ECOSYSTEM SERVICES OF LAKES

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ABSTRACT: Lakes provide a wide range of ecosystem services. We compile information on ecosystem services, focusing on those that are a result of lake ecological functioning. The key species, habitats, and processes underpinning important lake ecosystem services are discussed. The current status and trends in these services are assessed by examining recent data on lake ecological indicators. These allow inferences to be made on the current state and trends of lake ecosystem services, while also pointing to the main anthropogenic pressures that threaten these services. Many ecological processes contribute to the assimilation and sequestration of nutrients and contaminants, thereby improving water quality and habitats. However, assimilation and purification processes are vulnerable to excessive nutrient loading rates and to invasive species and the deterioration of these processes is often rapid and difficult to reverse in lakes. We provide evidence that these processes have deteriorated in many lakes due to land-use intensification in sensitive lake catchments and to the proliferation of non-indigenous invasive species. We also discuss valuations of lake ecosystem services, which show that lakes provide substantial economic benefits to various regions of New Zealand. Finally, we present a case study illustrating the complex interactions between multiple anthropogenic pressures and lake ecosystem services.

Key words: biodiversity, carbon, climate change, dam, denitrification, eel, fishing, fishery, lake, nitrogen, phosphorus, recreation, reservoir, trout, contaminants, valuation.

INTRODUCTION

The concept of ecosystem services encourages us to exercise a utilitarian perspective on lakes. The ecological structure and functioning of lakes provide a wide range of services that can be valued in conventional monetary terms. However, many values, such as scenic, cultural, and biodiversity values, are more difficult to monetise or even quantify. In this chapter, we describe a number of ecosystem services provided by lakes. While some of these will already be apparent to the reader, some will be less obvious, but nevertheless important.

Here we define lakes as closed bodies of fresh or brackish water, larger than 1 hectare in surface area. Based on this definition, New Zealand has 3820 lakes, with the eight largest each having a surface area greater than 100 km^2 (Figure 1). Most lakes drain catchments that have a land area at least as large as the lake, and usually many times larger. The morphology and climate of a lake and its catchment and the activities taking place in its catchment affect the ecological conditions of each lake and the ecosystem services it provides.

Before human arrival in New Zealand, lakes provided habitat for New Zealand freshwater biota and they performed the role of regulating water flows (e.g. through changes in volume) and water quality (e.g. by facilitating sedimentation). These 'services' were provisioned only to the ecosystems with which lakes were connected. Thus, the 'services' embodied only intrinsic ecological values. The arrival of Polynesians and then Europeans to New Zealand, and their subsequent utilisation of the catchment (e.g. vegetation clearance, farming) and lake resources (e.g. mahinga kai harvesting, sewage disposal), put pressures on the intrinsic values, functions and services of lakes and demanded new services defined by human needs and wants. Thus, the full suite of ecosystem services provided by lakes constitutes both intrinsic and human-valued services, the latter only existing due to the activities/pressures derived from human needs and desires to interact with lakes in specific ways.

In this chapter, we discuss some of the human-valued ecosystem services that New Zealand lakes provide. For some of these services we are able to present provisional monetary values, but for most ecosystem services discussed here acceptable ways of attributing monetary value to the services have not yet been developed. Nevertheless, their importance to our individual and societal well-being should not be underestimated.

This chapter is written by limnologists and lake ecologists and, thus, its focus is to bring some important ecosystem services provided by lakes to wider public attention. Lakes provide some ecosystem services that can be quantified relatively easily, even in terms of monetary contributions to the economy (e.g. commercial fishing, recreational fishing, hydroelectricity generation) and these are also addressed in this chapter. Our descriptions of these services should be seen as preliminary, as there are experts in other fields who could more adequately estimate and detail the dollar values of these industries to New Zealand. In contrast, most of this chapter focuses on the species, communities, habitats, and ecological processes that contribute less well recognised ecosystem services, though they are no less important than the recognised industries that depend on lakes.

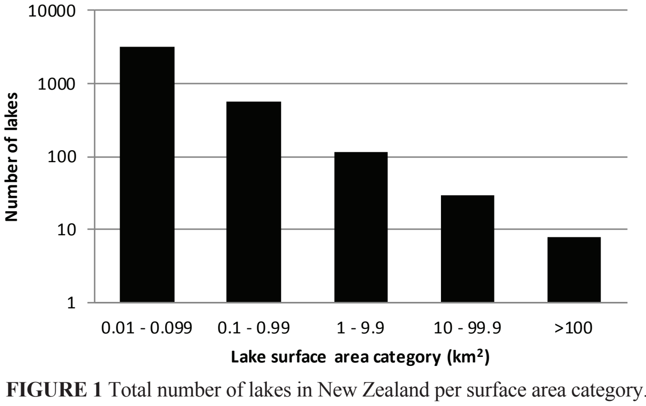

FIGURE 1 Total number of lakes in New Zealand per surface area category. (Data source: Leathwick et al. 2010).

There are many important ecosystem services that we have not dealt with in this chapter simply because we are not qualified to discuss these. These include spiritual, scenic, historical, climatic, and other services. Even in terms of ecological services, our treatment is not exhaustive, but merely a first attempt at raising awareness of some of the important ones.

As well as providing descriptions of key ecosystem services, we also assess current status, trends, and pressures affecting these services. In doing so, we employ lake monitoring data and scientific information. Most ecological monitoring and studies focus on a set of ecological factors (e.g. water quality indicators, invasive species distributions) that are not direct measures of ecosystem services, but are indicators that illustrate ecological status and trends. Thus, we discuss status and trends of lake ecosystem services via a set of commonly measured limnological and ecological indicators (Table 1). This allows us to link ecosystem services to measured indicators and ultimately to anthropogenic pressures on the ecosystem services, which can either be direct pressures (e.g. harvesting on fisheries) or indirect pressures (e.g. agricultural intensification on sediment and nutrient processing).

We have divided lake ecosystem services into four types: (1) services that are globally recognised via treaty obligations, (2) services that provide resources directly, (3) services that support and regulate useful ecosystem processes and components, and (4) services that are culturally important. Table 1 ‘maps’ these services to their key species, communities and processes, to their habitat requirements and key indicators of these, to the current status of, and trends in, the indicators and, finally, to the relevant anthropogenic pressures or drivers of change affecting the ecosystem services.

ECOSYSTEM SERVICES DERIVED FROM LAKES

Biodiversity

Biodiversity contributes indirectly to provisioning, supporting/regulating, and cultural services (MEA 2005). In addition to these contributions, biodiversity is an ecosystem attribute that New Zealand aims to preserve and enhance, due to the significance of New Zealand’s biodiversity within the global context. Therefore, New Zealand, as well as 149 other countries, is a signatory to the United Nations Convention on Biological Diversity (1992).

Ecological theory suggests high biodiversity is associated with greater efficiency of resource use within ecosystems (Gamfeldt and Hillebrand 2008). Biodiversity might also determine the resilience or maintenance of ecosystem services (Haines-Young and Potschin 2010), as systems with high biodiversity can better adapt to future conditions or are potentially more resistant to biological invasions (Taylor and Duggan 2012). Nevertheless, how exactly biodiversity influences ecosystem functioning and goods and services in aquatic systems is still poorly understood (Covitch et al. 2004; Giller et al. 2004; Gamfeldt and Hillebrand 2008; Stendera et al. 2012).

The biodiversity provided by New Zealand lakes can be measured as genetic, species, population, functional group, and food-web diversity. Although introduced alien and invasive biota might contribute to biodiversity, in this chapter we consider the ecosystem services related strictly to biodiversity as those provided only by native biodiversity.

When comparing the diversity of aquatic macroinvertebrates, fish, and submerged plants of the littoral zone in lakes of New Zealand with those of other larger land masses, our native biodiversity is considered depauperate (Kelly and McDowall 2004; de Winton and Schwarz 2004). Thirteen native fish species commonly inhabit lakes (Kelly and McDowall 2004). The number of species decreases from lowland lakes to alpine lakes due to the increasing number of barriers to fish passage with increasing distance from the sea. Macroinvertebrate diversity is much lower in lakes than in flowing waters, with 50 species reported to occur among 20 South Island lakes, with an average of 12.4 taxa per lake (Timms 1982). In contrast to fish and macroinvertebrates, species richness of native submerged plants is maximal in lakes rather than flowing waters (de Winton and Schwarz 2004) at approximately 50 species (as indicated by records on the National Institute of Water and Atmospheric Research Freshwater Biodata Information System). Surveys in 171 lakes recorded a maximum of 29 native submerged plant species per lake and an average of 6.9 species, but species richness varied across a gradient of lake trophic state (de Winton et al. 2012).

