatively high in turbid lakes such as Pukaki and Tekapo, indicating they can also tolerate relatively turbid waters. Koaro may be better off in turbid lakes because trout predation is reduced.

In comparison, smelt appear to be more sensitive to increases in turbidity and/or a decline in water transparency. Densities of larval smelt were inversely related to water transparency in 11 Rotorua lakes, and depth distributions of juveniles were both shallower and more restricted in turbid lakes than in clear ones (Rowe 1996). The decline of a lacustrine smelt population in Lake Waahi was attributed to increased turbidity (Hayes et al. 1992), although a number of concurrent changes in this lake's environment may have contributed to the demise of the smelt.

Smelt are primarily visual feeders, so their feeding could be more affected than that of bullies and koaro, whose adults are benthic feeders. Mean feeding rates of juvenile smelt (on *Daphnia*) were not greatly affected by turbidities of up to 620 NTU (Rowe and Dean 1998) and adults were not affected by turbidities up to 320 NTU, both of which far exceed levels likely to occur in lakes. As with common bullies, smelt may be more affected by the effects of settled solids on sediments than by turbidity from suspended solids. The mortality of smelt eggs can be increased by siltation (Stephens 1984), and larval smelt numbers in 11 lakes were inversely related to secchi disc depth and hence organic turbidity (Rowe and Taumopeau, submitted), suggesting that recruitment is reduced in turbid lakes.

Rainbow trout are primarily visual feeders and sustained reductions in water transparency can be expected to affect their populations. Laboratory studies have indicated that their capability to see prey is reduced by turbidities as low as 15 NTU (Barrett et al. 1992), but feeding rates on planktonic prey in tanks were only reduced at turbidities over 25 NTU (Vinyard and Yuan 1996). Field studies in a South African lake have indicated that rainbow trout avoid turbidities much over 28 NTU (Dorgeloh 1995), presumably because this restricts feeding. Where avoidance is not possible (the turbidity is pervasive), rainbow trout can resort to benthic feeding, which is not as dependent on vision. For example, trout fed on chironomid and *Deleatidium* larvae at turbidities of up to 320 NTU, but their ability to select the largest individuals is reduced at this level (Rowe 1996).

Pervasive turbidity can therefore be expected to change the feeding behaviour and depth distribution of trout. For example, in North Island lakes where secchi disc depths were greater than 3 m, trout fed mainly on smelt and rarely on bullies, but this pattern was reversed in turbid lakes where secchi disc depths were less than 2.5 m (Rowe 1984a). Such changes in prey imply a shift from pelagic feeding in the open water of clear lakes to benthic feeding in the littoral zone of turbid lakes. These changes may be related – at least in part – to differences in prey densities between turbid and clear lakes, but similar turbidity-induced shifts in prey type and feeding grounds have been recorded for rainbow trout in rivers (Tippets and Moyle 1978), and for other fish species in estuaries (Hecht and van der Lingen 1992).

Such changes in feeding behaviour indicate that where prey are mostly benthic (as in many South Island lakes), an increase in turbidity may not greatly affect trout feeding and growth. This is supported by observations in turbid lakes such as Ruataniwha and Tekapo in the South Island, where the rainbow trout were in good condition, indicating that obtaining food was not a problem. In comparison, brown trout – which are more piscivorous than rainbow trout, and hence may rely more on visual feeding – were in a poorer condition (James et al. 2002). Effects of turbidity and reduced water transparency on trout will therefore depend on the prey species present as well as on the structure of the food web (see section 4).

Although turbidity may be of minor concern to most fish in lakes, and have little affect on feeding and growth, the effects of settled solids on the lake bed and benthos (the flora and fauna of the lake bed) is another matter. Populations of common bullies and smelt appear to be lower in lakes where settled solids affect the benthos. Turbidity may therefore affect these fish more through its effects on lake sediments and fish food supplies than through effects on their feeding ability due to reductions in water clarity and light levels. This aspect of turbidity clearly requires more study.

Alkalinity, conductivity and pH

A number of overseas studies have indicated that measures of dissolved solids are correlated with fish production in lakes (Ryder et al. 1974; Oglesby 1977), and Hubert and Chamberlain (1996) found that trout abundance and size were correlated with total dissolved solids, pH and alkalinity. It appears likely that the chemical content of water can influence the structure of planktonic food webs in lakes and therefore has a pervasive, if indirect, effect on fish production.

Rowe and Chisnall (1997b) found that dwarf inanga were more abundant in lakes with high alkalinities, but abundance was also associated with higher levels of silica, calcium and magnesium and low levels of chloride. Dwarf inanga were more abundant in slightly basic lakes (pH 7.5–7.7) than in acidic ones (pH 6.6–6.8), although this may be coincidental.

High levels of chloride ions (from sea spray) characterise a number of west coast dune lakes and no doubt interact with land use and geology to influence lake water chemistry. Similarly, land-use changes and geothermal springs can influence the water chemistry of lakes (McColl 1972) and therefore influence planktonic food webs.

Many lakes in Europe have been degraded over the past two decades by acid rain. This is not an issue in New Zealand lakes, although some are naturally acidic because they lie within peaty soils or are fed by streams that run through peat swamps. Native fish may be sensitive to pH as they can be categorised according to the pH of waters where they commonly occur (Rowe 1991). Some species appear to be acidophils (preferring acid conditions of pH 6–7), whereas others are basophils (preferring alkaline conditions of pH 8–9). The remaining species are neutrophilic, preferring neutral waters with a pH close to 7. Ph preferences were determined for nine native fish species by West et al. (1997), who confirmed that banded kokopu are acidophilic and that most other species (longfin eels, inanga, common bully, smelt, redfin bullies) are basophilic, preferring waters with a pH of 8–9. Most species avoided pH levels under 6 and over 9.5. These levels are rarely

encountered in lakes, so pH is unlikely to greatly influence fish habitat, although such preferences are believed to influence stream selection by juvenile whitebait such as inanga, koaro and banded kokopu (McDowall and Eldon 1980). These responses could influence access to lake inlet streams.

Eutrophication and habitat squeeze

A number of overseas studies in the 1960s and 1970s on the effects of eutrophication on fish indicated that it tends to be detrimental for some (for example, salmonids) and beneficial to others (such as cyprinids). Reasons for this are now becoming apparent. One of the main effects of eutrophication in lakes is hypolimnetic⁸ deoxygenation. Trout avoid oxygen levels below 2.5–3.0 mg/l, and during summer/autumn, when lakes stratify, the oxygen content of the hypolimnion may drop below this level, which restricts trout to waters above the hypolimnion. However, high summer water temperatures (over 21°C) in the epilimnion⁹ may simultaneously restrict trout access to surface waters. The result is a reduction in trout habitat through their depth distribution being compressed from above and below.

Such habitat 'squeeze' due to eutrophication has also been recorded for striped bass and northern pike in North American lakes (Coutant 1985; Headrick and Carline 1993), and for rainbow trout in several North Island lakes (Rowe 1984b; Rowe and Chisnall 1995). This reduction in habitat was sufficient to reduce feeding and growth rates of trout in Parkinson's Lake over summer (Rowe 1984b). A similar effect would have restricted the development of trout fisheries in the Waitakere versus the Hunua water supply reservoirs near Auckland (Rowe 1989a).

Hypolimnetic deoxygenation can also be expected to influence some native fish species. It prevented the autumnal descent of post-larval planktonic bullies in Lake Rotoiti (Rowe 1994), so it may have reduced juvenile settlement in the demersal zone. Adult common bullies and koaro are benthic, and in oligotrophic lakes occur on the lake bottom down to at least 70 m. Complete deoxygenation occurs each year in mesotrophic Lake Rotoiti at all depths below about 30 m (max depth 93 m) and therefore restricts the distribution of both these species to waters above 30 m (Rowe 1994). In eutrophic lakes such as Okaro and Ngapouri (Rotorua district), hypolimnetic deoxygenation restricts the depth distribution of smelt from maximum depths of 15 and 25 m respectively to less than 5 m during summer (Rowe 1996). The effects of this more than 70% reduction in habitat on fish density and growth are not yet known, but are unlikely to be beneficial. Although some of the smaller South Island lakes – such as Lake Hayes and Johnson near Queenstown, and Lake Alexandrina – are eutrophic, most large South Island alpine lakes are oligotrophic, with very deep thermoclines. These deep lakes generally have oxygenated hypolimnions and support fish at all depths.

Eutrophication also increases algal biomass in lakes, which increases the level of suspended solids and hence turbidity. Reductions in water transparency and/or light from the increased turbidity can reduce the depth distributions of pelagic species and change feeding patterns for species or life-history stages that rely on

⁸ The hypolimnion is the lower layer of water in stratified lakes, below the thermocline.

⁹ The epilimnion is the upper layer of water in a stratified lake.

the visual senses for locating prey. As we have seen (above), the depth distributions of larval bullies and smelt were shallower in turbid, eutrophic lakes than in clear oligotrophic ones (Rowe, D. K., unpublished data), and the abundance of common bullies was increased in turbid, eutrophic lakes (Rowe 1999a), whereas the density of smelt larvae was reduced (Rowe 1996). Such changes were related more to the effects of settled solids (silt) on fish habitat and food supply than turbidity *per se*.

However, turbidity may also affect water quality in lakes. Increases in turbidity in surface waters can alter the thermal structure of lakes by increasing surface water temperatures, and hence the depth of the epi- and hypolimnion (Mazumder and Taylor 1994). Therefore increased turbidity from eutrophication can be expected to increase the size of the hypolimnion in some lakes, pushing it closer to the lake surface and further restricting the volume of habitable water for fish.

Eutrophication, therefore, has profound effects on the volume of fish habitat in lakes, and hence on fish-depth distributions. Overall, these effects tend to favour shallow-living fish species that prefer warm, turbid waters and reduce habitat for deeper-dwelling fish that prefer colder waters. These restrictions on habitat may reduce foraging and affect growth and abundance, depending on the species present and the depth of the lake. Such effects are independent of those that occur in the invertebrate populations, which may affect fish production.

Water quality: key points

Oxygen	<ul style="list-style-type: none"> • trout and smelt avoid levels < 3.0 mg/l • larval bullies may be more sensitive than other species
Temperature	<ul style="list-style-type: none"> • trout and koaro are coldwater species and avoid temperatures over about 20 °C • shortfin eels and coarse fish are warmwater species and cope with temperatures up to 30 °C • temperature influences fish habitat in lakes
Turbidity	<ul style="list-style-type: none"> • trout, bullies smelt, inanga, koaro can all feed at turbidities up to 160 NTU • increased turbidity reduces limnetic feeding and increases benthic feeding • reductions in light may affect fish depth distributions in lakes
pH	<ul style="list-style-type: none"> • acidophilic species prefer waters with pH 6-7 • basidophilic species prefer waters with pH 8-9 • neutrophilic species prefer waters with pH 7 • all species tolerate a wide range pH 6-10

One of the growing issues facing lake and fishery managers is the introduction of new, usually exotic, fish species into lakes and reservoirs. Trout stocking has long been practised in many lakes and reservoirs by fish and game councils, and in many lakes (such as the Rotorua and more northern lakes) it is an essential part of fishery management. However, in some stocked lakes trout may be preying on native fish species. Coarse fisheries are becoming more popular in some parts of New Zealand and are leading to requests to introduce new species such as perch and tench, but the potential effects of such introductions on other fish or lake environments are largely unknown. Grass carp are also being increasingly requested for weed control in small ponds and lakes.

Apart from such formal introductions, there are also concerns over what can be done about the accidental and illegal ones. Koi carp, which are designated as a noxious species, were recently discovered in Nelson ponds, catfish are still spreading to new North Island waters, and *Gambusia* (mosquitofish) are still being released into new waters for mosquito control.

Introductions and transfers of native fish into lakes can also create problems. For example, smelt were introduced to many lakes to provide a forage fish for trout, but have reduced koaro stocks (Rowe 1990). Elvers are being increasingly stocked into lakes and reservoirs to provide commercial fisheries, but may affect native fish such as bullies and dwarf inanga (Rowe and Chisnall 1997b; Rowe 1999a).

The issue for lake users and managers alike is whether the potential benefits of such introductions and transfers outweigh the impacts. Such decision-making necessarily involves planning for individual lakes, but lake planning should involve all lake users, not just fisheries agencies. The various requirements for lake planning, including the different agencies responsible for developing plans to cover their respective responsibilities, are well beyond the scope of this report. Nonetheless, to contribute to lake planning both managers and users need some knowledge of what fish introductions may be contemplated, what illegal introductions may occur, the effects such introductions may have on the fauna and the lake environment, and the control options and technologies available to them.

The pest status of exotic fish, the statutory responsibilities for dealing with fish introductions, and appropriate control technologies available are dealt with in the review of plant and fish pest species in New Zealand lakes (Champion et al. 2002). This also covers deliberate and accidental transfer leading to the spread of exotic fish. It should be noted that a relatively complex system of approvals based on the status of fish and their presence or absence in receiving waters is required for the taking and transfer of any fish from one location to another. This is outlined in Clayton et al. (2002).

In this report we summarise what is known about the impacts (actual and potential) that fish introductions may have on lakes. A review was provided by McDowall (1987), but at that time the information on exotic fish interactions

with native species was scarce because little work had been done on 'interactive segregation' (sensu Nilsson 1967), or the change in distribution of a resident species caused by the introduction of an exotic species for New Zealand lakes. It is only in the past five years that the problems of pest fish species have been appreciated and attention has focused on their impacts on the native fish fauna. This new information is presented below.

Salmonids

During the early 1900s trout (brown and rainbow) were introduced into most inland waters in New Zealand (McDowall 1984). Trout fisheries developed in many lakes and reservoirs, but in others, fisheries either failed to develop or have remained small, isolated and insignificant. It is now clear that predation by trout had a significant impact on the native fish populations in many lakes, particularly those containing galaxiids (McDowall 1990; Rowe 1990; Rowe and Chisnall 1997a; Rowe, Konui et al. 2002).

The introductions of rainbow trout to many North Island lakes were generally followed by heavy predation on koaro, with a consequent decline in the Maori fishery (McDowall 1990; Rowe, Konui et al. 2002). Trout predation has also played a role in the decline of dwarf inanga populations in Northland dune lakes (Rowe and Chisnall 1997b). Brown trout are known to be more piscivorous than rainbow trout, so no doubt have had a similar – if not greater – effect, but knowledge of the effects of brown trout on native fish in lakes is scarce.