The functional diversity of native New Zealand lake ecosystems is also considered low compared with overseas, with an abundance of generalist benthic macroinvertebrates in lakes (Wissinger et al. 2006), an absence of fish herbivores and large fish benthivores (Rowe 2007), and an absence of large surface-floating plants and water lilies (de Winton and Schwarz 2004). As yet, it is unclear what this lack of functional diversity means for the ability of lakes to deliver ecosystem services or to exhibit resilience against pressures to change. Functional roles are thought to have a greater importance for ecosystem process and services than does taxonomic diversity (Garcia-Llorente et al. 2011). Services might depend on native species with complementary functions or other interactions that have co-evolved over time (Haines-Young and Potschin 2010), that taxonomic or functional diversity may not be able to fulfil.

Lakes may be considered evolutionarily isolated, insular systems (Cox and Lima 2006) that promote genetic novelty and diversity. Correspondingly, fish speciation is common for lake-locked populations of formerly diadromous fish species in New Zealand, with migratory and non-migratory ecotypes of the common bully, *Gobiomorphus cotidianus*, identified (Michel et al. 2008), and evolutionarily significant units distinguished for *Galaxias gracilis* from different founding events (Ling et al. 2001). There is also evidence for recent, rapid radiation of one charophyte (macroalgae) group within New Zealand’s glacial lakes (Casanova et al. 2007). On the other hand, the relatively low endemism of lake macrophytes (33%, M. de Winton, NIWA, unpubl. data) suggests limited genetic novelty. This is probably due to continued gene flow via wind and waterfowl transportation of propagules from Australia (Champion and Clayton 2000), with these dispersal mechanisms also potentially reducing scope for inter-lake variation in genetic character. Intra-lake genetic diversity of lake plants is also likely to be low because of a perennial nature and strongly clonal growth, although seed banks deposited in lake sediment can represent an unrealised source of genetic biodiversity (de Winton et al. 2000).

Despite the limited biodiversity in New Zealand lakes, lake shores are ‘hot spots’ of biodiversity because they are ecotones with high species turnover over short distances (Schierner et al. 1995). Higher species biodiversity related to shore zones is associated with physical complexity and the interplay of physical factors along elevational and exposure gradients, with high connectivity to other habitats, and greater levels of biological interaction (Strayer and Findlay 2010). Other unique features

TABLE 1 A selection of ecosystem services provided by lakes. Associated key species habitats and processes are identified. Indicator data show current state and trends. Pressures or drivers of change impinging on the ecosystem services are also identified. Question marks identify where there is insufficient information to make a judgment

Type of service	Ecosystem service	Species, community or process of interest	Primary habitat	Conditions favouring species, community or process of interest (indicators)	Current state	Trend	Main anthropogenic pressures on ecosystem service (drivers of change)
Fulfilment of responsibilities under global conventions	Biodiversity (e.g. International Convention on Biodiversity, Ramsar Convention)	Mainly native species, habitats and ecological functions	Most habitats	● Low–moderate nutrient enrichment ●Low–moderate turbidity ●Lack of invasive, non-indigenous species	Poor	Declining	●Invasive species ●Land use intensification/eutrophication ●Harvesting
	Climate change mitigation (Kyoto Protocol and other conventions on climate change)	Sequestration of carbon	Sediments	●Sufficient depth to inhibit sediment resuspension ●Oxic sediment for inhibition of methane production	Fair	Declining	●Land use intensification/eutrophication
Provisioning	Drinking water	N/A	Open water of some lakes	●No blue-green algae/cyanobacteria blooms ●Low contaminant levels ●Low turbidity	Poor	Declining	●Land use intensification/eutrophication
	Fisheries	Eel/tuna	Most accessible lakes	Migration pathway	Fair	Declining	●Harvesting ●Modified hydrological regime
		Salmonids	Most accessible lakes	●Cool temperature ●High dissolved oxygen ●Low–moderate nutrient enrichment ●Low–moderate turbidity ●Migration pathway	Good	Static	●Land use intensification/eutrophication ●Modified hydrological regime ●Climate change
		Flounder	Brackish, tidal lakes and lagoons	●Low–moderate nutrient enrichment ●Migration pathway (connection to sea)	Fair	?	●Land use intensification/eutrophication ●Modified hydrological regime
		Whitebait	Coastal lakes for spawning	●Spawning sites ●Migration pathway (connection to sea)	Fair	Static	●Invasive species ●Modified hydrological regime
	Waterfowl	Swans, geese, ducks	Coastal and lowland lakes	●Macrophytes or macroalgae ●Nesting sites	Good	Static	●Harvesting ●Modified hydrological regime ●Land use intensification/eutrophication ●Climate change
	Recreation and tourism	Salmonids	Most accessible lakes	See above	Good	Static	See above
		Other sports fish	Many lakes	Various requirements	Good	Improving	Various
		Swans, geese, ducks	Coastal and lowland lakes	See above	Good	Static	See above
Support and regulation	Nutrient and sediment processing	Removal of reactive nitrogen (denitrification)	Sediment and water column	●Oxic/anoxic boundary ●Organic matter	?	?	●Land use intensification/eutrophication ●Modified hydrological regime
		Removal of excess nitrogen (anammox)	Sediments and water column	●Anoxic environment	?	?	None

		Filtering of water (*Daphnia* spp.)	Water column	●Low–moderate turbidity ●Low salinity ●Low blue-green algae/cyanobacteria	Fair	Improving	●Land use intensification/eutrophication ●Modified hydrological regime
		Filtering of water (freshwater mussel, *Echyridella menziesii*)	Sediments	●Appropriate substrate ●Low–moderate turbidity ●Low–moderate salinity ●Fish hosts for larval stage ●Adequate oxygen	Fair	Static	●Land use intensification/eutrophication
		Nutrient uptake and sediment stabilisation (macrophytes)	Illuminated parts of lake beds	●Low–moderate nutrient enrichment ●Low turbidity ●Appropriate substrate ●Low–moderate water level variation	Fair	Declining	●Land use intensification/eutrophication ●Invasive species ●Modified hydrological regime
		Sedimentation out of water column (water purification)	Water column and sediments	Sufficient depth to inhibit sediment resuspension	Fair	Declining	●Land use intensification/eutrophication ●Modified hydrological regime
	Sequestration	Long-term seques-tration of nitrogen, phosphorus, sediments and contaminants	Sediments	●Sufficient depth to inhibit sediment resuspension ●Oxic surficial sediment for phosphorus retention	Fair	Declining	●Land use intensification/eutrophication
	Hydrological regulation	Flood control	All lakes	All lakes	Good	Improving	●Modified hydrological regime
		Water retention in the landscape	All lakes	All lakes	Good	Improving	●Modified hydrological regime
Cultural	Recreation and tourism	Contact recreation	Many lakes	●Low–moderate nutrient enrichment ●Low levels of contaminants ●Low levels of blue-green algae/cyanobacteria ●No or low levels of faecal microbial contaminants ●Low–moderate turbidity	Fair	Declining	●Land use intensification/eutrophication ●Invasive species
		Navigation	Many lakes	Sufficient depth	Fair	Static	●Land use intensification/eutrophication ●Modified hydrological regime
	Fisheries	Eels/tuna	Most accessible lakes	Migration pathways	Fair	Declining	●Harvesting ●Modified hydrological regime
		Crayfish/kōura	Many lakes	●Low–moderate turbidity ●High dissolved oxygen	Fair	?	●Land use intensification/eutrophication ●Modified hydrological regime
		Salmonids	Most accessible lakes	●Cool temperature ●High dissolved oxygen ●Low–moderate nutrient enrichment ●Low–moderate turbidity ●Migration pathways	Good	Static	●Land use intensification/eutrophication ●Modified hydrological regime ●Climate change
		Other sport fish	Many lakes	Various	Good	Improving	Various
	Waterfowl	Swans, geese, ducks	Coastal and lowland lakes	●Macrophytes or macroalgae ●Nesting sites	Good	Static	●Harvesting ●Modified hydrological regime ●Land use intensification/eutrophication

of lakes include high internal connectivity, transportation, and disturbance (Giller et al. 2004) that serve to transmit local impacts to the wider system.