The effects of brook trout on native fish and lake faunas are not known, possibly because this species was largely supplanted by rainbow and brown trout. It has been stocked into small lakes in Auckland, Hawke's Bay and Rotorua to supplement populations of rainbow trout, and in some high-country lakes in the eastern South Island (McDowall 1990), but no adverse changes have been associated with these introductions. It is now restricted to small lakes and headwater streams above the influence of trout, particularly brown trout.

The effects of lake trout and sockeye, Atlantic and chinook salmon on native fish faunas in lakes are also unknown. Although sockeye salmon are mostly pelagic and planktivorous, they can feed heavily on small fish such as bullies (Graynoth et al. 1986). The adults of the other species are mainly piscivorous (McDowall 1990). Impacts on native fish can therefore be expected to be related more to the predatory effects of these salmonids on fish than to competition for habitat or food. However, sockeye salmon may also reduce zooplankton populations and so influence the water transparency. Clearly the introduction of any of these salmonid species to a lake can be expected to reduce any galaxiid populations present, so any further introductions would need to be carefully considered.

Today the value of galaxiids and their role in the overall biodiversity of New Zealand lakes is becoming better appreciated. As a result, the presence of trout in waters where there are no fisheries is now being questioned, and the feasibility of removing them from some locations is being contemplated and trialed. For example, in lakes where trout fisheries are small and insignificant, but where koaro are still present and would increase following trout removal, the removal of trout may well be warranted to increase the number of North Island koaro. Lakes such as Lake Pukaki in the South Island and Waikare-iti (close to Waikaremoana)

in the North Island may also fit such a category. However, practical issues, such as the feasibility of removing or reducing trout stocks, need to be carefully addressed, along with the possibility that other factors may now be inhibiting koaro. Consultation through planning processes would be required before any decisions on fish population restructuring are made.

Although trout have undoubtedly reduced some native fish stocks in lakes, they may now play an important ecological role in controlling planktivorous fish, or other small pest fish. For example, when trout stocking was halted in Lake Waikere (Northland), mosquitofish numbers increased (Rowe et al. 1999), suggesting that trout predation kept these pest fish in check. Similarly, after trout stocking rates were reduced in Lake Okareka (Rotorua), smelt numbers apparently increased and water transparency declined (Rob Pitkethley, personal communication). This suggests a 'top-down' role for trout in these lakes (see section 4).

The removal of all fish, including planktivores, in Lake Parkinson (Pukekohe) resulted in a noticeable improvement in water transparency (Rowe and Champion 1994), probably due to a reduction in fish predation on zooplankton. Such observations indicate that, at least in some lakes, reductions in piscivore populations may increase planktivorous fish and reduce water quality through top-down effects on plankton, whereas decreases in planktivorous fish may improve it. Similar observations have been made in a number of North American and European lakes (Power 1992; Scavia et al. 1986) and indicate that caution is needed before reducing piscivore populations in lakes.

Eels

The stocking of elvers into lakes and reservoirs they could not normally access because of natural or man-made barriers has increased recently. The intent is to provide a harvestable supply of eels. However, the practice involves a number of environmental risks to be weighed against the benefit of establishing a fishery. In particular, large eels (total length over 400 mm) are piscivorous and high densities from unharvested stocks may affect other native fish species such as common bullies and galaxiids. For example, the abundance of common bullies has been found to be lower in lakes with eels than in lakes without them (Rowe 1999a). Conversely, removal of large, predatory eels by commercial fishing may explain the increased abundance of common bullies in Lake Ellesmere (Glova and Sagar 2000).

Galaxiids may also be affected. Large eels preyed heavily on adult banded kokopu when they spawned in one of the inlet streams of a small water reservoir (Mitchell and Penlington 1982), and dwarf inanga are less abundant in lakes with eels than in lakes without them (Rowe and Chisnall 1997b). Eel fishermen are suspected of inadvertently spreading some coarse fish and exotic macrophytes between lakes in fyke nets (Rowe et al. 1999). Catfish, koi eggs and plant fragments can withstand desiccation if they are kept moist (in the folds of an eel net, say) and can easily be transferred between lakes by eelers who fail to check their nets carefully. Such possibilities raise the need for good education programmes as well as for lake management planning to address fishery development issues such as eel stocking.

Galaxiids

The only case of galaxiids being stocked into a lake to create a fisheries resource is the introduction of dwarf inanga into Lake Ototoa to provide a forage fish for the stocked trout population (Thompson 1989). This was successful in as much as the dwarf inanga thrived and became abundant (Rowe and Chisnall 1997a), but neither the effects on trout growth rates nor the fate of the existing banded kokopu population is known.

Koaro quickly colonised Lake Mahinerangi after its formation in 1911 (McDowall 1990) and established a land-locked population. This occurred naturally, probably from adult stocks in streams above the dam. This natural introduction shows that the species can quickly colonise lakes provided suitable habitat is present. Introductions of galaxiids may benefit trout fisheries and/or increase biodiversity, although the juvenile stage of these species is highly plantivorous so they may also influence water quality through top-down effects on plankton populations.

Smelt

Common smelt have been successfully released into many North Island lakes to provide a food source for trout, but introductions to a number of South Island lakes were unsuccessful (Jolly 1967; McDowall 1990). Today smelt are the main prey for rainbow trout in most of the Taupo and Rotorua lakes, and occur in a number of smaller lakes as far north as Kaitaia. In Lake Taupo and many of the Rotorua lakes, they are responsible for the particularly fast growth of the trout, probably because they provide a relatively large and easily caught prey item for the larger fish. In lakes where smelt are absent or scarce, growth rates of the rainbow trout are slower.

However, in Lake Rotopounamu (near Turangi), the introduction of smelt resulted in the extinction of the resident koaro population (Rowe 1993a). This shows that smelt can displace koaro, and that the current rarity of koaro in many lakes containing smelt and trout is likely to be attributable as much to smelt as it is to trout. Because large populations of planktivorous fish can influence water quality in lakes (Power 1992), it is possible that smelt may contribute to reduced water clarity in some lakes by changing the structure and abundance of zooplankton populations, thereby increasing phytoplankton density (top-down effects). However, more study is needed to substantiate such ecological interactions in New Zealand waters.

Bullies

It is clear that bullies have historically been introduced into many New Zealand lakes as many populations are found in lakes where they would not occur naturally. Like smelt, bullies provide a large prey item for trout. They are also an important prey for large eels, so their main role in lakes is as a forage fish. Bullies are not known to influence other fish, although their populations increase greatly as lakes become more productive (Rowe 1999a) and their larvae are planktonic, so they may exert top-down effects in some lakes (Jeppesen et al. 1997). Bullies probably colonised Lake Rotoaira soon after 1974 as none were present at this time (Rowe, Cudby et al. 2000), but they are now abundant (Rowe, Konui et al. 2002). This change coincided with a decline in koaro, and while this may have been related to other changes in the lake, there may be an interaction between

these two species. For example, common bullies were not found in Lake Rotopounamu when koaro were abundant, but are now abundant there (Rowe 1993a).

Non-salmonid exotic fish

Perch

Perch were historically introduced to many small lakes in both the North and South Island as a sports fish, and many small fisheries persist today. They have been extensively studied overseas and sporadically in New Zealand, but as yet there is no substantive evidence of effects on either lake ecosystems or other fish species. They are found mostly around lake margins or in shallow waters close to weed beds, and while they can prey heavily on bullies in rivers (Griffiths 1976), they may be less piscivorous in lakes (Duncan 1967; Schipper 1980). However, bullies are likely to be more important for the largest perch, and the difference in predation between rivers and lakes may be due to size-stunting in lakes and the consequent paucity of large fish. Recently, studies in the South Island have revealed that common bully populations are low in ponds where large perch are present, and increased when the perch – especially the larger piscivorous fish – were culled (Closs and Ludgate 2001). In a survey of a perch lake near Auckland (Lake Wainamu), catch rates of bullies in G minnow traps were less than one fish per trap, much less than in lakes lacking perch (D. K. Rowe, unpublished data).

Catfish

Catfish were found in Lake Taupo in 1985 and have since spread throughout the lake and established a breeding population. There has been no observable impact on the trout or smelt in this lake so far, but exotic fish populations sometimes take many years to build up to levels where impacts become apparent. Adult catfish feed heavily on crayfish in Lake Taupo (Barnes 1996), so may affect crayfish stocks. The diet of juvenile catfish is unknown. If they feed on fish eggs they may pose a danger to fish species whose eggs are deposited in the littoral zone and not defended (such as smelt). Effects of catfish on the trout fishery of Taupo may therefore take time to become apparent.

Eel fishermen have noticed an inverse relationship between catfish and eels (McDowall 1987) which, if substantiated, could represent either the expansion of catfish into areas depleted of eels by fishing or the displacement of eels by catfish. The decline of species such as perch and goldfish in some shallow lakes may also be related to the invasion of catfish. Catfish have poor eyesight and disturb lake sediments with their barbells to detect small prey items. Effects of this disturbance of lake sediments on nutrient cycling, benthic invertebrate populations, and plant regeneration are not yet known. In short, there is too little information available to be certain whether the spread of catfish poses a threat to other fish, or to lake ecosystems. In the absence of such information, a precautionary approach to new introductions is warranted.

Goldfish

Goldfish have been present in many lakes in New Zealand for many years and have not been associated with any noticeable changes in lake ecosystems or fish populations. However, they have proved to be a problem species in some Canadian ponds, by reducing aquatic vegetation and increasing turbidity (Richardson and Whoriskey 1992; 1995).

Rudd

Rudd were widely introduced into small lakes and reservoirs in the top half of the North Island, mainly to provide sport for coarse fish anglers. These introductions were unauthorised, and although it is illegal to introduce such fish into new waters without proper authorisation, liberations continue. No direct impacts of rudd on trout were detected in Lake Parkinson (Rowe 1984b), but rudd produce large populations of small, stunted fish which readily take anglers' lures. This degrades trout fishing, and the trout fishery in Lake Parkinson collapsed because the anglers could only catch rudd, even though trout were still common in the lake (Rowe and Champion 1994). Rudd therefore disrupt trout angling rather than the trout and, as a consequence, can reduce the recreational values of lakes.

There has been no systematic study of the role of rudd in lake ecosystems, so their effects in lakes are not well known. A hundred-fold increase in the abundance of rudd in Lake Rototuna (North Kaipara Head) had no long-term effect on the dwarf inanga population (Rowe et al. 1999). Similarly, smelt, common bullies and trout were not greatly affected by rudd in Lake Parkinson (Rowe and Champion 1994). Rudd were abundant in Lakes Parkinson (up until 1980) and Rototuna (over a five-year period), but their browsing had little observable effect on the macrophyte cover in these lakes (Rowe and Champion 1994; Rowe et al. 1999). However, in lakes where macrophytes are scarce, or cover is greatly reduced by other factors, rudd browsing of seedlings may prevent the re-establishment of plant cover (see, for example, Wells 1999; Dugdale 2000).

Tench

Little is known about tench in New Zealand because they are rarely encountered and are a secretive species. One fish census in a lake thought to be dominated by rudd revealed that tench were the dominant species in terms of both numbers and biomass (Rowe and Champion 1994). Tench are essentially benthivorous, feeding on benthic invertebrates and detritus. They may therefore compete with other benthivores such as common bullies for both habitat and food in lakes. In shallow lakes their number and biomass may increase to the point where nutrient cycling between the sediments and the water column accelerates, and trophic status is increased. They may also disturb lake sediments through their foraging activities, and in shallow lakes this could increase turbidity and help prevent the re-establishment of macrophytes.

Koi carp

The koi carp in New Zealand waters is an ornamental variety of the common carp (*Cyprinus carpio*). Hanchet (1990) reviewed knowledge of the common carp with a view to predicting the impacts of koi carp in New Zealand waters. In the US and Australia the prolific reproductive rate of common carp produces high densities of fish. The adults, which can weigh 10–20 kg each, are mainly herbivorous, but unlike other herbivores they pull plants out by their roots and grub among the roots. The reduction in macrophyte cover reduces the buffering action of weed beds on wave action, and both shoreline erosion and re-suspension of silt by wave action can then increase and elevate turbidity levels. Other factors no doubt also come into play, such as the effect of increased silting of plants and reduced light levels, which can both be expected to reduce weed growth.

Koi carp may not be as much of a problem in New Zealand as the strains of common carp present in the US and Australia. Unfortunately, there is little hard

information on the impacts of, and hence the risk posed by, koi carp to New Zealand lakes. It may only prove to be a problem in lakes where spawning habitat is plentiful and where a shortage of predators allows its population to increase greatly. Or it may only prove to be troublesome in shallow, soft-bottomed lakes with large beds of macrophytes, and not in deeper lakes with sandy or rocky shores and few macrophytes. However, populations of koi carp appear to have built up very quickly in New Zealand waters, so a precautionary approach is warranted. Koi carp can hybridise with goldfish (Smith and Pullan 1987), but the extent of this is unknown.

Gambusia (mosquitofish)

Gambusia have a reputation for eating mosquito larvae and therefore controlling mosquitoes. These fish were widely distributed into ponds and lakes in the US, and following this to New Zealand, Australia and many other countries around the world. Although they have probably had some impact on mosquitoes, it is becoming clear that they pose a danger to some native fish species. Gambusia are prolific breeders but stocks crash during the winter, so high densities only occur towards the end of summer (Wakelin 1986). In New Zealand lakes they have reduced populations of dwarf inanga, mainly through antagonistic behaviour (Rowe 1998). They appear to displace bullies from inshore weedy habitats and may also reduce invertebrate prey and exclude native fish from feeding in the littoral zone (Rowe et al. 1999). They are also known to attack black mudfish (Barrier and Hicks 1994).

Unfortunately, the role of native fish species in controlling mosquito larvae was never properly evaluated, and one or more native species (such as the banded kokopu) may have been just as effective as mosquitofish (Graham 1939). The spread of gambusia has increased rapidly in the North Island because of the growth in horticulture and the resultant need for irrigation during summer months. Many small dams and ponds have been constructed to store water for irrigation; they create problems with mosquitoes and so are stocked with gambusia.

Gambusia can readily spread downstream from these dams. In Whangarei, they quickly spread to the stream below a farm pond and colonised the stream all the way down to the harbour. In the harbour they adapted to seawater and are now thriving in the mangrove swamps. From here they can be expected to spread around the harbour and colonise many of its inlet streams, where they will undoubtedly interfere with native fish species. Unless a satisfactory alternative to mosquito control in such dams is found, the spread of gambusia can be expected to continue in areas of intensive horticulture as climate warming produces warmer summer conditions and problems with water supply and mosquitoes increase.