Climate change mitigation

Lakes mitigate the effects of climate change in two main ways: carbon sequestration and hydrological buffering. It has been estimated that, on a global basis, inland waters sequester around 20% of the carbon transferred from land, reducing carbon losses from inland waters to the atmosphere by around one-third (Tranvik et al. 2009). Therefore, lakes can perform an important ecosystem service in reducing the effect of climate warming.

However, lake sediments can also produce substantial amounts of methane and while this is largely oxidised to carbon dioxide within lakes when it is produced in deep hypolimnia, when the methane escapes as bubbles, or originates from shallow sediments, it is largely lost as methane to the atmosphere (Tranvik et al. 2009). This is significant because over a one hundred year time frame methane is 25 times more more potent as a greenhouse gas than carbon dioxide (IPCC 2007). Thus, when terrestrial soils and vegetation are not removed before flooding to create new reservoirs (e.g. as was proposed for the Mokihinui Hydroelectric Reservoir, West Coast, South Island) or to enlarge existing lakes (e.g. Lake Monowai, Fiordland), large standing stocks of flooded, decaying vegetation can release substantial quantities of the greenhouse gases carbon dioxide and methane to the atmosphere (St Louis et al. 2000; Bastviken et al. 2011).

Extreme weather events, such as floods, will become more frequent in a warmer climate in New Zealand (Mullan et al. 2008). Snow and glacier melt are likely to occur earlier and will result in greater stream flows. Thus, the importance of lakes and reservoirs as hydrological buffers increases as climate change progresses, floods intensify and the contributions of melt waters increase.

Fisheries

The contribution of aquatic ecosystems to harvestable food is a significant resource for the New Zealand population and economy. The New Zealand seafood industry harvests about 600 000 tonnes from wild fisheries and aquaculture each year. The value of this harvest ranges from NZ$1.2 to $1.5 billion per annum, of which the aquaculture industry contributes about $200

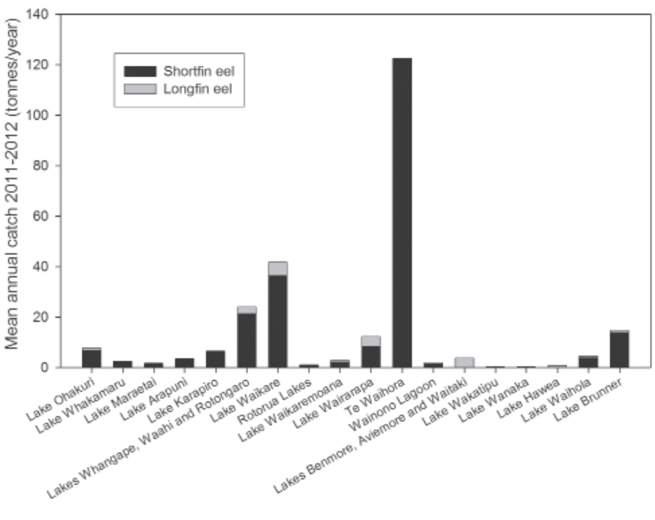

FIGURE 2 Mean commercial catch of eels in 2011 and 2012 from a number of lakes. Source: M. Beentjes, National Institute of Water and Atmospheric Research, and M. Griffiths, Ministry of Primary Industries, unpubl. data.

million dollars per annum. Seafood exports consistently rank as New Zealand's fourth or fifth largest export earner. The main freshwater contributions include the eel and flounder fisheries and salmon aquaculture, as well as some smaller-scale culturing of other freshwater fish and crayfish.

Commercial fisheries occurring in New Zealand lakes include predominantly the shortfin eel and, to a lesser extent, longfin eel fisheries, and the flounder fishery, which is confined to a few coastal water bodies. Commercial trout or salmon fishing for wild stocks is not permitted in New Zealand; however, there is a small amount of chinook salmon (*Oncorhynchus tshawytscha*) aquaculture in lakes. The whitebait fishery, although considered a recreational fishery managed by the Department of Conservation, does supply catch to the commercial market, which is sold within New Zealand and overseas. However at present, because it is managed as a recreational fishery and does not even require a recreational licence, it is very difficult to obtain catch statistics.

The eel fishery is the most significant commercial freshwater fishery. The majority of eels and eel products are exported, mainly to South-East Asia, Europe, and Canada, with the growth of annual export sales ranging from NZ$800,000 to $3.5 million between 1990 and 2004.

Eel fisheries are managed by the Ministry of Primary Industries under a quota system. Quotas are determined on a regional basis; however, recently commercial eel fishers have voluntarily reported catches for sub-regional classes, making it possible to report catch statistics from coastal, riverine, and lake habitats (M. Beentjes, National Institute of Water and Atmospheric Research and M. Griffiths, Ministry of Primary Industries, unpubl. data.). Eel catch from lakes in 2011/12 averaged 238 tonnes per year, with 92% being shortfin eels (Figure 2). Just over half of this catch was taken from a single lake, Lake Ellesmere/Te Waihora, and was exclusively shortfin eels. Other significant fisheries include Lakes Whangape, Waahi, Rotongnaro and Waaikare in the Waikato and Lake Brunner/Moana on the West Coast

The eel fishery associated with Lake Ellesmere/Te Waihora has been the subject of considerable study (see summary in Jellyman and Smith 2009). Following the establishment of the commercial fishery in the lake in the 1970s, harvests peaked in 1975 at over 800 tonnes per year, and then rapidly declined by 1982 to their present levels (Figure 3). There has been concern about eel growth rates and the size of emigrating eels (Jellyman 2001; Kelly and Jellyman 2007) as well as catch per unit effort data, which show that the harvestable catch of eels in the lake declined 10-fold between 1991 and 2006 (Jellyman 2012). A recent report by the Parliamentary Commissioner for the Environment has called for a moratorium on commercial eel fishing as a necessary measure to halt the decline of longfin eels in New Zealand (PCE 2013).

Small commercial flounder fisheries are present in New Zealand coastal lakes and lagoons. However, the dominant portion of the fishery is caught from marine coastal areas. The only significant documented commercial flounder fishery occurs in Lake Ellesmere/Te Waihora (Jellyman and Smith 2009), where commercial catches of yellowbelly, black, and sand flounder have occurred since 1945. High variability in catch rates has been a feature of the fishery (Figure 4), largely thought to be linked to intermittent recruitment of juveniles into Lake Ellesmere/Te Waihora due to the timing of openings of the lake to the sea (Jellyman 1992). However intra-annual variability in flounder recruitment across much broader regional scales is known to affect site recruitment in Lake Ellesmere/Te Waihora

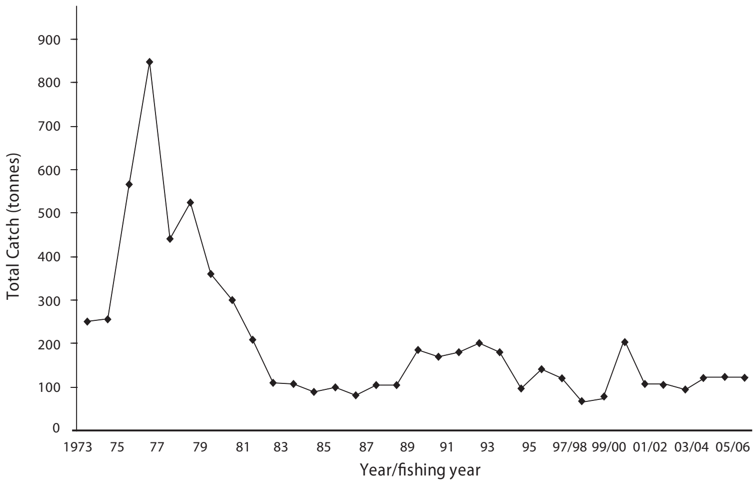

FIGURE 3 Trends in commercial eel catches from Lake Ellesmere/Te Waihora between 1973 and 2006 (Source: Jellyman and Smith 2009).

(Jellyman 2011). The commercial fishery is controlled under the 'total allowable commercial catch' quota management system administered by the Ministry of Primary Industries, and approximately eight fishers target flounder in Lake Ellesmere/Te Waihora (Jellyman and Smith 2009). Although quite variable, the annual catch is between 10 and 150 tonnes from the lake (Figure 4).

Commercial trout fishing and aquaculture are not permitted in New Zealand, and thus freshwater finfish aquaculture is almost solely confined to chinook salmon. Although some salmon farming is carried out in fresh water within net pens located in hydro canals and reservoirs, the majority of farming is in sea pens located in sheltered coastal embayments. Organic enrichment beneath salmon farms from fish faeces and uneaten food is an environmental problem and locating farms in areas with high water exchange is an attempt to mitigate this problem. As such, hydroelectric canals and reservoirs have been the predominant sites in freshwater environments. New Zealand is the world's largest producer of chinook salmon. Annual production is around 10 000 tonnes, but there are plans to increase this to 15 000 tonnes. Half the product is sold in New Zealand, with the rest going to Japan, Australia, and North America.

Other, smaller-scale aquaculture industries are based on freshwater crayfish, and both grass carp and silver carp; the carp species being cultivated for use as biological control agents of aquatic plants and phytoplankton, respectively. The cultivation of carp is conducted in ponds not connected to natural waterways in an attempt to prevent escape of cultured fish.

Recreation and tourism

Services provided by lakes in terms of recreation are numerous and include a range of activities such as boating, fishing, swimming, hiking, kayaking, and water fowl hunting. It is expected that these services are significant in terms of resource provided to the population, with several small city centres built around significant lakes, such as Rotorua (population: 56 100), Taupo (22 800), Queenstown (20 000), and Wanaka (5000). However, quantification of the usage of New Zealand lakes by some of these activities is poorly reported. We do not detail the recreational ecosystem services provided by lakes beyond those provided by recreational fishing and by recreational use of reservoirs.

Lake recreational fisheries for brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*) and chinook salmon are widespread throughout inland waters in New Zealand. Following successful introductions by acclimatisation societies over three decades from about 1875 (McDowall 1990, 1994), all three species rapidly became the basis of lively sports fisheries. Chinook salmon are well established on the east and west coasts of the South Island, rainbow trout occur throughout the central North Island and South Island high country, and brown trout are widely distributed over the whole of the South Island and the North Island south of Auckland (McDowall 1990). Smaller and more localised fisheries also occur for other introduced salmonids (such as brook trout *Salvelinus fontinalis*), and other species such as European perch (*Perca fluviatilis)* and tench (*Tinca tinca)* (McDowall 1994).

Recreational angling for salmonids is a popular activity amongst New Zealanders and also provides a major attraction for overseas visitors. New Zealand is internationally renowned for its trout fisheries, with a significant feature being the opportunity to catch large wild fish in clear waters and in highly scenic conditions. Fish and Game New Zealand (FGNZ) manage the fisheries and oversee fisheries regulations. Anglers partaking in these fisheries require recreational fisheries licences, which provide resources to FGNZ for managing and advocating for the fishery. This also provides a means by which to assess participation in the fishery, and during the last national angling survey published by FGNZ there were a total of 97 215 angler licences sold (Unwin 2009). This included more than 12 000 licences sold to visitors from overseas, predominantly trout anglers who participated in recreational fishing on their visits. The Lake Tāupo fishery is excluded from these statistics and has its own fishery management process overseen by the Department of Conservation in conjunction with Ngāti Tūwharetoa iwi. The Tāupo fishery had a further 50 000 licences sold during the 2007/08 season. The level of participation in the recreational trout fishery has ranged from an estimated one in six people for the southern South Island to approximately one in 100 for people in the Auckland/Waikato Region.

Angler effort, measured as the number of individual angler days fishing a waterbody, has been assessed by FGNZ through angler survey forms provided to a large subset of licence holders (Table 2). Lakes fisheries comprised a significant attraction for anglers as evidenced by an estimated 544 000 total angler usage days per annum.

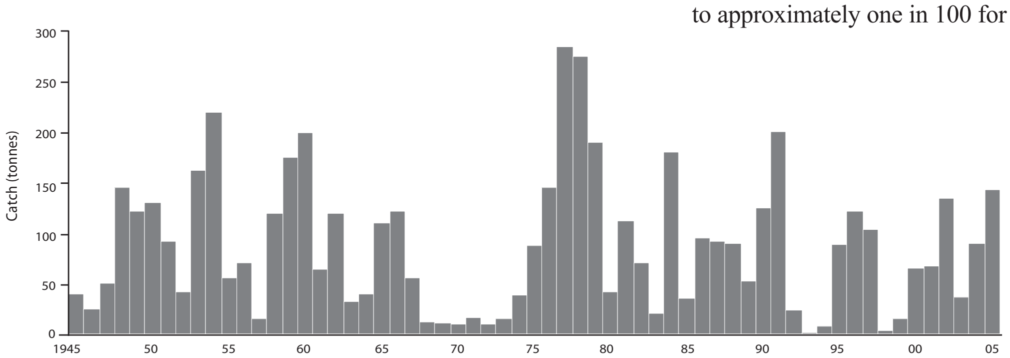

FIGURE 4 Commercial flounder catches from Lake Ellesmere/Te Waihora between 1945 and 2005 (Source: Jellyman and Smith 2009).

TABLE 2 Angler effort in New Zealand lakes and rivers as measured in the Fish and Game NZ annual angler survey in the 2007/08 angling year (Source: Unwin 2009)

Fish and Game NZ Region	Lakes (angler days × 1000)	Rivers + Lakes (angler days × 1000)	Lake fishing (% of total)
Northland	1.7 ± 0.4	3.7 ± 0.5	46%
Auckland/Waikato	9.8 ± 1.9	30.7 ± 2.4	32%
Eastern	165 ± 6.9	215.6 ± 8.6	77%
Taranaki	4.2 ± 1.0	16.9 ± 1.4	25%
Hawke's Bay	2.6 ± 0.8	36.1 ± 2.6	7%
Wellington	1.2 ± 0.4	45.1 ± 2.6	3%
Nelson/Marlborough	5.2 ± 0.8	41.1 ± 2.1	13%
West Coast	17.1 ± 1.5	51.3 ± 2.4	33%
North Canterbury	32.3 ± 2.5	200.1 ± 8.6	16%
Central South Island	128.4 ± 6.4	252.2 ± 9.0	51%
Otago	136.7 ± 7.6	224.9 ± 9.4	61%
Southland	39.6 ± 3.3	153.7 ± 6.2	26%
Total	544.0 ± 13.2	1271.4 ± 19.7	43%

This made up nearly 43% of the total national angling effort (Unwin 2003, 2009), and lakes dominated the focus of anglers for the Bay of Plenty, Otago, and Central South Island regions. It is generally considered that lakes offer a different experience for anglers than river fishing, in particular providing more family-friendly opportunities in safer non-flowing waters, as well as access to fishing from boats and wharfs.

Recreational 'whitebait' fisheries for five native species of galaxiids (*Galaxias maculatus* or inanga, *G. fasciatus* or banded kōkopu, *G.brevipinnis* or kōaro, *G. argenteus* or giant kōkopu, *G. postvectis* or shortjawed kōkopu) are prevalent throughout the country, but particularly along the west coasts of both the South and North islands (McDowall 1984, 1991). Although these fisheries occur almost exclusively in the lower reaches of rivers, as the larval whitebait migrate upstream from the sea, adult inanga, kōaro and giant kōkopu can colonise and breed in coastal lakes (Kelly and McDowall 2004). Thus a significant portion of these fisheries is sustained by lake-dwelling populations of adult fish.

There is a small and relatively undocumented recreational fishery for native longfin and shortfin eels; however, both the customary and commercial fisheries for these species comprise a far greater portion of the fishery.

Reservoirs can have subsidiary human benefits related to recreation and tourism and there are approximately 570 artificial lakes in New Zealand (Leathwick et al. 2010). Notable examples where major dams are now nationally valued recreational assets and features of the landscape include Lake Karapiro, the final hydro dam along the Waikato River, and Lake Benmore on the Waitaki River, which is the most utilised recreational trout and salmon fishery in New Zealand, next to Lake Taupo (Unwin 2009). Lake Karapiro is a rowing venue of world renown and is also valued for power boating, water skiing and swimming. Similarly, artificial Lake Ruataniwha, which feeds into Lake Benmore on the Waitaki River system, is also an important rowing venue. Although originally both natural lakes, Lakes Tekapo and Pukaki located in the Mount Cook area have been modified with dams at their outlets, but remain large tourist attractions on the South Island with an estimated 250 thousand visitors in 2001 (O'Neill and Phluger 2004).

Sediment and nutrient retention and processing

Water may reside in lakes for periods of hours (e.g. in some hydro dams) to several years (e.g. Lake Tāupo). This period of time provides an opportunity for mitigation of incoming contaminants, particularly nutrients, through a variety of physical, chemical and biological processes. Nutrients may thus be sequestered to the bottom sediments of lakes (Peters et al. 2011) or released to the atmosphere (Seitzinger et al. 2006; Tranvik et al. 2009), to some extent purifying the lake water that flows downstream. This self-purification process is the principle behind the use of some artificial lakes to protect sensitive downstream ecosystems from potentially damaging levels of nutrient, sediment or other contaminant loading (e.g. heavy metals and acids from mine tailings).