Orfe

Orfe were recently introduced into New Zealand and are believed to exist in one or two lakes near Auckland. Like tench and rudd, they have no teeth, so are unlikely to be serious predators. However, they are reported to feed on a wide range of benthic invertebrates, plus fish and vegetation (Cala 1970). In this respect they are similar to rudd and likely to prove highly resilient. They are different to other cyprinid species in being more tolerant of salinity (McDowall 1990), so can be expected to proliferate in the lower, estuarine areas of large rivers,

where they may interact with native fish species. For this reason alone their spread needs to be halted until more is known about their life history and biology in New Zealand waters. Although they may have a reputation as an angling fish in Europe, their role in New Zealand waters is unknown and would be very difficult to establish (McDowall 1990). If the potential environmental risks of their spread outweigh any benefits they may need to be eradicated.

Introduced fish	Impact on resident species
Rainbow trout	Reduces koaro
Brown trout	Reduces koaro
Sockeye salmon	None known (but is a planktivore)
Quinnat salmon	None known (but is piscivorous)
Perch	None known (but is piscivorous)
Tench	None known
Rudd	Degrades trout angling
Koi carp	Degrades fish habitat
Goldfish	None known in New Zealand
Catfish	None known (but preys on koura)
Mosquitofish	Displaces littoral species
Eels	None known (but is piscivorous)
Smelt	Reduces koaro

Dams and fish passage

Dams inundate river valleys and replace large reaches of riverine habitat with reservoirs. They may also prevent the re-colonisation of upstream riverine reaches by diadromous native fish species (species that carry out part of the life cycle in the sea and the remainder in freshwater). In addition, reservoirs may become colonised by pest fish species, which then move down-river, forming populations in the riverine reaches below dams. These issues are separate to those involving changes in the hydraulic regimes and hence in fish habitat below dams.¹⁰

In New Zealand there are few diadromous native fish species (four galaxiids, one smelt and three bullies) that can fully adapt to lake dwelling and so form land-locked populations in reservoirs. Even so, the establishment of many of these species in reservoirs is not guaranteed, as smelt-spawning habitat is often lacking and the galaxiid species will only become established if riverine stocks already occur upstream. Koaro have colonised Lake Mahinerangi (Dunedin) and banded kokopu some of the Waitakere and Hunua water supply reservoirs (near Auckland), but neither of these species occur in the Waikato hydroelectric reservoirs, or those in the Rangitaiki River (Bay of Plenty).

Galaxiids tend to be reduced by trout, which are found in nearly all reservoirs. Most reservoirs therefore tend to have a sparse fish fauna dominated by salmonids and bullies, with small populations of galaxiids in some, and smelt in the Waikato River reservoirs. Remnant populations of eels may also be present unless fish passage is provided or stocking is used to increase elver numbers (see below). In the North Island non-salmonid exotic fish species have been introduced to many reservoirs (such as the Hunua dams near Auckland, and the Waikato hydro dams) to increase the variety of angling. This may increase overall species diversity, but effects on trout fisheries and on native fish abundance are yet to be determined. In general, many reservoirs tend to support adequate trout fisheries, but fish size, or catch rate (or both), tends to be lower (Richmond 1981) than in comparable lakes, indicating that the standing stock is likely to be lower.

Dams can block the upstream and downstream movement of riverine fish, limiting the recolonisation of rivers upstream and reducing diadromous native fish stocks. Small dams and weirs close to the coast often restrict or prevent the upstream movement of giant kokopu, inanga, mullet, smelt and bullies, although some barriers can be surmounted by climbing species such as eels (longfins and shortfins) and some of the whitebait species (banded kokopu and koaro). Juvenile migrants of these species can ascend almost vertical rock faces provided a film of water is present (McDowall 1990). The fish noted above are all known to form populations in lakes, but other diadromous species such as short-jawed kokopu, torrentfish, bluegill bully, redfin bully and lamprey do not. As a consequence their populations will be limited to river reaches below the lowest dam.

¹⁰ For an overview, see Davis and Teirney 1987.

Large dams constructed without fish passes on the Clutha and Waitaki Rivers have blocked the upstream passage of chinook salmon, eels, koaro and other fish (Graynoth 1982; Pack and Jellyman 1988). Although trout and land-locked chinook salmon fisheries have developed in the reservoirs, the overall impact on chinook and sockeye salmon, eels and other native fish is probably negative. The major effect of dams on salmonids has been to disrupt upstream spawning migrations. Consequently, many fish passes and lifts have been constructed (with few successes) to create fish passage past dams. These are outlined by Jowett (1987).

A major effect of many high dams has been to restrict the upstream migration of eels to both the reservoirs and river catchments above them. As a result, considerable work in the past decade has gone into facilitating the upstream migrations of juvenile eels and galaxiids over dams. Various passes, lifts and ladders have been designed (Mitchell et al. 1984; Mitchell and Boubée 1989; Boubée 1995; Boubée et al. 2000). In some situations it has proved impractical to protect fish from predators (birds, rats) and/or maintain these passes to ensure they do not become blocked with debris. Where this occurs, elvers are captured at the foot of dams and then transferred by truck over the dam. This approach is labour intensive but may, in the long term, prove more reliable than fixed structures which require constant monitoring and cleaning. The arrival time of elvers at the foot of dams depends on distance from the sea (see section 3), so the critical period for the operation of fish passes will vary between sites.

Elver passes and upstream transfer operations have seen many reservoirs that lacked eels become repopulated and new fisheries established (Beentjes et al. 1997). However, with the general decline in the natural recruitment of longfin elvers throughout the country, attention is now focused on ensuring the downstream passage of large mature eels past dams so they can migrate to sea and spawn. Passage through the turbines of hydro-electric power stations can damage fish, more so with Kaplan than with Francis turbines (Mitchell and Boubée 1992). Where mortality is high it may be necessary to provide an alternative route. This has proved problematic because it is difficult to direct or attract mature eels into structures that will allow their safe passage downriver. Research is now being focused on this problem in New Zealand as well as overseas.

Where dams block fish passage upstream and fish passes are impractical (for example, due to the height of the dam), fish are replenished through stocking in reservoirs. This has only been used for salmonids (mainly rainbow trout) as the techniques and hatchery facilities for the artificial rearing of other species have not been developed in New Zealand. An account of stocking programmes implemented in New Zealand reservoirs is provided by Hutchinson (1987). Today most stocking involves yearling trout (fish 150–200 mm long) rather than fry, because survival of yearlings is much higher.

Providing artificial spawning channels is another way of increasing the recruitment of fish whose spawning migrations are blocked. Those created below the Aviemore Dam were successful (Jowett 1987; McDowall 1990).

Artificial water outlets

Artificial structures are often used to take water out of reservoirs. There are two main types: in one the water flows out by gravity, in the other the water is pumped out of the reservoir. Both can create problems for fish. Where the amount of water being abstracted is large, and localised currents occur, fish can become entrained within the flow. This is mainly a problem when flows are large and/or current velocities fast, which affects small or weak-swimming fish that cannot escape the current. They are either taken out of the reservoir with the outgoing water, or, if screens are present, they may impinge on these and can be damaged, or become trapped and die. As a result many intakes from reservoirs now have large inlets (to reduce water velocities near their mouths), and these are screened to prevent the exodus of entrained fish.

Rotary and Johnston T-screens are commonly used on water intake structures in reservoirs to minimise the incidence of entrainment and reduce impingement problems. They are designed to produce low water velocities across the face of the screen, which minimises impingement, and have relatively narrow slot sizes, which ensures that even the smallest fish cannot pass through the meshes. This prevents the exodus or impingement of juvenile and adult fish, but larvae are not protected. If fish larvae are at risk of entrainment, intakes may need to be sited in locations where their densities are low (as in deeper waters, or embayments). Alternatively, larvae may only be present at certain times of the year or at night, and abstractions can be timed to avoid these periods.

Outlet structures that take water from the deep, cold, hypolimnetic zone of reservoirs (where there are few fish) may minimise entrainment and impingement problems, but can create gas bubble disease in fish. This occurs when an abrupt reduction in water pressure occurs (from the depths of the lake hypolimnion to the shallows of the receiving waters), resulting in the formation of small bubbles of gas in fish tissues. This has not proved to be an issue in New Zealand reservoirs, perhaps because most intakes are surface-based.

Fish deterrent devices, such as electric and bubble fields, have not proved very effective in keeping fish away from outlet canals or water intakes, although screening the outlet from Lake Waikaremoana reduced the loss of rainbow trout (Jowett 1987). Bright lights deter some species, but recent success using combined high-frequency sound and bubbles indicates that acoustic deterrents may prove to be a useful technology for the future.

Outlets may also need to be screened to prevent the transfer of undesirable species out of the lake and into other water bodies. For example, rotary drum screens on the Wairehu Canal, which takes water from the Whanganui River and Lake Otamangakau to Lake Rotoaira, were designed to prevent the transfer of lampreys and eels into Lake Rotoaira and on into Lake Taupo. Lamprey proved not to be an issue, but the screens now help prevent the downstream migration of eels into Taupo and brown trout into Rotoaira (see also below).

Artificial water inlets

Artificial inlets bring water and suspended sediment into lakes, and the large flows – or, in some cases, the planktonic or invertebrate food present in the source water – may attract some species of fish into the inlet canals. Some migratory fish

(for example, land-locked juvenile koaro) are attracted to the large inlet flows in inlet canals, such as those in Lakes Rotoaira and Coleridge, possibly because they are greater than those in inlet streams and so mimic a large river (Rowe, Konui et al. 2002). Other species (for example, trout) may use them as thermal refuges during late summer when temperatures in lake waters exceed avoidance levels. All such seasonal movements of fish into lake inlets can result in aggregations, with a resultant increase in mortality rates from predators or anglers.

Perched culverts and/or velocity barriers (as in Wairehu Canal) can be incorporated into such inlets to prevent unwanted upstream movements of fish. However, culverting natural inlets (for example, to pass streams under roads) may restrict the upstream movement of some fish and create problems for lacustrine species requiring access to natural streams for spawning (salmon, trout, koaro). Problems and solutions with fish passage past culverts are detailed in Boubée et al. (2000).

Further problems may arise if inlet waters bring new fish into the lake or reservoir. The nature of such problems depends on the species involved, any fisheries present, and the size and nature of the inlets. In the Rotorua lakes large migrations of smelt from Lake Rotoiti into Lake Rotorua occur through the natural canal joining the two lakes. This clearly benefits Lake Rotorua, as smelt form a major prey for trout, but may be disadvantageous to the trout fishery in Rotoiti, particularly if it reduces its smelt numbers. In Lake Otamangakau, water diverted from the Whanganui River introduces both juvenile trout and eels into the lake. Whereas the increase in trout recruitment can be expected to benefit the fishery, the addition of eels probably has little effect. Similarly, the rotary drum screen on the Wairehu Canal between Lakes Otamangaku and Rotoaira restricts the downstream movement of eels into Rotoaira, although juvenile brown trout can move through the screens (Turner 1979). A few periodically enter Rotoaira and grow to adulthood (Rowe, Konui et al. 2000), but an adult spawning population has not yet established. Should it do so, the brown trout might reduce recruitment of juvenile rainbows (Tilzey 1999) and affect the trout fishery. This possibility was not foreseen and has only become an issue because the brown trout population in Lake Otamangakau has increased (Dedual et al. 1997).

Constructed inlets and outlets that may result in significant entrainment and impingement problems for fish, or attract fish, should not be sited close to natural streams, as large numbers of adults may enter such streams to spawn and juvenile fish and/or larvae can be expected to leave the streams at certain times of the year. Where this is not possible, the operation of inlets and outlets may need to be restricted at times of the year when major fish movements occur (see section 3).

Water-level changes

Natural changes in water level play an important ecological role in lakes. Seasonal rises may initiate annual events such as spawning for some fish species (for example, cyprinids and galaxiids) and may allow other species (eels and trout) periodic access to new feeding grounds in inundated areas. Changes to the natural water-level regime of lakes can therefore affect the seasonal use of littoral resources by fish and may affect growth and abundance. Although such impacts have been recorded overseas (Gafny et al. 1992), none have been reported in New Zealand lakes or reservoirs¹¹.

¹¹ See Lake Level Management in this series for further information.

Many town and city water supply reservoirs and some hydro reservoirs in New Zealand undergo marked changes in water level (over 2 m per year). This also occurs in small lakes and ponds, especially where water is abstracted for agriculture or horticulture. Problems for fish may arise when the water levels fall and expose major areas of the littoral zone to desiccation. In particular, the eggs of fish species that spawn in shallow waters, such as smelt and perhaps some galaxiids (for example, dwarf inanga and inanga), may be exposed and die. This will only occur when ramping rates are high and the drop in lake level is fast enough to expose the eggs before they hatch. A more gradual drop in water depth may reduce the size of spawning grounds and affect fish recruitment. In such situations the change in size of the spawning grounds can be determined for any given lake level by the use of GIS-based habitat models, as was developed for Lake Taupo (see section 9).

Large drawdowns (over 2 m per year) can greatly alter the physical structure and ecology of the littoral zone. In lakes with large fetches, wave action can be a major factor influencing the structure of the shallow littoral zone. Wave action tends to restrict macrophytes to waters deeper than 1–2 m, the actual depth depending on the degree of exposure. In these lakes a change in lake level up to 1 m or so is unlikely to have as great an effect on macrophyte depth distribution as in a smaller, more sheltered lake, where macrophytes grow close to the lake surface. However, water-level changes over about 2 m per year, and certainly of 5 m or more per year, can be expected to affect the shallow-growing plant species in large lakes and restrict the macrophyte zone to deeper waters. In some lakes increased turbidity from shoreline erosion, and/or the resuspension of silt, may also occur and reduce light penetration, reducing the maximum depth of macrophytes. The result would be a compression and reduction of the macrophyte zone to a point where it may disappear, as occurs in Lakes Tekapo and Pukaki in the South Island.

Where there is little wind exposure (as in reservoirs formed by blocking river valleys, or small lakes in valleys), and a lack of wave action allows plants to grow close to the lake surface, even small changes in lake level can be expected to decrease the upper depth limit of macrophytes. Conversely, where natural changes in water level are damped and minimal, plants may establish right up to the water's edge and the open, wave-washed zone between the water's edge and the start of macrophyte beds will be lost. This clear zone is important for fish. Large brown trout patrol such areas searching for Odonata larvae, which make periodic forays towards the shoreline during spring. Anglers, aware of such habits, target the brown trout at these times. Changes to this zone can therefore affect fish and fisheries.