Denitrification is the transformation of nitrate into gaseous nitrous oxide and di-nitrogen and results in the permanent removal of reactive nitrogen from aquatic systems. Bruesewitz et al. (2011) found that increasing nitrogen loads (e.g. from intensive agricultural land use) resulted in increased rates of denitrification in sediments from Lake Rotorua, possibly as a result of increased presence of anoxia, which is a prerequisite for the occurrence of denitrification. However, overseas literature indicates that the fraction of the nitrogen load denitrified in lakes declines with increasing nitrogen loading rates (Seitzinger et al. 2006). Thus, it would appear that denitrification cannot be relied on to fully purge excess nitrogen loads to lakes but it may partially explain the lower nitrogen-to-phosphorus ratios (Abell et al. 2010) and potential for cyanobacterial blooms (Smith 1983) observed in eutrophic lakes. Another bacterially mediated process that converts and transfers reactive nitrogen from water to the atmosphere is known as anaerobic ammonium oxidation (i.e. anammox), which oxidises ammonium using nitrite, converting it to di-nitrogen gas. While this process may account for approximately 50% of the nitrogen gas lost from global oceans (Dalsgaard et al. 2005), as yet, there is no consensus on the importance of anammox as a mechanism for removing reactive nitrogen from temperate lakes (Burgin and Hamilton 2007).

Filter-feeding organisms feed on algae, suspended detritus and other particles in the water column and through this activity may substantially affect water clarity, nutrient concentrations and sedimentation rates. The organisms with the greatest capacities are the zooplankton and freshwater mussels. Pelagic copepods selectively feed on smaller particles, producing relatively dense fecal pellets, which can facilitate sedimentation. However, the cladoceran *Daphnia* sp. is the zooplankter generally regarded as having the greatest potential to clear water of particulate matter in the size range 1–60 mm (Burns 1998; Burns and Schallenberg 2001). Thus, *Daphnia* is considered a keystone species in lakes and has been the focus of many pelagic food web manipulations specifically designed to enhance *Daphnia* abundance to improve water clarity, particularly in shallow lakes. Furthermore, the filtering capability of *Daphnia* is also able to reduce concentrations of the human pathogen *Campylobacter jejuni* in water (Schallenberg et al. 2005).

Similarly, a study of Lake Tuakitoto (Otago, mean depth = 0.7 m) found that the filtering capacity of the freshwater mussel, *Echyridella menziesii*, population in the lake was capable of clearing the lake's water of phytoplankton every 32 hours (Ogilvie and Mitchell 1995), which was sufficient to regulate phytoplankton biomass in the lake. A similar calculation for

Lake Rotoroa (Waikato, mean depth = 2.4 m) suggested that the population present could clear the lake water in 7 days (James et al. 1998). While the capacity to clear water depends on mussel densities and lake depth, these studies suggest that mussels can contribute to water clarity and nutrient retention, particularly in shallow lakes (Phillips 2007).

Hydrological regulation

Hydroelectricity contributes around 55% of the electricity generated in New Zealand. The three largest river systems in New Zealand, the Waikato, Clutha, and Waitaki rivers, have undergone extensive hydrological modification to create reservoirs for hydroelectricity generation (Table 3). The Waikato (central North Island) and Waitaki (central South Island) rivers have an extensive network of artificial lakes created by dams. There are eight dams along the Waitaki River, two along the Clutha River (Otago), and three along the Waitaki River. In addition, the Waitaki River is fed by an artificial lake, Ruataniwha, which is linked through an extensive artificial canal network to Lakes Pukaki and Tekapo. These two lakes existed naturally but now have regulated water levels due to damming. The largest hydroelectric scheme in terms of generation (800 MW) is at Lake Manapouri in Fiordland, where water levels are regulated but maintained within their naturally occurring historical range. There are more than 25 other hydro dams of small to modest generating capacity throughout New Zealand.

There are approximately 158 reservoirs for drinking water supply throughout New Zealand (Leathwick et al. 2010) and in some cases these incorporate hydro schemes. One example is Lake Karapiro, the terminal hydroelectric reservoir on the Waikato River, which supplies drinking water for the town of Cambridge (c. 15 000 people). The city of Auckland (population of 1.4 million) has 10 water supply reservoirs supplying about 80% of its water requirements (Gibbs and Hickey 2012), and other cities such as Wellington, Nelson, and Dunedin also have numerous municipal water supply reservoirs. Some of these reservoirs are integral parts of wildlife sanctuaries and reserves (e.g. the decommissioned Karori reservoirs in Wellington).

TABLE 3 Hydro dams on three major river systems in New Zealand, ordered from upstream to downstream. Year refers to the timing of commissioning of the dam. Adapted from table 37.1 in Young et al. (2004), and table 1.1 in Collier et al. (2010)

River	Discharge ($m^3 s^{-1}$)	Dam	Year	Generation (MW)	Area (km^2)	Height (m)
Waikato	340	Aratiatia	1964	84	0.6	5
		Ohakuri	1961	112	12.6	52
		Atiamuri	1958	84	1.7	44
		Whakamaru	1956	100	7.4	56
		Maraetai	1953–62	360	4.1	87
		Waipapa	1961	51	1.6	34
		Arapuni	1929–46	197	9.4	64
		Karapiro	1947	90	7.7	52
Waitaki	356	Benmore	1965	540	75	110
		Aviemore	1968	220	29	58
		Waitaki	1935–49	105	6	37
Clutha	614	Clyde	1992	432	26	100
		Roxburgh	1956–61	320	6	76

TABLE 4 Selection of natural and artificial lakes from around New Zealand that are used for hydrological control (floods, urban stormwater) and aesthetic purposes. NI is North Island and SI is South Island

Lake	Location	Area (ha)	Type	Purpose
Pegasus	Waimakariri, North Canterbury, SI	14	Artificial	Aesthetic (housing subdivision)
Tewa	Remarkables, Queenstown, SI	5	Artificial	Aesthetic (housing subdivision)
Waikare	North Waikato, NI	2032	Natural	Flood control, lower Waikato River
Rotoroa	Hamilton City, NI	221	Natural	Urban stormwater control
Virginia	Wanganui, NI	19	Natural	Urban stormwater control
Albany lakes	Auckland, NI	<1	Artificial	Urban stormwater control
Te Ko Utu	Cambridge, NI	25	Natural	Urban stormwater control
Hood	Ashburton, Mid-Canterbury, SI	80	Artificial	Recreation and aesthetic (housing subdivision)
Lake Pupuke	Pupuke, Auckland, NI	110	Natural	Urban stormwater control
Waikato University lakes	Hamilton, NI	2.1 (3 lakes)	Artificial	Aesthetic, campus stormwater

Hydrological modifications associated with dams can have negative effects on ecology and ecosystem services by, for example, preventing fish passage along river systems and reducing habitat for wading birds that would otherwise nest on river flats (e.g. the critically endangered black stilt, *Himantopus novaezelandiae*). The diverse ecotonal gradients of shores and littoral zones are often negatively impacted by the rapid and/or large water level variations common in hydroelectric reservoirs. For example, the frequency of immersion and the duration of exposure to more extreme water levels have been shown to be major factors affecting submerged aquatic macrophyte communities in lakes (Riis and Hawes 2002). These communities are often important in terms of lake productivity, biodiversity, and sediment stabilisation (Table 1). In contrast, the nationally vulnerable North Island dabchick (*Poliocephalus rufopectus*) may benefit from an outlet structure on Lake Rotoiti (Bay of Plenty, North Island) that stabilises water levels, protecting floating nests that might be more vulnerable under a natural regime of greater water level variability. This artificial water level regulation has been strongly contested, however, including by iwi who have sought a more natural water level regime to allow for beach re-establishment and to improve access for recreational and food harvesting.

Both natural and artificial lakes have had hydrology altered for a variety of purposes intended to benefit humans. Examples include drainage to increase agricultural land area, mostly in fertile lowland locations, stormwater control to attenuate increased-intensity discharges from hard surfaces in urban areas, and flood control (e.g. Hamilton et al. 2010). Many artificial lakes have been created for a dual role of stormwater control and aesthetic purposes, and these systems may also play an important role in nutrient and contaminant processing (e.g. through sedimentation, denitrification or volatilisation), which can help protect sensitive downstream aquatic ecosystems (e.g. estuaries and harbours; Snelder and Williamson 1997). On the other hand, many natural lakes have been adversely affected by excessive nutrient loads arising from drainage water, often leading to eutrophication (Schallenberg and Sorrell 2009). Table 4 provides a list of natural and artificial lakes that have been used for a variety of purposes (e.g. stormwater control) and indirect human uses (e.g. aesthetics).

STATUS AND TRENDS OF LAKES

Habitats and species

Despite the fact that lakes contain many species that are important for subsistence, cultural, commercial, water purification, and recreational uses (Table 1), the monitoring of lakes in New Zealand has predominantly focused on measuring water quality for the purpose of assessing bathing water suitability and /or the degree of nutrient enrichment (i.e. the trophic state or Trophic Level Index – TLI).

In some lakes, other aspects of the lake ecosystems are also monitored, such as phytoplankton species composition, freshwater crayfish/kōura and freshwater mussels/kākahi (e.g. Environment Bay of Plenty), and occasionally fish (e.g. Auckland Regional Council monitoring). However, directly monitoring biological features of lakes only became widespread with the development of the Lake Submerged Plant Indicators (LakeSPI; Clayton et al. 2002), which is an index for assessing lake ecological condition based on macrophyte composition (native vs non-indigenous), macrophyte cover of the lake bed and the maximum depth limit of macrophytes.

Hamill and Verburg (2010) found that 257 lakes have had regular monitoring to assess trophic state or ecological condition using LakeSPI – less than 7% of all New Zealand lakes. The monitoring has been biased towards larger lakes and low-altitude lakes, with about 25% of lakes over 10 hectares monitored and 47% of lakes over 50 hectares. This bias reflects the perceived values and pressures on lakes, with many of the unmonitored lakes having catchments dominated by alpine or native bush.

While it captures many of the important processes driving lake ecosystems, the emphasis on the use of the TLI in lake monitoring in New Zealand limits our ability to assess changes in key species and habitats that provide ecosystem services. Maintaining species and processes of interest and the ecosystem services they provide depend additionally on the prudent management of the harvesting of populations, the minimisation of interspecific competition and the safeguarding of habitats that promote the growth and reproduction of species of interest (Table 1).

Lacustrine species of importance include species used for food gathering and which have cultural value (e.g. eel/tuna, salmonids, freshwater mussel/kākahi, waterfowl), species used for recreation (e.g. salmonids, waterfowl), species or communities that contribute to habitat integrity such as the filter feeders (e.g. *Daphnia* sp. and the freshwater mussel/kākahi, *Echyridella menziesii*), and aquatic macrophyte communities, which not only provide habitat for fish and invertebrates, but also suppress sediment resuspension and remove nutrients from the water. The maintenance and enhancement of these important biota require specific conditions including intact migration pathways, adequate dissolved oxygen concentrations (DO), cool temperatures, appropriate salinities, low to moderate levels of inorganic suspended sediment, the presence of suitable substrates, restriction of invasive non-indigenous species, etc. Many anthropogenic pressures such as the damming of rivers, anthropogenic climate change and nutrient and sediment loading to lakes from activities in the catchment negatively impact the species that provide important ecosystem services.

Of all ecosytems globally, fresh waters have the highest proportion of species threatened with extinction (MEA 2005). Based on the New Zealand Threat Classification System (Townsend et al. 2008), six native vascular plant species from lake shores are listed as 'nationally critical', 'endangered' or 'vulnerable' (de Lange et al. in press). A further two plant species are listed as 'at risk' due to declining populations, while four 'naturally uncommon' species are best known from coastal lagoon habitats that are under substantial pressure from land use intensification. Six fish species are listed as either 'declining' (giant kōkopu, kōaro, inanga, longfin eel) or 'naturally uncommon' (dune lake galaxias, Chatham Island mudfish) (see chapter on freshwater biodiversity; Allibone et al. 2010). The lake macroinvertebrates, the freshwater mussel (*Echyridella menziesii*) and crayfish (*Paranephrops planifrons*) are listed as gradually declining.

Nutrient enrichment

Nutrient enrichment negatively affects habitats and species that provide important ecosystem services (Table 1). Verburg et al. (2010) found that 44% of lakes monitored for water quality were found to be in a eutrophic or worse state of nutrient enrichment (i.e. TLI > 4) and 33% were oligotrophic or better (i.e. TLI < 3). For lakes in alpine, native, exotic forest and pasture catchments, the median TLI was microtrophic, oligotrophic, eutrophic, and eutrophic, respectively (Table 5). Much of the variation in TLI scores among lakes is explained by catchment land cover types (Figure 5).

Water quality trends were analysed using TLI data for 68 lakes for a 5-year period from 2005 to 2010. The trend analysis found that 28% of monitored lakes had deteriorated while 12% had improved. The lakes that had declined were generally in the oligotrophic category while the improving lakes were generally eutrophic. Similarly, ecological condition was also assessed using LakeSPI for 155 lakes since 2005. Thirty-three percent of lakes had 'high' or 'excellent' ecological condition (i.e. LakeSPI score >50%), while 37% of lakes had poor ecological condition (i.e. LakeSPI score <20%). Half the lakes in the pasture land use category had poor ecological condition or were not vegetated.

Eighty-seven lakes have been assessed more than once by LakeSPI, with changes in the LakeSPI index being predominantly negative (i.e. declining ecological condition) over time (Figure 6). Examining the nature of events leading to changes in scores identified lakes that had changed due to invasion impacts, the retraction or extension in

TABLE 5 Distribution of 3820 lakes in New Zealand larger than 1 hectare in each of the regression-tree water quality groups. (Defined by regression tree groups in Sorrell (2006). Source: Verburg et al. 2010)

Group	Water quality description	Number of lakes	% of lakes	Median TLI
1	Microtrophic or oligotrophic lakes in very cold climates; largely unmodified catchments	1,638	43.0	2.3
2	Oligotrophic and mesotrophic lakes with cold winters	674	17.6	3.2
3	Good water quality in mild climates and high native cover	275	7.2	3.6
4	Aupori Peninsula subset	15	0.4	3.7
5	Larger eutrophic lakes with mixed land use in catchments	278	7.3	4.2
6	Small, shallow, pastoral lakes; mild climate; mostly supertrophic	906	23.6	5.0
7	Large hypertrophic lowland and coastal lakes	34	1.0	6.2
Total /	Weighted mean TLI	3,820	100	3.4

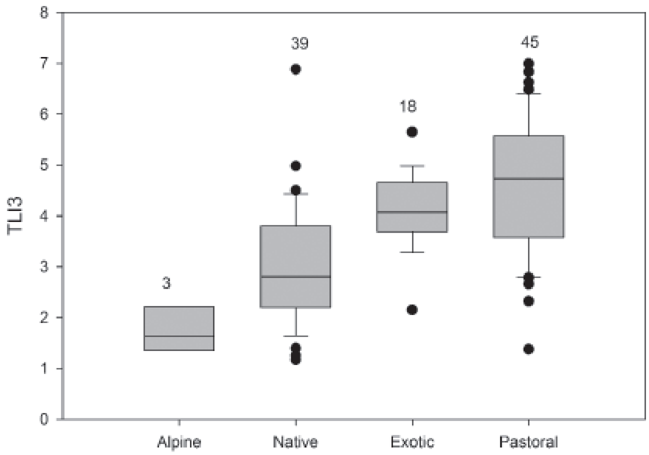

FIGURE 5 Box and whisker plots showing differences in Trophic Level Index (TLI3: based on chlorophyll a, total nitrogen and total phosphorus) in four classes of predominant catchment land cover. Numbers indicate sample size. Horizontal lines within boxes show median values, boxes show 25–75% data ranges, whiskers show 5–95% ranges, and circles outliers outside the 5–95% ranges (Source: Verburg et al. 2010).