Many fish species obtain invertebrate foods (such as snails) from the littoral zone, and macrophyte beds are expected to be a major source of such prey. Macrophytes may also provide cover for young fish, but despite their importance there are few quantitative data on the types of macrophytes favoured by fish and their role in providing fish habitat. The effects of water-level changes on fish caused by changes in macrophytes are now becoming an active area of research overseas.

GIS-based models (see section 9) can be developed and used to determine changes in the amount of general fish habitat (for example, the area of weed beds, sandy area or rocky substrate) at various lake levels. However, as with other habitat-

based approaches to impact assessment (such as IFIM/RHYHABSIM¹²), changes in habitat do not necessarily result in changes to fish abundance, as other factors (such as predation and the extent of spawning grounds) may be limiting.

Other potential impacts of lake-level changes can include altered access to spawning tributaries by mature salmonids, smelt and koaro. If lake levels are too low during the spawning migration, access to streams may be restricted by small falls or, where the stream channel is wide, reduced water depth. Conversely, access may be increased when water levels are high. Knowledge of the timing and location of fish spawning migrations in lakes is therefore important for managing water-level variations in lakes (see section 5).

When drawdowns are relatively large (over 2 m) and prolonged (over summer or autumn, say), a large expanse of lake shore can become exposed. Seeding this zone with ryegrass, particularly areas with soft substrates or a heavy overlay of silt, has proved beneficial to some fish when water levels rise (Strange et al. 1992). Such riparian planting may also help reduce runoff and so maintain water quality.

Circulation patterns and currents

When large volumes of water move through hydro lakes (such as the Waikato hydro lakes, Lake Rotoaira, or Lakes Dunstan and Waitaki), currents can develop which may affect fish distribution patterns. Distributions of limnetic species such as smelt and inanga are affected by wind action (Glova and Sagar 2000), and by the subsurface currents created by this. Such currents may be beneficial in that water circulation in lakes is improved, and with it oxygenation. However, one-way flows may result in longitudinal gradients in nutrients, sediment and water-quality variables such as turbidity, which will influence fish habitat and distribution patterns in reservoirs. Also, fish larvae and fry may be carried passively by internal currents, and either concentrate in certain areas or be transported out of the lake. Impacts on fish populations from spatial displacements of water are as yet unknown. However, the larvae of bullies, galaxiids and smelt may all be susceptible to such movements, particularly at night, when they move to the lake surface.

Sediment removal

One of the major problems facing the management of many reservoirs, such as Roxburgh and Dunstan on the Clutha River, and the Hinemaiaia Dam near Taupo, is the build-up of sediment to a point where it limits the inflow and/or significantly reduces water storage capacity. When this occurs, the sediment needs to be removed, and the methods used may impact on fish life, particularly if the removal process increases turbidity levels and/or results in changes to the lake bed and its biota. Sediment needs to be removed in such a way as to minimise turbidity and prevent re-entry of the sediment to the lake basin. Suction dredging and the deposition of spoil above large bunds on the shoreline have proved useful to overcome these problems.

¹² IFIM - Instream Flow Incremental Method. RHYHABSIM – River Hydraulic Habitat Simulation.

PART III: Monitoring and managing lake fish populations

There have been a number of innovations and improvements in methods for assessing fish distribution, abundance, movements, habitats and biological attributes, such as age, condition and maturation in lakes. Good reviews of basic methods are provided in Nielsen and Johnson (1983), Schreck and Moyle (1990) and Murphy and Willis (1996). In this section, new methods applicable to fish in New Zealand lakes are outlined.

Echosounding

Acoustic techniques are now routinely used for determining fish abundance and distribution in many overseas lakes. In essence, these constitute a downward-looking transducer mounted on a boat or in a towed body behind the boat. Sound from the transducer is pulsed into the water, and echoes from objects below the transducer are detected and converted to digital or analogue signals displayed on a chart recorder, or stored on data files. A high-frequency (200 kHz) acoustic system, which can detect very small fish (for example, larval bullies), was used in the Rotorua lakes during the early 1980s to determine changes in the distribution of smelt and larval bullies related to depth gradients in temperature, oxygen and light (Rowe 1993b; 1994). This machine also proved useful for assessing changes in the relative abundance of dwarf inanga in the hypolimnion of Lakes Taharoa and Waikere in Northland (Rowe et al. 1999), and the distribution of larval bullies in Lake Coleridge (Taylor et al. 2000).

In the late 1980s a 70 kHz (medium-frequency) split-beam sounder was used to routinely monitor trout abundance in Lake Taupo (Cryer 1991). The split-beam transducer and associated software allowed the target strength of echoes (a measure of fish size) to be measured, so that adult trout could be distinguished from smaller fish such as smelt. This machine was later used to measure the abundance of smelt in Lake Rotongaio (Forsyth et al. 1990), and the depth distribution of trout in several Rotorua lakes in relation to temperature, oxygen and light levels (Rowe and Chisnall 1995).

Although acoustic techniques have proved useful for measuring the abundance and distribution of fish in the pelagic zones of lakes, there are blind spots within several metres of the transducer face and within 1 m of the lake bottom. This, coupled with large changes in trout distribution between the shallows and deeper waters of lakes, can limit the accuracy of estimations of trout population (Rowe, Macaulay et al 2001).

Acoustic methods are therefore of limited value for determining the abundance of fish in shallow lakes, in littoral zones or for benthic species. This is changing as techniques for deploying transducers in a horizontal (sideward-looking) mode are currently being developed. The major remaining limitations are the accuracy of measurements of fish size based on target strength, and assumptions about fish distributional patterns in lakes (Rowe, Macaulay et al. 2001). Both of these can lead to uncertainty about the identity of some echoes, and hence to concerns over the reliability of fish abundance estimates in lakes where several species of fish are present.

Fyke netting and minnow trapping

The use of conventional netting/trapping techniques in lakes has been much improved since the 1980s. 'Super-fykes' have been developed for sampling a wide range of species, particularly eels, in the littoral zones of lakes (Chisnall and West 1996). Super-fykes are relatively large nets with a fine mesh (2 mm) for securing both the smallest and largest fish present. They also contain meshed-off compartments for trapping different-sized classes of fish and ensuring that the larger predatory species do not eat the smaller prey species.

In addition, a 5 mm-mesh version of the standard fyke net used by eel fishermen now provides a practical way of obtaining abundance estimates for small fish such as adult bullies, smelt, koaro, dwarf inanga and rudd in lake littoral zones (Rowe and Chisnall 1997a; Rowe 1999a; Rowe, Konui et al. 2002). Whereas such fyke nets are limited to shallow waters and lake margins, arrays of G-minnow traps placed at various depths down a transect have proved useful for determining depth distributions of small littoral and demersal fish such as adult bullies and koaro (Rowe, Nichols et al. 2001; Rowe, Konui et al. 2002a).

Fine-meshed seine nets are also effective (especially at night) for catching samples of littoral species such as juvenile salmonids, perch, smelt and common bullies (Graynoth 1999b). Electric fishing, manta boards, small-beam trawls, brush traps, gill nets, trap nets and small purse seines have also been successfully used to sample or count fish in New Zealand lakes (McDowall 1990; Jellyman and Chisnall 1999).

Larval fish sampling

A number of native fish in New Zealand lakes have planktivorous larvae (common bully, smelt, koaro, banded kokopu, dwarf inanga). A large, coarse-meshed ichthyoplankton or zooplankton net can be towed horizontally (Rowe 1993b; Taylor et al. 2000), or, in shallow lakes, smaller zooplankton nets can be mounted on a small boat and pushed through the water to obtain samples of larvae. In deep lakes, where ichthyoplankton are in deeper waters (over 30 m), such methods are not viable and drop-netting with a Wisconsin, throttlable plankton net has been used to determine depth distributions and measure the areal abundance of fish larvae (Rowe 1993b; Rowe et al. 1999). Light traps have proved popular for the larvae of some cyprinid species overseas, but are ineffective for most New Zealand native fish species in lakes.

Radio and acoustic tagging

Fish movements in lakes can now be determined by sophisticated radio and acoustic tagging methods. These tags are still relatively large, even though the battery size is small and longevity short. For example, the smallest radio tags available are 18 mm by 8 mm and last about 30 days. As such tags need to be implanted in, or attached to, the fish this technique is limited to the larger species such as adult salmonids, eels and carps. Such techniques have been used to determine the movements and territories of trout in lakes (James and Kelso 1995), and to identify the movements of eels in lakes and around dams (Jellyman et al. 1996). Data recorders within some of these tags can measure changes in pressure (depth) and temperature at intervals of seconds to minutes for periods of weeks to months. On recovery of the tags, these data can be downloaded and used in

conjunction with knowledge of the lake's bathymetry and thermal structure to reconstruct the fish's movements and preferred habitat.

Modelling tools

Knowledge of the area (or preferably volume) of fish habitat in lakes is useful, particularly if it may be changed in some way. GIS modelling provides a potentially valuable tool for measuring fish habitats and for determining the effects of changes in water quality, lake levels, macrophyte growth, etc. Although knowledge of the variables that determine habitat is still lacking for many species and life stages, GIS-based methods have proved valuable in determining changes in the amount of habitat related to changes in lake level.

For example, smelt-spawning habitat in Lake Taupo consists of clean, sandy substrates at depths of 0.5–2.5 m (Stephens 1984). A GIS-based model was developed using a map of the lake's inshore bathymetry (obtained by acoustic surveys) and a substrate map (determined by aerial photography and ground-truthing). The model was constructed to calculate the total area of smelt-spawning habitat at any given water level, and hence to show changes in the amount of habitat present at each water level (Rowe, Shankar et al. 2002). Such GIS modelling can be used to determine the effects of changes in water levels, or of other lake variables such as light and turbidity, on fish habitat. However, it also gives the ability to predict the effects of changes in these variables on macrophytes. This versatility means that GIS modelling will become increasingly important as a tool in lake management. However, knowledge of fish habitats in lakes will still be needed before this can become a reality. For small lakes GIS modelling can be replaced by mapping and diver-based manual estimation of habitat areas.

Bioenergetic models are also finding an increased use in lakes. For example, the Wisconsin bioenergetics model (Hewett and Johnson 1992; Hanson et al. 1997) is used to estimate consumption rates of forage fish by piscivores such as salmonids. It can also be used to detect seasonal bottlenecks in growth and/or to assist in stocking decisions. Such models can be combined with food-web models (for example, Beauchamp et al. 1995) to provide a wider ecological understanding of species interactions in lakes.

Feeding rates, prey species and measures of condition

Where there are concerns over fish food supplies in lakes, the food web needs to be determined and measures of feeding activity, condition and ultimately growth rate need to be developed and compared with either historical data or data from control lake populations.

Measurement of prey species by gut analysis usually forms the basis for constructing the food web, and new numerical methods for comparing gut contents (for example, Mansfield and McCardle 1998) can be useful for assessing changes in diet. Such comparisons do need to be approached cautiously, as the diet of many species can change with age/size, sex, and season. Also, some prey species may vary in abundance between years and will not provide a useful index of change. Ideally, large samples (50–100 fish) spanning the size range present need to be taken at least quarterly to provide even a rudimentary picture of the main prey species and their role as fish food.

More general measures of food web structure can be provided by measuring stable isotopic ratios for carbon, oxygen and nitrogen. These have proved useful for determining whether fish production is based mainly on terrestrial, macrophyte or planktonic sources of primary production, or some combination of these (see, for example, James et al. 2000; Campbell et al. 2000). This technique is based on the different isotopes (of carbon, say) synthesised by aquatic versus terrestrial plants. The ratios of these isotopes in the flesh of fish changes depending on their food base. For example, fish dependent on a purely aquatic food base (such as trout in Lake Taupo) can be expected to have a very different carbon isotope profile to fish from lakes where significant amounts of terrestrial prey are consumed.

Although useful in distinguishing the relative importance of terrestrial versus aquatic prey, and in identifying the likely prey species for some fish, the technique is limited. The current cost of the analyses generally limits application to only a few fish, and terrestrial food sources are generally a minor component of fish diets. Such analyses also cannot distinguish changes in fish diet related to the interplay of seasonal and ontogenetic factors.

Feeding rates of fish can provide a guide to whether food supply is adequate. The feeding rates of smelt were measured after the Ruapehu eruptions caused reduced chlorophyll levels in Lake Taupo (Gibbs 1998) to see if feeding activity in Taupo had been reduced. Both the mean amount of food present in fish stomachs and the proportion of fish feeding in Taupo provided useful data to compare with that for control lakes as well as historical data from Lake Taupo (Rowe 1997). Results indicated that food intake was reduced after the eruptions.

However, feeding activity may vary from day to day, and fish are capable of withstanding long periods without food. Starvation for periods of weeks is followed by 'compensation' growth, wherein the growth rate of starved fish exceeds that of fed fish (Broekhuizen et al. 1994), resulting in a larger size for the starved fish. Therefore, longer-term measures of food intake are needed to determine whether fish populations have been affected by a reduction in food supply.

Condition factor is one of these. It is commonly used to measure whether a fish's overall weight is acceptable for its length. A number of numerical indices are available for calculating this and are provided in standard fisheries texts, but care is needed to select the appropriate one. A more useful approach is to compare length-weight relationships by analysis of covariance. This compares the slopes and intercepts of the length-weight regression lines. Problems with both approaches can occur if males and females vary greatly in size (so need to be separated), or if fish are sampled during the spawning season when the weight of individual fish can be expected to vary greatly depending on whether they have a fully developed gonad or not, and whether they have spawned. Some fish may also have a higher weight than others because they have been feeding recently and have full stomachs. Fish can be eviscerated and the weight of the carcasses compared. However, evisceration removes much of the visceral fat, which can be an important nutritional reserve.

Another (and perhaps better) approach to determining the nutritional status of fish is to determine their total fat content. For example, after the Ruapehu eruptions and consequent reduced feeding of Taupo smelt, their fat

concentrations were lower than in comparable control lakes (Rowe 1997). Adequate fat stores need to be acquired by fish before they can mature, and such stores are highly sensitive to changes in food intake (Rowe et al. 1991). Fat content can be reduced by restricted feeding and increased when feeding resumes without any change in fish length or weight being apparent (Rowe et al. 1991). This is because water replaces fat when it is depleted from tissues. Such changes would not be detected by measurements of fish weight and length, but would be detected by whole-body fat analysis.