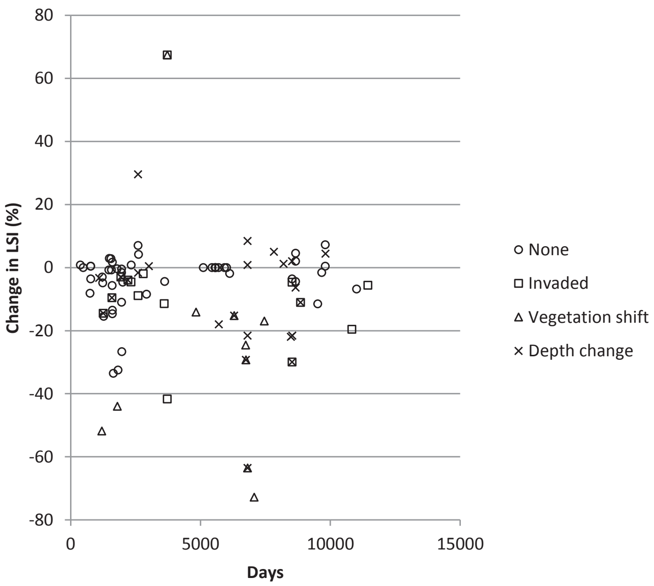

FIGURE 6 The direction and magnitude of change in LakeSPI score (LSI %) with time (days) between lake surveys, where the nature of change is identified as: Depth change (vegetation maximum depth changed by an average of ≥ 2 m; 24 lakes); invaded (recorded the presence of a more invasive weed; 15 lakes); vegetation shift (switch between vegetated and non-vegetated status at the majority of lake sites; 10 lakes); none (no obvious cause of change; 48 lakes).

vegetation depth extent, or due to regime shifts between vegetated and non-vegetated states. Generally, the latter group showed the greatest degree of change.

Barriers to migration

Eels/tuna and salmonids are key providers of ecosystem services (Table 1). Many of New Zealand's freshwater fish are migratory. While some species can maintain landlocked populations behind dams, eels must migrate to the sea to complete their life cycle. Dams impede both this migration as well as access of elvers to productive upstream habitats. With New Zealand deriving around 55% of its electricity from hydroelectricity generation, around 10% of the area of the North Island and 22% of the area of the South Island are affected by hydro dams (Jellyman 2012). It has been estimated that the presence of hydro dams restricts access of longfin eels to 36% of their potential inland habitat (Jellyman 2012). Dams built for other purposes, such as drinking and irrigation water storage, also restrict fish migration, but to a lesser extent. Historically, little attention was given to facilitating fish migration past dams, but recently more effort is being made to understand fish behaviour around dams and to facilitating eel movement across dams (Jellyman 2007). Martin et al. (2005) reported that around 3 million eels were actively 'seeded' into lakes upstream of dams. The success of such efforts to replenish upstream stocks is encouraging and downstream migrations are also being facilitated in many cases using 'trap and transfer' techniques. However, adult eel mortality due to passage through turbines has been estimated to reduce the commercial catch of eels by 5–10%, killing 5–15% of migrating longfin eels (Jellyman 2012).

There is a large salmonid stocking programme in New Zealand sponsored by fishing licences, and, salmonid stocking often compensates for the lack of recruitment caused by the presence of dams. The status of important freshwater/brackish water fisheries, including the eel and salmonid fisheries, is discussed elsewhere in this chapter.

Dissolved oxygen

Dissolved oxygen (DO) is a key indicator of lake condition and has a strong link to a number of ecosystem services (Table 1). It is essential for maintaining habitat for fish and benthic biota. To protect freshwater salmonid fish, the 7-day mean minimum DO concentration should be more than 5 milligrams per litre (Franklin 2010). Dissolved oxygen also exerts a strong control on internal nutrient cycling. For example, when DO in bottom waters drops below 2 milligrams per litre, lake sediments tend to become anoxic. Under anoxic conditions, the oxidised minerals that bind phosphorus become reduced, releasing a pulse of phosphate into pore water, where it diffuses into the water column and can stimulate phytoplankton growth (Vant 1987; Burger et al. 2007). This internal loading of phosphorus creates a positive feedback whereby high algae biomass promotes anoxic bottom waters under stratified conditions, which causes a release of phosphorus that supports further algae productivity and further deterioration in water quality. Another negative consequence of bottom water anoxia can be the release of toxic hydrogen sulphide gas and potentially ammonium into the water column at levels that may be toxic. Subsequent diffusion and mixing of these substances into the upper water column may lead to toxic effects on many biota including those providing key ecosystem services (Table 1).

Hamill and Verburg (2010) collated DO and temperature profiles for 63 lakes. During periods of stratification 81% of lakes in this dataset had average bottom-water DO concentrations of less than 5 milligrams per litre, suggesting that low DO may limit the potential fish habitat in over 80% of the lakes for which DO data exist. Furthermore, during periods of stratification 45% of the lakes in this dataset had average bottom-water DO concentrations of less than 1 milligrams per litre. Besides being inhospitable to most biota, such hypoxic bottom waters are likely to promote the release of phosphorus, ammonium and toxic hydrogen sulphide from the lake sediments. The depletion rate of oxygen in the bottom waters of lakes is positively correlated to the phytoplankton biomass of lakes (Burns 1995; Schallenberg and Burns 1999). Therefore, in many lakes, nutrient enrichment and eutrophication leads to bottom water anoxia and the loss of important habitats for biota that provide ecosystem services.

Temperature

Temperature, as a component of climate, is a factor that contributes to biogeographic patterns of species distributions in New Zealand (Leathwick et al. 2007). Therefore, it is not surprising that temperature is also an important habitat factor for some species inhabiting lakes (Table 1). New Zealand's lake biota exhibit a wide range of temperature optima and tolerances and it is important to recognise that these may vary for different life stages within particular species. Salmonids have an upper temperature threshold of around 20°C (Blair et al. 2013). This means that in many lakes, salmonids must access cooler hypolimnetic waters in summer. If bottom waters become anoxic due to excess algal productivity, then severe reductions in fish condition, and even fish kills, can result. Lake Hayes, Otago, is an example of a lake where habitat for brown trout is compromised by the combined effects of warm summer temperatures in the epilimnion and anoxia in the hypolimnion (M. Schallenberg, University of Otago, unpubl. data).

Anthropogenic climate change and hydrological modification (e.g. abstraction, diversion) are probably the main drivers of anthropogenic temperature changes in New Zealand lakes. For most lakes, climate warming will result in warming of lake waters, but in the short term, increased glacier melt could result in the cooling of lakes that receive a substantial component of their water from glaciers (Bayer et al. 2013; Hamilton et al. 2013). Hydrological alterations can either remove or add heat to lakes, depending on the waters being abstracted and/or diverted. The effects of both climate change and hydrological alteration on ecosystem services are discussed in more detail elsewhere in this chapter.

Salinity

Salinity plays a major role in structuring biodiversity in brackish ecosystems (Remane & Schlieper 1971), with different aquatic species displaying a wide range of salinity optima and tolerances. Large salinity fluctuations occur in coastal lakes and lagoons, with the main drivers being sea levels (Schallenberg et al. 2012), storms, droughts (Schallenberg et al. 2003) and artificial openings of gravel barrier bars separating lakes/lagoons from the sea (Schallenberg et al. 2010). On average, there are 74 coastal lakes and wetlands per 1000 kilometres of shoreline that are at an elevation below 1 metre above sea level (Schallenberg et al. 2003). This indicates the number of coastal freshwater and brackish systems that are vulnerable to rising salinity in the foreseeable future. Sea level around New Zealand has risen 17 centimetres in the past century (Hannah 2004) and sea level rise is projected to accelerate until at least 2100 due to anthropogenic climate change (IPCC 2007). In addition, climate change is expected to increase the frequency of extreme weather events such as storms and droughts, which will increase salinity variations in brackish and tidal lakes. Furthermore, increasing farming intensity not only results in more irrigation in drier areas, resulting in less fresh water flowing to coastal lakes/lagoons, but also seeks to minimise flooding of coastal lakes and lagoons by increasing freshwater drainage and artificially increasing connections to the sea (Schallenberg et al. 2010).

The impact of salinity on a key filter-feeding zooplankter (*Daphnia carinata*) was demonstrated by Schallenberg et al. (2003) in a tidal lake. This keystone organism, capable of clearing water of algae (Burns 1998), detritus (Levine et al. 2005) and human pathogens (Schallenberg et al. 2005), was only observed in the lake during periods of low salinity, confirming laboratory studies that showed it to be far more susceptible to salinity toxicity than two other zooplankters found in the lake. The inland migration of brackish waters over the past 100 years and its predicted acceleration for at least the next 100 years will likely reduce the lowland lake habitats available for *Daphnia* and other cladocerans to survive. Thus, their contributions to improving water quality in some coastal lakes will diminish.