A range of chemical methods are now available to measure total fat levels in fish. Limitations on these are related to fish size. For example, small fish, such as juvenile smelt or galaxiids, may need to be pooled to provide a sufficiently large sample (for example, 10 g) of tissue for analysis. Conversely, all the tissue from large fish may need to be blended to extract a small enough representative sample. Electronic scanners are also now available for estimating the fat content in the fillets of large fish, such as salmonids, but they do not provide a whole-body measure.

Age, growth, maturation and population structure

The ultimate, long-term measure of whether fish populations are affected by changes in food supply, or other environmental factors influencing feeding, is growth rate. In the 1970s calculation of several freshwater species' growth rates was largely based on examining fish scales to estimate age, but this was often hindered for many species and in many lakes because the fish scales failed to show annual growth checks. Ageing in these situations therefore relied mainly on expensive tag and recapture studies, or analysis of size frequency distributions from monthly sampling.

Tagging techniques have improved considerably over the past decade with the advent of micro-tags and PIT (passive internal transponder) tags. Micro-tags are small metal bars (approx. 3 mm long by 1 mm diameter), which are implanted into fish either near the nose or in the dorsal musculature. They can be used on fish as small as 5 cm long so are generally used to batch-mark large numbers of fish, which are later stocked into lakes. They have good retention and are detected in adults by a metal detector. They could also be used to identify fish individually. PIT tags are slightly larger (10 mm long by 2 mm diameter) and are generally implanted inside a fish's abdominal cavity. They each have a unique number, which is read by an electronic wand. Although other tag types and their retention have greatly improved, tag and recapture studies are still relatively time-consuming and costly.

The discovery of annual growth rings on fish otoliths (ear bones) has removed many of the former limitations to determining growth. Techniques for preparing and reading otoliths have now been developed for many species, and are routinely used to age trout, eels and other freshwater fish (Graynoth 1996; 1999b). The discovery of daily growth rings on otoliths raised the prospect of putting a finer time scale on changes in growth. For example, patterns of daily growth rings have proved useful in identifying the location (stream versus lake) of early rearing environments for juvenile trout (Rosenau 1991; Hayes 1995) and for ageing smelt (Ward and Boubée 1996).

More recently, techniques to analyse the chemical composition and radio-isotopic content of otoliths against the time base of daily growth rings has increased the ability to determine features of early life history, such as whether fish were raised in inlet rivers of lakes or the sea (Northcote et al. 1992).

However, where it is possible, scale reading still provides a useful and cost-effective method for ageing fish in lakes. Scale reading was successfully used to determine the growth rates of trout in lakes Otamangakau and Rotoaira (North Island), which both experience relatively cold water temperatures (less than 8°C) during winter (Dedual et al. 1997; Rowe, Konui et al. 2000). An advantage of scales over otoliths is that spawning marks are apparent on scales, so age at first maturation and the years a fish spawned can also be determined. This is important for trout, as the age at first maturation can influence the maximum size fish attain and is affected by changes in growth rate and food type (see, for example, Rowe and Thorpe 1990b; Rowe et al. 1991). In Lake Rotoaira age at first maturation for rainbow trout increased between the 1970s and 1990s, and the mean size of spawning fish increased (Rowe, Konui et al. 2000).

Ageing by measuring scales or otoliths needs to be validated for each species in each lake, as the first annulus (annual ring) may not be present, there may be false growth checks, and annuli may not be laid down each year. For example, annuli in rudd scales are caused by resorption of calcium that occurs during maturation and not by a reduction in winter growth. Also, rudd do not mature in their first year of life, so the first annulus is missing (Rowe, D. K., unpublished data). Scales from most rainbow trout captured, released and recaptured after a winter in Lake Otamangakau exhibited a clear winter growth check, but some did not (Dedual et al. 1997). Growth checks were not caused by reduced water temperature (which would affect all fish) so much as by a reduction in food supply during winter. It was apparent that some trout were able to find a food source in the lake during winter months (such as the mouth of an inlet stream) and continued to grow over winter.

Where ageing from otoliths or scales is not possible, but there are clear modes (representing age groups) in the size frequency distribution, computer programmes such as MIX (Macdonald and Green 1998) can be used to determine the age structure of the population. This is useful when a single large sample of fish is obtained. Other more sophisticated computer programmes (such as MULTIFAN) rely on changes in the modes of size frequency distributions over time. Size-at-age scatter plots are generally used to compare changes in growth for fish in lakes. Curves can be fitted to these plots, the most useful and generally applicable being the von Bertalanffy growth curve. This has been found to provide a good approximation to fish growth, and statistical techniques can be used to compare the parameters of this growth model between different populations of fish (see, for example, Gallucci and Quinn 1979).

Fish health indices

Fish health profiling is now used to determine whether fish in lakes are showing signs of disease or damage caused by pollutants (Richardson 1998). This technique involves capturing a representative sample of fish for a given species, and systematically recording a number of key external and internal features such as gill colour, eye condition and liver state. The state of these variables is assessed

and scored for each fish. The scores are weighted and combined to produce an overall index of the health of each fish in the sample. The mean health index for a sample is then taken to reflect that of the fish population in the lake.

Such an index was used to determine whether trout and common bullies in Lake Maraetai (which is affected by pulp mill discharges) were healthy compared with fish up and downstream of this reservoir. Key indicators of health and metrics for scoring these have been developed for both eel species, rainbow trout and common bullies. Samples of fish from un-impacted lakes were analysed to provide baseline or control values (Richardson 1998). Although such indices may show differences in the 'health' of a fish population between sites, or over time at a specific site, they do not indicate whether population parameters such as mortality, growth, or fecundity differ. They are also specific to the 'health' parameters examined. For example, the health index may record the presence of external but not internal parasites. Care needs to be taken when applying such indices to avoid introducing biases related to differences in the sex, size, or maturation status of fish.

Bioassessment, biodiversity and fish-based indices of lake health

Fish-based indices of biodiversity, lake trophic status or environmental stress are proving popular overseas (US EPA 1998), but would be of limited use in New Zealand lakes and reservoirs because there are too few species of fish present. For example, the ratio of pollution-sensitive species (salmonids, say) to pollution-insensitive species (such as cyprinids) is used to provide a measure of lake trophic status and pollution in some US lakes. However, in New Zealand, both salmonid and cyprinid species are few in number and do not occur together in many lakes.

The ratio of some native fish species may prove useful in this respect. For example, the ratio of smelt to bully larvae declines between various Rotorua lakes and reflects a decline in water transparency associated with changes in lake trophic status (Rowe, D.K., unpublished data). However, such a ratio would not be possible for South Island lakes because smelt are generally absent. Similarly, measures of fish species diversity based on the apportionment of total fish numbers (or some measure of their abundance) among the species would be limited. Such measures would only be feasible in localised lakes that contain the same species (for example, the Rotorua lakes, or the Waikato hydro reservoirs).

Main assessment methods for fish in lakes	
<p>FISH ABUNDANCE</p> <ul style="list-style-type: none"> • echosounding (pelagic fish, all stages) • purse seine netting (schooling, limnetic fish) • drop netting (larval fish) • fyke netting (eels, littoral fish) • G minnow traps (benthic fish) <p>AGE, GROWTH, MATURATION, POP^N. STRUCTURE</p> <ul style="list-style-type: none"> • scale and otolith reading • tagging and recapture • bioenergetics modelling • size frequency distribution analysis 	<p>FISH MOVEMENT</p> <ul style="list-style-type: none"> • acoustic and radio tags • trapping streams <p>FEEDING, FOODS AND CONDITION</p> <ul style="list-style-type: none"> • stomach analysis and gut fullness indices • condition factor • lipid content • fish health indices <p>HABITAT IDENTIFICATION AND MEASUREMENT</p> <ul style="list-style-type: none"> • acoustic, radio and data-logger tags • GIS modelling

Many aspects of lake management can potentially affect the fish populations in lakes, and a number of these were covered in Part II, especially with respect to water quality, contaminants, fish introductions and artificial water barriers and manipulations. Lake management is not, however, restricted to considering the impacts that such factors can have on fish. Some fish can themselves be used as control agents – for macrophytes, algal populations, or pest fish populations in lakes, and can therefore provide useful tools for lake managers. The issues relating to fish in these interactions are outlined in this section.

In addition, managing fish populations may sometimes conflict with the overall goals of lake management. Ideally potential conflicts can be identified and addressed by good planning and through liaison between the different management agencies involved. However, such issues are often overlooked because they are not anticipated. In this section we also outline some of the main ‘fishery’ issues that lake managers need to be aware of and anticipate.

Fish for macrophyte control

The weed problem

Exotic weed beds are perhaps the main management issue in New Zealand lakes today, and fish can play an integral role in plant management. The native plant species in lakes have not generally proved troublesome. Native plants are thought to provide cover, protecting fish from shag predation and from piscivores such as trout or eels. They also provide a substrate, and in some cases a food base, for important invertebrate prey species such as Odonata (dragonfly) larvae, caddis (mayfly) larvae, snails and crayfish. Aquatic plants also provide substrates for spawning by perch and coarse fish species such as tench and goldfish. However, the invasion of exotic macrophytes has changed the public perception of aquatic plants in lakes.

The foreign weeds have overwhelmed and replaced the low-growing native plant communities of lakes with dense, surface-reaching beds that restrict light and water circulation, and reduce oxygen levels within the weed beds. They attract large populations of swans, which may accelerate an increase in lake trophic status by voiding faecal matter directly into the water column. The exotic plant species hinder navigation, foul propellers, make swimming dangerous, interfere with and restrict angling (from boats as well as the shore), block water intakes, and are suspected of reducing fish habitat. When such large, exotic weed beds collapse in small, shallow lakes, algal domination and increased turbidity often occur. As a result the spread of exotic weeds has resulted in many undesirable changes to lake ecosystems. However, the undesirable effects of lake changes associated with the invasion of exotic plants should not blind people to the desirable attributes of native plant species.

The effects of weed removal

The removal of macrophytes in lakes tends to increase the area of benthic habitat, and this has been associated with increases in benthic species such as eels

and bullies (Mitchell 1986; Hayes et al. 1992), while species more dependent on the littoral zone (such as rudd and trout) may decrease (Rowe 1984b). Some planktivorous species (such as dwarf inanga) have increased following weed removal (Rowe et al. 1999), while others more sensitive to increased silting (such as smelt) may have declined (Mitchell 1986). Littoral species in New Zealand lakes which utilise plants for food, cover and as a spawning substrate are generally coarse fish such as rudd and perch. However, trout (brown and rainbow) may be dependent on littoral zones in lakes where limnetic forage fish are scarce (most South Island lakes). In such lakes they would be adversely affected by weed removal if it greatly reduced trout food supply.

Using fish to control weeds

While excessive growths of exotic weeds can affect fish populations in lakes, some fish species can affect aquatic plants. The grass carp was introduced into New Zealand in 1971 in response to problems with exotic weeds in the Rotorua lakes. Although it cannot reproduce naturally in New Zealand waters, controversy surrounded its importation and use because of confusion with the common carp, which is a noxious species in many countries. A number of trials in New Zealand have since proved its value for weed control in lakes and indicated that environmental problems are no greater than with other equally effective forms of weed control (Rowe and Schipper 1985; Rowe and Hill 1989; Rowe et al. 1999). However, a major limitation to the use of grass carp for weed control is their propensity to escape. If they can be confined within a water body (for example, by screens), they will remain and any weed problems will be controlled. However, if they can escape, then the numbers remaining may be too few to exert any control over the weed beds.

The value of using grass carp to eradicate exotic plants was thought to be that once the exotic species were eliminated, so too was the weed problem because the main exotic plant species do not set seed in New Zealand waters. However, before native plants could regenerate from seeds present in the lake sediments, grass carp would need to be removed, or their numbers drastically reduced, to reduce browsing pressure. If they could not be easily removed by netting (as in most lakes), they must either be left to die out, which could take 10–15 years, or removed using a piscicide. Recently, a piscicide-impregnated bait system (Prentox) was used with limited success to reduce grass carp numbers in a Northland lake (Rowe 1999c). More recent trials with Prentox have since indicated that grass carp quickly develop resistance to the treated baits, so they can only be used once.

If other phytophagous fish species that reproduce naturally in lakes (such as rudd, goldfish and koi carp) are present, they may prevent the regeneration of native plants from seedlings by feeding on the emergent shoots. For example, exclusion experiments have shown that browsing by rudd can prevent regeneration of plants in Lake Rotorua in Hamilton (Wells 1999). Other species (catfish, tench) may contribute to this process by disturbing seedlings through their foraging activities. In lakes where such species are present it may be necessary to remove all fish using a piscicide such as rotenone, and then restocking with desirable species. Such an exercise was successfully carried out in Lake Parkinson near Pukekohe (Rowe and Champion 1994). It enabled native plants to regenerate from seeds in the lake sediment, and native fish were later re-introduced to the lake to restore its ecological values.

More recently a degree of long-term control versus complete eradication was demonstrated by low-density grass carp stocking in several Florida lakes (Leslie et al. 1987; Cassani et al. 1995). In these lakes weed cover remained at 5–10% for up to five to seven years. No such trials have been carried out in New Zealand lakes, although Lake Omapere (Northland) has recently been stocked with a low number of grass carp and may provide an opportunity to test this.

Fish for algal bloom control

Silver carp, along with a range of other fish, were routinely stocked into Israeli drinking water reservoirs to reduce algae. They were thought to reduce the algal populations in these reservoirs by about 25%, which was sufficient to prevent blooms forming (Leventer 1981). Silver carp were imported into New Zealand and evaluated for the control of blue-green algae in a small Hawke's Bay lake. Periodic observations indicated that they ate the blue-green algae and noticeably improved water quality (Carruthers 1986). However, the duration of this effect was not measured, and trials in other lakes were not successful, either because the fish died, too few were stocked, or there was insufficient monitoring to determine a result (Rowe 1989b). As with grass carp, silver carp do not breed naturally and must be propagated by artificial methods. Their status as a bio-control agent is therefore still unknown, but there is increasing interest in this technology overseas (see Wu et al. 1997).

The role of fish in lake restoration

Restoration is generally employed to improve water quality or aquatic plant communities in lakes, and fish may benefit from this. The many techniques in current use are described in Cooke et al. (1986) and Olem and Flock (1990). Lake restoration has usually been separated from fishery restoration, wherein fishery managers manipulate fish stocks through stocking, forage fish introductions, selective harvesting, or piscicides. However, just as lake restoration may either benefit or reduce fisheries depending on the species present, so too can fishery management enhance or hinder lake restoration. Because these two processes may conflict at times, managers need some background knowledge of the potential issues related to fish, particularly as lake restoration seems likely to increase during the next decade.

Lake restoration is the responsibility of lake managers, including regional or district councils, and the Department of Conservation (DOC) on public conservation land. However, fishery management for acclimatised fish species – mainly trout – is exercised by the regional fish and game councils, and by DOC in Taupo. To confuse this multi-agency approach to management further, eels are increasingly likely to come under the aegis of the Ministry of Fisheries and/or iwi control. The goals of these different management authorities may conflict at times, so co-ordination of planning is advisable. Statutory management planning processes provide a way of identifying and resolving issues, but at present there are few formal linkages between fish management plans (prepared by fish and game councils and DOC in Taupo) and lake management plans (prepared by regional or district councils and DOC for lakes in public conservation land).

Where the goal of lake restoration is the removal of exotic weeds and their replacement by native plants, stocking with grass carp has provided a cost-effective technique (see above). However, such large changes in aquatic vegetation

may affect certain fisheries, and the subsequent regeneration of native plants may require the reduction of other herbivorous fish such as rudd or koi carp, which may be important to coarse fish anglers in some lakes. Other species, such as catfish and tench, may also restrict plant regeneration in lakes by uprooting seedlings when they forage for benthic prey. Of these, tench are highly regarded by coarse fish anglers. There is therefore potential for conflict between lake and fishery managers.

However, some technical resolutions are possible. Problem fish species could be removed by piscicides in some lakes (see, for example, Rowe and Champion 1994) to allow the establishment of native plants, and then be re-introduced. Bio-control agents may also allow reductions of pest fish. No bio-control agents for rudd or other coarse fish species have been evaluated so far, but brown trout are reputed to exert some control over rudd numbers in small lakes.

Where the goal of restoration is improvement in water quality, a reduction in nutrients is required. External supplies of nutrients to lakes can be reduced, but recycling of nutrients from sediments back into the water column may also need to be looked at. The role of benthic invertebrates and fish in this process is not understood at present. Little research has been done on this issue in New Zealand lakes, but a number of overseas studies have implicated benthic omnivores in nutrient recycling within lakes. Some fish species may also affect benthic communities by the bioturbation of sediment during feeding. This realisation has led to recommendations to control such fish in order to improve water quality (see, for example, Andersson et al. 1978; Horppila 1994). In particular, species such as catfish, tench, koi carp and goldfish may play a role in nutrient cycling and transport within small shallow lakes, and they may also affect colonisation of sediments by plants and invertebrates.

Midges are a problem in the vicinity of some highly productive shallow lakes such as Rotorua. Their aquatic larvae are generally found in the sediments of these lakes and are a major food for benthic fish species such as the common bully (Forsyth and James 1988), and no doubt the koaro. Both these fish have been found in the benthic zones of lakes at depths ranging from 0 m down to 70–100 m. They are not confined to littoral zones, so may exert widespread control over midge larvae in lake sediments. Conversely, loss of such benthic fish populations, or a reduction in their numbers, could allow midges to proliferate. The maintenance of a healthy benthic native fish fauna in lakes may therefore be important for this aspect of lake management. Hypolimnetic deoxygenation restricts the colonisation of the demersal zone by fish (Rowe 1994), which may reduce benthic fish populations, leading to reduced predation pressure and the proliferation of midges.

Tree planting around lake edges is often used to reduce nutrient inputs from diffuse surface and groundwater inflows. However, the location and type of riparian planting needs to take account of the wind-driven water circulation patterns in lakes. The maintenance of water quality and habitat for fish such as trout in small lakes (Lake Parkinson, for example) is highly dependent on wind mixing (Rowe 1984b). Wind also creates wave action, which limits the upper depth for macrophytes and forms an open, shallow-water habitat behind weed beds that is important for foraging by some fish. Where tall trees are planted and form a wind break, both water circulation and wave action may be reduced and water quality could decline as a result of increased stratification. Fish habitat can

be reduced in vulnerable lakes such as those protected from prevailing winds or with small fetches. Exposure of small lakes to wind therefore needs to be maintained, and the height and location of riparian strips carefully planned to avoid this.

A number of recent overseas studies have indicated that high densities of planktivorous fish can, in some lakes, reduce zooplankton. This increases algal biomass and therefore turbidity (top-down effects). Such effects are yet to be demonstrated in New Zealand lakes, although top predators such as salmonids can exert a degree of control over planktivorous fish in some lakes (Power 1992; Scavia et al. 1986). The subtle effects of this control may not be apparent until the trout populations crash and planktivorous fish can then flourish (Scavia et al. 1986).

Trout stocking therefore has the potential to influence limnetic communities and water quality in lakes with large populations of planktivorous fish. The Eastern Fish and Game Council experimented with overstocking of rainbow trout in Lake Okareka to determine maximum stocking rates before growth was affected. They noted some symptoms of top-down control (R. Pitkethley, personal communication), but concurrent sampling of water quality and planktivorous fish was insufficient to fully appreciate the significance of these results. Until such top-down processes are better understood, care needs to be taken with lake or fishery restoration activities that will increase planktivorous fish densities.

Fishery restoration generally requires an increase in the number of target fish species, but may also require reductions in other competing fish species (such as coarse fish), or increases in forage fish. In future, fishery restoration may also involve efforts to restore native fish populations that have been reduced by salmonids. For example, where trout predation on native fish species (dwarf inanga or koaro, for instance) is an issue, trout numbers can be reduced by reducing the stocking rate in stocked lakes, or by reducing the amount of, or access to, spawning habitat in inlet streams. The latter requires the construction of barriers to prevent the upstream migration of spawning trout. However, the addition of predators may be required to thin stunted populations of coarse fish. Brown trout and/or eels may serve the purpose, but this has yet to be evaluated. As a rule, species introduced to lakes for bio-control should not be able to breed there, so that if they prove to be a problem or ineffectual they will eventually die out.

Siting of recreational facilities and fish habitats

Little attention has been paid to the ecological consequences of siting structures in lakes, such as jetties, marinas, wharves, ski-lanes, launching ramps, or shoreline stabilisation works. However, the siting of certain types of structure and the cumulative effects of some facilities can be expected to have ramifications for fish life in some lakes (Beauchamp et al. 1994).

In particular the installation of marinas, wharves, launching ramps and shoreline stabilisation works may alter fish habitats around lake margins by either increasing or decreasing them. For example, in New Zealand lakes spawning habitat for common bullies would be increased by structures that provide hard surfaces and cover from predators. However, such structures may reduce spawning habitat for other species, such as smelt. Knowledge of how and when fish species

utilise littoral habitats in New Zealand lakes is still rudimentary and predicting changes is not always possible. Therefore care needs to be taken when a certain type of habitat is to be reduced to ensure it is not essential to fish and in short supply in the lake.

An example of such essential habitat is the sandy beaches in North Island lakes. Smelt spawn in shallow water (0.5–2.5 m deep) on the clean sand of such beaches during summer months (Stephens 1984). Such beaches are often scarce compared with the more steeply shelving weedy or rocky shores that characterise most lake edges, and in some lakes they may be relatively scarce. In these lakes smelt spawning could be highly dependent on just a few sandy beaches. However, such beaches are also the preferred locations for water-skiing during summer months and ski lanes are often sited near the middle of these beaches. There is therefore the potential for smelt spawning habitat to be reduced, and/or egg mortality to be greatly increased if ski-lanes are sited in all such beaches. This would not be an issue in lakes where such shallow, sandy habitat is extensive (Lakes Taupo and Rotorua, for instance), but it may be significant in lakes where sandy beaches are scarce (Lake Rotoiti), or where weed beds now cover large tracts of shallow sand. In these lakes, sandy beaches provide essential spawning habitat for smelt, and some protection from other lake uses may be required.

The types of fish habitat likely to be in short supply in lakes therefore need to be identified, mapped and then recognised in lake management plans to ensure a level of protection from other lake uses. In this respect the spawning season and spawning habitat for galaxiids, such as inanga and dwarf inanga, need to be determined in lakes where these fish occur to ensure that the use of the lakes is compatible with fish recruitment.

Marinas are constructed to provide shelter for boats in lakes, and therefore create habitat more suited to weed-dwelling fish. In New Zealand lakes these include non-salmonid exotic fish such as goldfish, catfish, koi carp, rudd and mosquitofish. Marinas can provide good nursery areas for these species, and can therefore increase the risk of pest fish becoming established, especially if they provide public launching facilities. As pest fish can be transferred from one lake to another in boat trailers and in bilge water, public launching sites in marinas increase the risk of a pest species being introduced and becoming established. This means that good public information and disinfection facilities may be needed at such sites.

PART IV: A case study

The following case study is provided to illustrate both the range of issues and the complexity involved in resolving potential problems with fish caused by anthropogenic changes in lake ecosystems. It illustrates the five stages of investigation (Table 3) typically required before sufficient information can be obtained to prepare an assessment of environmental effects (AEE) report. It also indicates that where there is little baseline information, timeframes of three to four years may be needed to fully complete investigations on fish.¹³

Table 3: Typical stages and timeframes for the resolution of fishery issues in lakes related to projects requiring AEEs and resource consents

STAGE	ACTIVITY	TIMEFRAME
1	Review of information and scoping of potential issues	1–2 months
2	Initial investigations to identify the real issues and to confirm whether or not there are environmental problems	15–18 months
3	Secondary investigations to identify whether the changes in the lake environment have contributed to the problems, and whether other factors could also be responsible	15–18 months
4	Identification of options for avoidance, remediation or restoration, including economic assessments	1–6 months
5	Settlement of issues by agreement and preparation of AEE	1–2 months
6	Resource consent hearing (conditions and appeals if agreement not reached)	1–2 years

The complexity in resolving fish issues is partly due to fish being at the top of most food webs in lakes, and therefore integrating a number of environmental changes occurring at lower trophic levels. The Lake Rotoaira case study provides some useful insights into such trophic interactions.

The long timeframe for pre-AEE investigations is because:

- fish populations are subject to seasonal variations, and these need to be taken into account in investigations
- environmental changes may take several years or more to manifest their effects up through the food web and into fish populations.

Some changes (such as those affecting growth, mortality and recruitment) may take several generations before the fish population is affected, and for long-lived species this can be up to several decades. In the Lake Rotoaira case study, a decade was needed before a decline in the fishery could be substantiated.

¹³ The views expressed in this case study are not necessarily those of Genesis Power Ltd.

For Lake Rotoaira a large amount of pre-development data were available, so a before-and-after approach for resolving issues was possible. Where baseline data are not available, and before-and-after studies are not possible, comparative studies in the potentially impacted lake and in a 'control' lake may be required. Ideally, a full BACI (Before, After, Control, Impact) approach is used, but this was not possible for Rotoaira. Nevertheless, some comparative studies did prove useful for resolving some of the issues.

The Rotoaira case study also illustrates the involvement of different management groups, each with separate responsibilities for a different aspect of lake or fishery control. In this case the owners of the hydro power station worked with the lake owners, who were also the fishery managers. This simplified management responsibilities. In other situations the lake owners and fishery managers are likely to be different agencies. In some situations fisheries management goals may conflict with fish biodiversity issues. However, in this case they were linked: issues related to the trout fishery were entwined with issues related to a native galaxiid fish, and hence biodiversity. The Rotoaira case study illustrates many of these interactions and considerations, which need to be taken into account when developing an AEE for resource consents and when resolving fishery issues.

Background

Lake Rotoaira is a small (15.3 km²), relatively shallow lake (mean depth 8.9 m, maximum depth 14.0 m) just south of Lake Taupo in the North Island of New Zealand (see Figure 3). At 564 m above sea level it is 200 m higher than Lake Taupo and ideally situated for hydroelectric power generation. In the early 1970s Rotoaira was turned into a water reservoir as part of the Tongariro Power Development (TPD) scheme. In particular, flows from two rivers draining the flanks of Mt Tongariro (the Tongariro and Whanganui Rivers) were channelled into the lake, increasing its combined inlet flow from 6.9 to 57 cumecs (a 726% increase). Flows from the upper reaches of the Whanganui River were diverted into the lake via the Wairehu Canal, and water from the Tongariro River was channelled into the lake via the Poutu Canal (Figure 3).

The Poutu Stream near the southern end of the lake once drained water from the lake into the Tongariro River. However, in 1972 this stream was dammed and the dam raised the lake level by about 50 cm. A new outlet was built on the northern edge of the lake to take water from the lake to the Tongariro Hydroelectric Power Station. After the TPD was fully commissioned the greater volume of water moving through the lake was estimated to decrease the water residence time from 247 to 28 days.

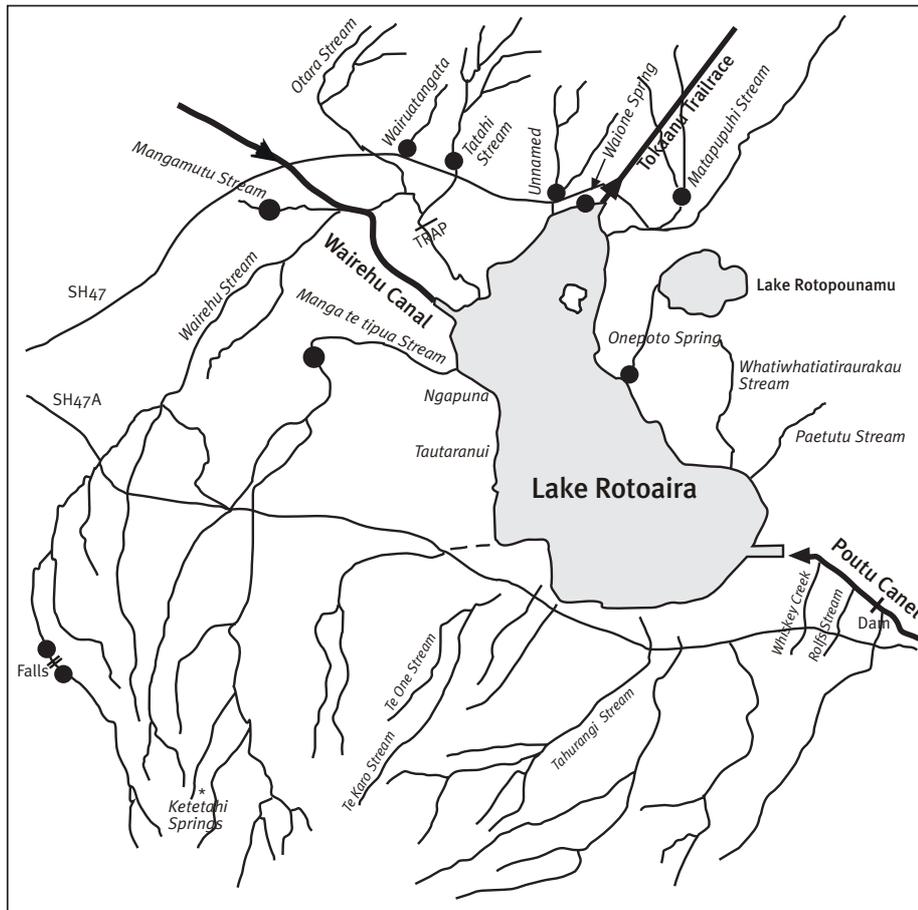


Figure 3: Map of Lake Rotoaira showing its main inlet tributaries and canals and the water outlet to the Tokaanu Power Station. The Poutu Canal now replaces the Poutu Stream. Before 1970 water flowed out of the lake via the Poutu Stream. Water now flows into the lake via the Canal.

Before construction of the TPD scheme little attention was paid to its effects on Lake Rotoaira or its fishery. For example, the main impact assessment for the TPD (Woods 1964) addressed fishery impacts on the eel and trout stocks in the Whanganui and Tongariro Rivers in some detail, but made little mention of the trout fishery in Rotoaira. Even though it was known to contain an important trout fishery, no data collection was focused on the lake. Woods (1964) suggested that the greater volume of water passing through the lake would result in clearer water and that there would be greater variations in water level associated with flood flows. He speculated that these two changes would not alter biological production, but that there could be a change from larger to smaller prey species for trout. In conclusion, he proposed that consideration be given to introducing smelt to the lake to provide a forage fish for trout. Introductions of smelt had proved highly successful in many other local lakes, so this recommendation was probably based more on this fact than on the identification of a real need for an additional prey species.

A further concern over trout, raised later in the TPD evaluation process, was that the large water flow down the Wairehu Canal and into the lake could attract large numbers of trout into it, particularly as its proposed location was close to the mouth of the Wairehu Stream. This was a major spawning tributary, up which many trout migrated to spawn. As a consequence the location of the Wairehu Canal outlet in the lake was shifted further away from the Wairehu Stream mouth, and velocity barriers were installed in the canal to stop any upstream movement of trout.

It was apparent at this time that the Department of Internal Affairs (DIA) was aware of potential problems for trout in Lake Rotoaira, particularly where they might also affect trout in Lake Taupo. Lampreys were known to inhabit the Whanganui River, and there was a concern that they could enter Rotoaira via water diverted into the lake from the river, and could then move downstream (through the power station turbines) to Taupo, where they could parasitise the trout. At this time lampreys were spreading into some of the Great Lakes of North America, where they were affecting salmonids. This generated concern that a similar scenario could occur with the TPD scheme and Taupo. To prevent this, a drum screen was installed on the Wairehu Canal to prevent the downstream movement of lampreys into Rotoaira and on to Taupo.

DIA was also aware that other potential damage to the Rotoaira trout fishery could be caused by the TPD scheme, but it had no jurisdiction over the lake and this information was not acted upon.

Twenty-five years later, in 1997, the need to renew resource consents for the TPD scheme, including Rotoaira, provided an opportunity to examine any potential adverse environmental effects of the TPD on the lake. Representatives of both the Tuwharetoa Maori Trust Board and the Lake Rotoaira Trust Board (representing the owners of Rotoaira) expressed concern over the deterioration of the trout fishery in the lake to the Electricity Corporation of New Zealand (ECNZ) (the current owner of the power station) and NIWA. A review of the information on the lake relating to its fishery was requested by the Tuwharetoa Maori Trust Board and subsequently prepared by NIWA (Rowe 1997).

Stage 1: Review of information and scoping of potential issues

This review collated historical information on the trout population gathered in the early 1970s by the Fisheries Division of the Ministry of Agriculture and Fisheries (MAF). It summarised records of trout catch rates from Rotoaira that had been published in various reports from time to time and, in order to identify changes in the lake that may have affected the trout, examined reports analysing physico-chemical and biological data on the lake. Fortunately, a relatively large amount of historical data had been collected by both MAF and the DSIR even though it was patchy and often used different methods.

The review found that although the size of angler-caught trout had not changed greatly since the 1970s, catch rates had apparently declined by as much as 70% (Rowe 1997). Such a decline, if substantiated, could indicate overfishing by anglers or a decline in trout numbers in the lake related to some change in physical habitat and/or biological production. The physico-chemical and biotic data for the lake were therefore examined to see whether any changes had

occurred which might provide a plausible explanation for the decline in trout numbers. A number of potential changes in the fish populations and in the lake environment which might affect the fish were subsequently identified (Table 4).

Table 4: Possible changes in the Lake Rotoaira ecosystem that could reduce trout production and hence angler catch rates, and their potential causes

POSSIBLE CHANGES AFFECTING TROUT NUMBERS		POTENTIAL CAUSE(S)
1	Overfishing of trout	<ul style="list-style-type: none"> • increase in anglers • increased poaching
2	Decline in limnetic trout prey (<i>Daphnia</i> or koaro)	<ul style="list-style-type: none"> • reduced 1° production • emigration of koaro • colder water • abstraction via intake
3	Decline in littoral trout prey (Odonata)	<ul style="list-style-type: none"> • changes in lake level • increased macrophyte growth
4	Decline in trout habitat in the lake	<ul style="list-style-type: none"> • increased turbidity • reduced water temperature • reduced oxygen levels • increased macrophyte growth

The RMA required ECNZ to consult with the Lake Rotoaira Trust (owners of the lake and its fishery), and ECNZ's approach was to work with the Trust to resolve any potential issues so as to minimise objections to the application for resource consents affecting the lake. Ownership of the power station changed in 1999 and Genesis Power Ltd. assumed the responsibilities of ECNZ. A consultative group comprising representatives of the Lake Rotoaira Trust and Genesis Power Ltd was set up to provide joint co-ordination of the process. At the same time, a working party of technical experts was assembled to identify the issues and scope the studies that would be needed to resolve them.

Stage 2: Initial investigations to obtain baseline data and identify the issues

A number of the initial investigations focused on the fishery. The first of these involved the collection of more comprehensive data on angler catch rates to indicate whether the fishery had declined. Because the historical data were few and based on limited creel census data (synoptic records of anglers' catches obtained by rangers), the decline in angler catch rates presented in the review could have been an artefact of sampling times or frequencies. Also, data after 1983 were lacking and could show that catch rates had recovered. Consequently, approaches were made to local anglers to see whether further information could be obtained. Approaches were also made to obtain data on the number of anglers fishing the lake (from records of licence sales), as an increase in angler numbers could result in overfishing and account for any decline in catch rates.

The spawning migration of trout in the Wairehu Stream (the main inlet stream) had been trapped in 1974. As this was the main spawning stream in the lake at the time, and most trout could be expected to use it, a repeat of this exercise in

1998 could reveal whether trout numbers had dropped significantly over the past 25 years. The data would also provide an opportunity to examine any changes in the structure and/or growth rate of the trout population. The Wairehu Stream trap was rebuilt, and data collection on the spawning trout began.

The review by Rowe (1997) had also identified koaro as once abundant in the lake and utilised by trout as a major prey, but as possibly having declined since the early 1970s. As there were few studies of this species in New Zealand lakes, and little knowledge of its life history, distribution, foods, habitats or spawning requirements, a general ecological study was initiated to provide such information for Rotoaira.

Other investigations commissioned by ECNZ and Genesis Power Ltd together with the Lake Rotoaira Trust were broader in scope and focused on the wider lake environment. However, they also collected data relevant to trout habitat. The first of these involved a lake-wide chain of thermister probes designed to determine how water temperatures in the lake changed with depth and season. Monthly surveys were carried out to determine the main limnological characteristics of the lake, including depth profiles of nutrients, turbidity, oxygen and chlorophyll a levels. Additional surveys were commissioned to:

- determine the distribution and status of macrophytes in the lake
- compare the distribution and density of benthic invertebrates present with that recorded in the 1980s
- map the lake's bathymetry.

Results of the initial investigations

The results of these preliminary investigations were reported in 1998/99, and by ruling a number of concerns out they enabled future studies to focus on the real issues. The size of the trout spawning run in 1998 was 40% less than that in 1974, providing evidence to support the hypothesis that reduced catch rates were caused by a reduced abundance of trout in the lake. Discussions with anglers who had fished the lake since the 1970s supported the creel census-based reports of high catch rates before 1970. Limit bags of 10 fish per rod per day and multiple strikes wherein several trout were hooked and landed at the same time were common before 1970, but unheard of in the 1990s. These anecdotal observations again tended to support the view that trout numbers in the lake had declined. After several public meetings with and representations to the two main tenants organisations (representing local bach holders and residents who fished the lake), a number of anglers were located who had kept extensive diaries of catches, some dating back to the 1970s.

No useful data were available on trout-angling licence sales, so any changes in angler numbers and hence the potential for overfishing could not be examined. However, this issue was resolved by data on the trout. Fishing tends to be selective for adult rather than juvenile fish, so that over-exploitation of a fish stock results in a decline in both fish abundance and size. The size of the Rotoaira trout in 1998 was greater than in 1974, indicating that over-fishing by anglers, or over-exploitation of the stock, was highly unlikely.

Scales taken from the spawning trout allowed age at capture (in years) to be determined, along with the age at which they first spawned or matured. These

data showed that growth rate was no different between 1974 and 1998, but that trout matured a year later than in 1974. The change in trout population structure – from large numbers of early-maturing trout to fewer numbers of later-maturing trout – could partially explain the 40% reduction in spawning trout in 1998. However, a nearby smaller lake (Otamangakau) contained a population of later-maturing trout and, like Rotoaira in 1998, the trout spawned mainly in one tributary stream. DOC had monitored its spawning runs over a period of years, so good data on the size of the adult trout population in the lake were available. When the size of the annual spawning run in both lakes was compared on an areal basis for 1998, the density of adult trout in Lake Otamangakau was nearly double that in Rotoaira. In summary, data on trout size, catch rates and comparative densities in lakes all pointed to a decline in trout numbers in Lake Rotoaira after 1970. As this decline coincided with the construction of the TPD, further investigations were clearly warranted.

Examination of the temperature data for the lake indicated that there had been no major change in the thermal nature of the lake. Not surprisingly, analyses of the growing season for trout (the days and hours during which suitable temperatures for trout growth occurred) showed no major changes in either its timing or duration over the years. Instead, there was a reduced incidence of water temperature stratification over summer months, post-TPD. This was probably related to the larger inflows of water into the lake. As a result, the incidence of low oxygen levels was reduced post-TPD, thus improving trout habitat in the limnetic zone. Although turbidity in the lake increased at times of flood flows, the turbidity levels were generally well below those that affect trout feeding. Changes in the species composition of the macrophytes had occurred, but not their overall distribution. Similarly, surveys of the invertebrate populations in the lake revealed little change in benthic macro-invertebrates over time, suggesting that important trout prey species such as snails were not reduced.

Studies of the forage fish populations for the trout revealed a different picture. Common bullies, which are an important trout prey in other North Island lakes, had increased greatly in the lake since the 1970s. This was probably related to their introduction some time after 1974, but their increase could also have been related to a decline in the koaro. The study on koaro indicated that although adults were still common in the lake they were present mainly on one side of the lake and not throughout the lake as occurs elsewhere. Juveniles were scarce throughout the lake and in its tributary streams.

Studies in South Island lakes carried out in 1999 provided comparative data on the abundance of adult koaro in the littoral zones. These data indicated that koaro abundance in Rotoaira was well below what would be expected. Anecdotal reports of koaro abundance in the 1950s indicated they were relatively common in the lake at this time, but had since declined. For example, it was known that large numbers of juvenile migrant koaro used to climb the near-vertical concrete wall of the first velocity barrier on the Wairehu Canal (McDowall 1990). Examination of this canal in 1998 and 1999 indicated that koaro no longer climbed the wall and none were present in the canal above it, indicating that the numbers of juvenile migrant koaro in the lake had declined. An increase in trout predation was not a plausible explanation as trout numbers had also declined.

However, the large water inflows into the lake via the canals may have been partly responsible. They would have attracted large numbers of juvenile migrants

(whitebait) into the canals each year, and these fish would probably have all eventually perished as the canals provided poor fish habitat. Concerns over the decline of the lacustrine stock of koaro were related to its potential importance as a trout food, but it is also a threatened native fish species. Lacustrine koaro were once abundant in most central North Island lakes, but are now rare in nearly all of them. The koaro in Lake Rotoaira were also valued because historically they were harvested by Maori, for whom they have a special significance.

Stage 3: Secondary investigations to refine the main issues and identify the role of the TPD

The initial investigations allowed the main issues in Lake Rotoaira to be defined. It was becoming clearer that the trout population had declined, and that this was caused by some environmental change rather than by overfishing. However, several questions about the trout population remained. Inter-annual variation in spawning runs of rainbow trout can be large, so the 40% decline in 1998 may have been caused by a poor year rather than by a more general long-term decline. Furthermore, some of this decline in trout numbers in the Wairehu Stream could be related to the later age of maturation of the trout stock. More data were therefore needed to confirm the preliminary observations. It was decided to monitor the spawning trout for a further year and to examine the angler diary data in greater detail, as this provided a potentially less biased picture of changes in trout catch rates, which would complement the creel census data. These analyses were expected to help clarify the picture of trout decline in the lake.

Because a decline in trout numbers in the lake could be caused by either a reduction in recruitment, or an increase in natural mortality, or by emigration, it was also now time to examine the trout-spawning streams in the lake and factors that might increase the natural mortality or emigration of trout. An investigation of the streams was also required to determine any blockages that might have reduced trout access to spawning grounds and to confirm that most trout spawned in the Wairehu Stream, therefore justifying its use for monitoring the adult trout population in the lake.

The analysis of the physico-chemical data confirmed that physical habitat for trout in the lake had not decreased, so concerns over a reduction in water quality related to reduced water temperature, lower summer oxygen levels, or increased turbidity were all discounted. Similarly, concerns over macrophyte growth and loss of open-water habitat were ruled out. The physico-chemical data also indicated that either reduced limnetic production, or reductions in benthic invertebrates providing a food source for trout, was unlikely. The trout data indicated that there had been no change in growth rate post-TPD, confirming that the overall food supply for trout had not been reduced.

However, it was clear that there had been some major changes in the forage fish populations of the lake that could have affected trout population dynamics. A decline in consumption of koaro by trout could result in a later age of maturation, so an analysis of trout diet was required to identify the role of koaro for trout feeding, growth and age at maturation.

The koaro was also important because of its biodiversity and value to Maori, so the decline in its population required further investigation anyway. In particular, potential causes needed to be identified. The investigation therefore focused on

the inlet canals to determine whether koaro migrants that entered the canals could survive in them.

It was possible that some koaro larvae were being abstracted from the lake via the outlet flow. This would only occur if internal circulation patterns concentrated larvae near the intake. Examining this possibility required data and assessment of water circulation patterns within the lake, along with measurements of larval concentrations within the abstracted water. Knowledge of water circulation patterns was needed to determine sediment transport around the lake.

Results of the secondary investigations relating to trout

The trout-trapping data for 1999 revealed that the spawning population was still lower than in 1974. Analysis of these data confirmed the preliminary results on trout growth rate, size and age at maturation, and reinforced the contention that trout growth had not changed, but that the trout were now larger than in 1974 because they matured at an older age. Analysis of the angler diary data corroborated the decline in catch rates inferred from the creel census data. It also provided a more accurate temporal picture of the decline. A rapid drop from 0.9 to 0.4 fish per rod per hour occurred over the three years between 1972 and 1975, indicating a near 60% decline in catch rates compared with the 70% drop estimated from the creel census data. This was followed by a more gradual decline over the next decade (1978–88) to 0.3 fish per rod per hour. Catch rates over the following decade (1998–98) varied, but were relatively stable at around 0.4 fish per rod per hour.

The initial rapid decline in trout catch rates occurred in the three years following the completion of the Poutu Dam. A three-year period of decline is consistent with the average lifespan of rainbow trout in Rotoaira (it would take about three years for most fish to die out and not be replaced). The more gradual decline over the next decade was more consistent with a change in trout population dynamics, such as the change from a relatively early-maturing population to a late-maturing one.

Examination of the streams draining into Rotoaira revealed that there was a potential blockage to trout spawning in the Wairehu Stream. This was created by a fish ladder under State Highway 47A (owned by Transit NZ Ltd.) which sometimes became blocked with debris. However, historical reports indicated that while this may have prevented trout access to a large area of spawning habitat in the Wairehu Stream in some years, it had been periodically cleared and was working in most years. It could not account for the low trout population size and catch rate in 1998.

The other major stream entering the lake (i.e., the Manga te tipua Stream) was not utilised by many trout for spawning because its water quality was poor, through being affected by geothermal water from hot springs further up the catchment. All other inlet streams were relatively small, and if access to them was lost they would not provide sufficient spawning habitat to account for the large decline in trout numbers in Rotoaira in the early 1970s.

This left the single outlet stream to the lake that had been dammed in 1972. No historical data were available to indicate whether trout used this stream for spawning. However, an examination of old photographs, newspaper articles,

correspondence by officers of the Department of Internal Affairs, and interviews with long-time residents all indicated that it not only provided a major spawning ground for trout in the lake, but was also an important rearing area for juvenile trout. The construction of the Poutu Dam on this stream reversed its flow, deepened the channel, and prevented adult trout from accessing all the areas identified on the old aerial photographs as providing good spawning habitat. The loss of both the large spawning population that utilised this outlet stream and, more significantly, the extensive rearing habitat for juvenile trout produced by it, would easily account for the 60–70% reduction in trout numbers that occurred in the lake between 1972 and 1975.

Although the damming of the Poutu Stream would have reduced trout numbers in the lake, it was also possible that many juvenile trout entering the lake from the Wairehu Stream now emigrated from the lake via the nearby outlet (to the power station) and so exacerbated the loss of recruits from the Poutu Stream. However, this was considered unlikely: although many juveniles were observed around the entrance to the inlet embayment, they were feeding there and could easily resist entrainment in the flow through the embayment. Discussions with staff who periodically cleared the screens covering the water intake at the far end of the embayment revealed that whereas some goldfish were occasionally caught up in the weed on the screens, trout were not.

The study of the diet of rainbow trout in 1974 provided a good picture of the main prey species utilised by trout in Rotoaira at that time. It was clear that snails were the main prey over summer, with other littoral invertebrates such as caddis (mayfly larvae) and Odonata (dragonfly larvae) supplementing this. During the colder winter months, when littoral invertebrate prey were less abundant, the trout preyed mainly on the waterflea (*Daphnia*) and on koaro. Goldfish were also a significant prey species, but only during autumn. Overall, snails were the main prey by volume, with water fleas and koaro the next most important species. *Daphnia* were a staple food for most young trout (100–400 mm long), with snails and koaro the main fare for the larger, older trout (over 500 mm). Surprisingly, no common bullies were recorded in any of the 1200 trout examined. As they are readily eaten by trout, this could only indicate that their abundance in Rotoaira in 1974 was very low, or that they were not present at that time.

The analysis of trout diet and prey species indicated that in 1974 trout production in this lake was based on both the littoral (shore-based) and limnetic (open-water) food webs, with the latter being most important in winter, especially for juvenile trout (which depend on *Daphnia*) and for the largest trout (which prey heavily on koaro). Compared with other trout lakes, Rotoaira had a more complex and diverse food web, with summer and winter as well as littoral and pelagic components, and a range of different-sized prey species catering for the different sizes of trout. This diversity could be expected to buffer the effects on trout of a change in any one of the main prey species. For example, a decline in koaro would not be expected to affect trout growth rates, especially if common bullies increased in abundance. However, changes in the composition of the diet could well affect trout population dynamics. Adult koaro contain large amounts of fat, which are important for the early maturation of fish. It is possible that the replacement of a relatively fat-rich prey such as koaro, with a lean one such as common bullies, would lead to a later age of maturation in trout, and thereby alter the dynamics of the population. Unfortunately further data to test this hypothesis could not be obtained.

Results of the secondary investigations relating to koaro

The investigations on the decline of koaro indicated that whereas large numbers of shoaling juveniles (whitebait) could be expected to migrate into both the Poutu and Wairehu Canals, few would survive there for long. It was suggested that the canals could draw large numbers of juveniles out of the lake each year, thereby reducing the numbers of adult fish present. However, the investigations into water circulation patterns within the lake, and the possibility of entrainment of larval fish into the outlet, suggested another possible mechanism.

The large volumes of water entering the lake from the two canals (amounting to over a 700% increase in flow) were found to have a marked influence on water movement in the lake. In essence, the inflow from the Poutu Canal generated a large circular surface gyre, which transported surface water in a clockwise fashion around the main southern basin of the lake. Water from the Wairehu Canal also generated a gyre, and this moved in an anticlockwise direction around the northern basin of the lake. Water velocities in these large lake-wide gyres were relatively high at times, and it was apparent that they interacted with more complex sub-surface currents. Surface water currents produced by wind action could presumably override these effects, so the circular gyres probably occurred mainly during periods of calm weather and at times when water flowed down both canals and out through the outlet to the power station. The net result would be a series of within-lake currents that could readily transport larval fish and plankton in surface waters towards the outlet, where they would be entrained in the outlet flow and carried out of the lake. Measurements of plankton and fish larvae in water flowing through the outlet indicated that whereas the larvae of common bully were entrained during both the day and night, koaro larvae were only entrained at night. The combination of water circulation patterns in the lake, entrainment in outlet flows, and the mainly diurnal pattern of power generation whereby most generation occurred at night, could well have resulted in high numbers of koaro larvae being drawn out of the lake.

The conclusion reached was that two artificial hydraulic processes were drawing an unknown number of koaro out of the lake, although the extent of these losses and the relative importance of the two processes were unknown. Other processes could also be involved in the decline of koaro. Koaro populations in lakes have declined historically because of increased predation by trout and displacement after the introduction of smelt. Reduced access to spawning streams or destruction of spawning habitat in streams could also lead to a reduction of koaro in the lake. These factors would need to be ruled out before accepting hydraulic processes as the likely cause of the decline.

Increased predation by trout and the introduction of smelt were quickly ruled out in Rotoaira because the trout population had declined and no smelt were present. However, reduced access to streams for spawning remained a possibility. There used to be large migrations of adult koaro into and out of the sub-surface springs in Rotoaira during summer. The study of koaro confirmed that these migrations of adult fish coincided with spawning, so blocked access to the springs could reduce spawning migrations and hence the recruitment of koaro. This remains a possibility.

Stage 4: Identification of remediation and restoration options

The investigations into the ecology and fisheries of Lake Rotoaira revealed that there were no significant changes to the lake environment that could affect fish, but that the populations of rainbow trout and koaro had declined while common bullies had increased. Although some debate over the exact mechanisms and extent of decline for trout and koaro was possible, it was generally accepted that the construction and operation of the TPD was responsible for these changes. Common bullies may have been introduced to the lake after 1974, or may have increased as koaro declined.

The RMA requires that the adverse environmental effects of an activity be appropriately avoided, remedied or mitigated. Via the consultation process with Genesis Power Ltd., the Lake Rotoaira Trust identified a number of long-term objectives for Lake Rotoaira, relating to its range of ecological, cultural and economic values. In relation to the lakes's fisheries, two primary goals for restoration were to increase trout numbers in the lake, and to restore the pelagic fish food base for the trout. The third goal was to remediate the decline of koaro.

Removal of the dam on the Poutu Stream was not considered by Genesis Power Ltd. as an option, as it would significantly impact the viability of the entire power scheme, but in particular the Tokaanu Power Station. A range of other possible options for increasing trout numbers in the lake were:

- stocking the lake with hatchery trout each year in lieu of the lost natural recruitment from the Poutu Stream
- creating new spawning and rearing areas for trout in artificial channels, which could be built alongside the Wairehu Canal and could use the high-quality water from the canal to provide the necessary flow
- improving spawning habitat for trout in the new Poutu Canal
- diverting a large stream below the Poutu Dam into the Poutu Canal so trout from Rotoaira would have access to spawning habitat in its upper reaches
- improving spawning habitat for trout in small streams around the lake
- diverting water from the Wairehu Canal into the Mangatetipua Stream, to dilute the effects of geothermal water and increase trout spawning habitat in it.

The options for restoring pelagic fish as a food source for trout included:

- introducing and establishing smelt in the lake
- closing the Tokaanu water intake at times when koaro larvae were abundant
- using lights or bubble curtains to prevent the entrainment of larvae into the intake
- preventing the upstream migrations of koaro juveniles into the canals through the construction of sills.

The options for remediating the decline of koaro in Lake Rotoaira were:

- re-establishing the koaro population in Lake Rotopounamu by eliminating the smelt and restocking with koaro from Lake Rotoaira (water from lake Rotopounamu flows into Rotoaira, so the two lakes are hydrologically connected)
- installing structures on certain inlet streams in Lake Rotoaira to prevent trout access and so allow koaro to flourish once more in these streams.

The pros and cons of each option were explored, including a rough estimate of the likely costs and an assessment of potential benefits and risks. As the costs of any option with a reasonable chance of success were high, attention subsequently focused on the economic value of the trout fishery.

Stage 5: Economic assessments and resolution of issues for the resource consent

The assessment of the value of the fishery required an investigation of its current status and the likely revenues that could be generated by it if trout numbers were increased. This study was duly commissioned and provided a cursory assessment of values.

The Lake Rotoaira Trust and Genesis Power Ltd realised from the range of options identified, and the cursory assessment of their costs, benefits and risks, that a long term management plan for the lake was required. It was agreed that rather than identifying specific options at this stage, a management plan was needed to focus on both short-term and long-term objectives and projects that would be flexible enough to appropriately respond to increased information and the successes and failures of any options that might be implemented. The Lake Rotoaira Trust Board (representing the owners of the lake) and Genesis Power Ltd, therefore agreed to enter into a long-term formally constituted relationship and a Joint Management Group was formed to work together for the life of the resource consents (likely to be 35 years) to establish and implement a short and long-term Management Plan for the lake. The agreement sets out a number of common objectives for the lake which generally provide for its ecological, cultural and economic enhancement. The details of this agreement are confidential, but, in essence, the Lake Rotoaira Trust/Genesis Power Joint Management Group will receive annual funding from Genesis Power Ltd to implement a range of enhancement measures for the lake.

Conclusion

This case study demonstrates the complexity of issues that can confront both lake users and lake managers in resolving fishery problems in lakes. It also shows the relatively large time scales needed for the proper evaluation and resolution of issues, and the interplay and co-operation needed between developers, lake managers, fisheries managers, and even anglers. The processes used by Genesis Power Ltd (co-ordinating committees, technical focus groups, etc.) provided a useful management tool for overcoming the complexity of issues, and for eventually settling them. However, none of the achievements made in understanding the needs of the lake and its fisheries would have been possible without the active involvement and support of the Lake Rotoaira Trust,

representing the lakes owners. The RMA requirement for consultation was therefore a useful tool that, in this case, helped produce a partnership approach to problem resolution.

The preparation of the AEE for Lake Rotoaira required scientific expertise over a wide range of disciplines. Issues related to fish, water quality, plant and invertebrate communities, sediment dynamics, bathymetry, water circulation patterns, and the functioning of intakes and outlets were all involved. It is therefore an expensive and complex process. However, the end result is a much clearer understanding of the lake, its environment, and its values. This knowledge provides an invaluable stepping-stone for improved management of the lake and its fishery in the future. In this sense, the process required by the RMA can, when applied properly, result in environmental stewardship values over and beyond the needs of the resource consent.

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About the Ministry for the Environment

The Ministry for the Environment works with others to identify New Zealand's environmental problems and get action on solutions. Our focus is on the effects people's everyday activities have on the environment, so our work programmes cover both the natural world and the places where people live and work.

We advise the Government on New Zealand's environmental laws, policies, standards and guidelines, monitor how they are working in practice, and take any action needed to improve them. Through reporting on the state of our environment, we help raise community awareness and provide the information needed by decision makers. We also play our part in international action on global environmental issues.

On behalf of the Minister for the Environment, who has duties under various laws, we report on local government performance on environmental matters and on the work of the Environmental Risk Management Authority and the Energy Efficiency and Conservation Authority.

Besides the Environment Act 1986 under which it was set up, the Ministry is responsible for administering the Soil Conservation and Rivers Control Act 1941, the Resource Management Act 1991, the Ozone Layer Protection Act 1996, and the Hazardous Substances and New Organisms Act 1996.

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