The salinity tolerance threshold for *Echyridella menziesii* (freshwater mussel/kākahi) is not well known, but the larval glochidia and adult stages appear to be able to sustain periods of salinity of up to around 5 parts per thousand, while they appear intolerant of salinities above that threshold (M. Schallenberg, University of Otago, pers. obs. and C. Hickey, NIWA, Hamilton, pers. obs.). Thus, both of the important filter-feeders, *Daphnia* spp. and *E. menziesii*, are sensitive to salinity.

Turbidity, light and suspended sediment

Land use activities contribute to soil erosion. Soil particles transferred from land to water create many negative consequences for aquatic biota and ecosystems (Schallenberg et al. 2001; Rowe and Graynoth 2002). While lakes provide an important ecosystem service by allowing the sedimentation (retention) of some soil particles to the benefit of downstream aquatic ecosystems, the presence of suspended and sedimenting particles in lakes has numerous negative effects on habitats, species and ecosystem services. These include the reduction of light penetration into the lake (Hamilton et al. 2004), increasing nutrient loads (Schallenberg et al. 2010), 'smothering' aquatic plants and benthic invertebrates (Tanner et al. 1993), interfering with the mechanics of filter-feeding organisms such as *Daphnia* (Levine et al. 2005 and references therein), reducing the foraging ability of visual predators (Rowe and Dean 1998; Rowe et al. 2003), and rapidly infilling lakes (Schallenberg et al. 2012) and reservoirs, which reduces their volumes and water residence times.

The rate of sediment infilling of tidal Lake Waihola due to activities since European settlement in the lower Taieri Plain has been over 30 times greater than the average sediment infilling rate in the previous 3850 years (Schallenberg et al. 2012). Despite this rapid infilling rate, accelerating sea level rise will compensate for the infilling of the lake bed of Lake Waihola and other similar coastal lakes, but the increasing salinity will also decrease biodiversity (Schallenberg et al. 2003). However, in lakes not affected by sea level rise, sediment infilling due to soil erosion and intensifying land use will shorten the lifespan of these ecosystems, impacting on the ecosystem services that they provide.

While filter-feeding organisms like *Daphnia* sp. and *E. menziesii* can effectively remove organic particles from water, inorganic particles in high concentrations inhibit filter-feeding (Levine et al. 2005 and references therein). Thus, increasing inorganic loads could cause sudden regime shifts whereby the loss of filter-feeding organisms could further increase particle concentrations and light attenuation in the water column. Aquatic macrophytes play an important role in shallow lakes by damping turbulence, thereby reducing sediment resuspension by winds and currents. Excessive sediment loads can smother leaves and reduce light penetration to submerged macrophytes. The loss of macrophytes from lakes is a driver of sudden regime shifts in lakes from clear-water to turbid states (Scheffer 2004). Schallenberg and Sorrell (2009) showed that such regime shifts are common in shallow lakes and are related to the percentage of the catchment in either pasture or forest and to the presence of certain invasive macrophyte species, which apparently facilitate the sudden collapse of submerged macrophyte communities in lakes.

Invasive species

The presence of non-indigenous invasive species in a lake can have negative consequences on valued biota and on ecosystem services (Table 1). Schallenberg and Sorrell (2009) showed that the presence of the non-indigenous, invasive submerged macrophyte, *Egeria densa*, was related to the probability of a lake undergoing a sudden regime shift from clear-water to turbid conditions. Furthermore, the presence of benthic-feeding and herbivorous, non-indigenous fish also facilitated the loss of submerged macrophytes and, consequently, a sudden regime shift to a turbid-water state. In contrast the invasion of the Laurentian Great Lakes by zebra mussels (*Dreissina polymorpha*) resulted in enhanced grazing on phytoplankton and improved water clarity (e.g. Fahnenstiel et al. 1995). In New Zealand, the recent spread of the non-indigenous *Daphnia pulex* (Burns 2012) appears to have resulted in temporary regime shifts to clear-water states in some South Island lakes, while apparently extirpating the native *D. carinata* (M. Schallenberg, unpubl. data). Therefore, non-indigenous invasive species can enhance some ecosystem services (e.g. filter-feeding resulting in improved water clarity), but they usually do so at the expense of biodiversity values and, therefore, they may potentially reduce the ecological resilience of the lakes that they invade.

The LakeSPI index commonly assessed in New Zealand lakes includes the components 'Native Condition Index' and 'Invasive Impact Index'. LakeSPI monitoring indicates that the current ecological condition of many lakes is reduced from a pristine condition (100%: Figure 7) and that invasion by non-indigenous macrophytes is a common and serious problem in New Zealand lakes.

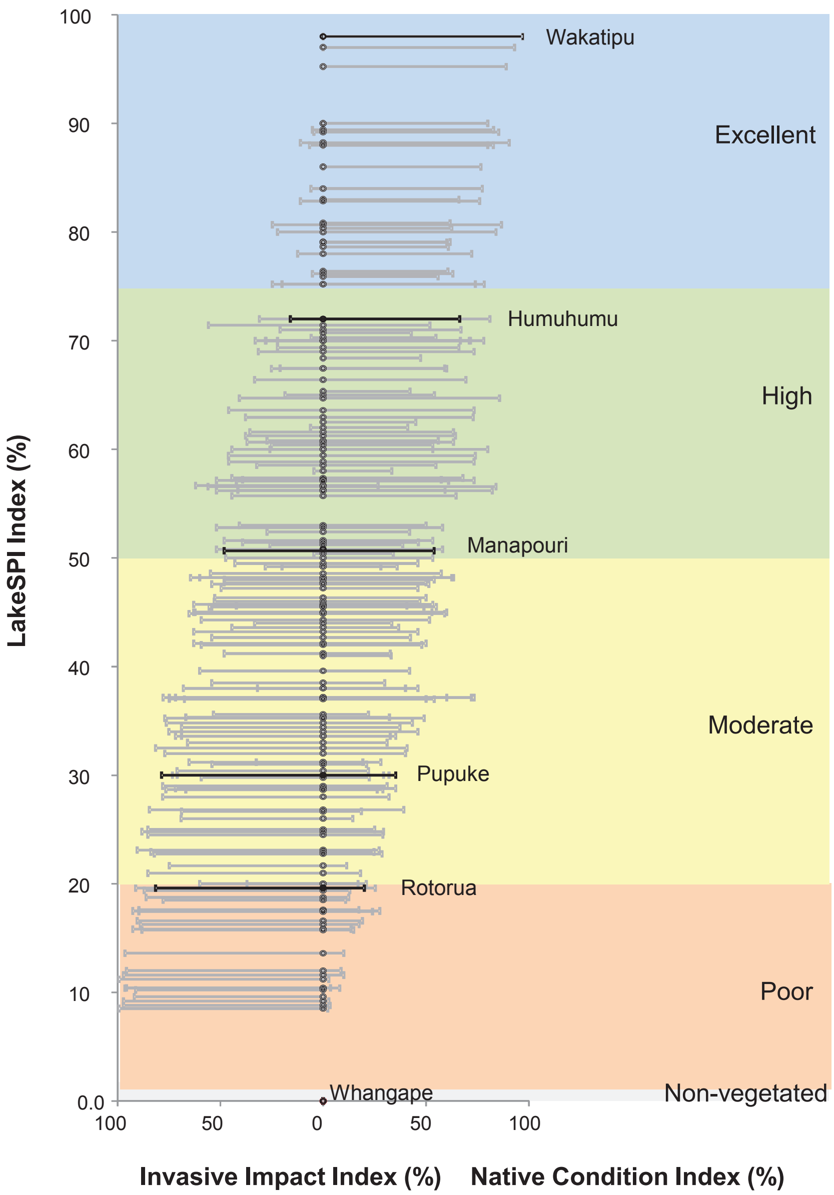

FIGURE 7 LakeSPI status for 236 lakes based on the most recent survey data. LakeSPI Index is plotted on the vertical axis (black circles), with the Native Condition Index plotted as a horizontal grey line on the right, and Invasive Impact Index on the left. Position of six benchmark lakes is indicated. A LakeSPI score of 0% represents the widespread loss of submerged plants from a lake (i.e., a non-vegetated state), which is recognised as more impaired than a lake dominated by an invasive macrophyte.

Contaminants (not including nutrients or sediments)

The presence of contaminants, such as industrial chemicals and biological pathogens, in New Zealand lake waters is an important factor restricting lake ecosystem services. The large number and diverse classes of environmental contaminants found in New Zealand fresh waters prevent a detailed examination of their impacts on ecosystem services in this chapter. The impacts generally affect the provisioning of drinking water, contact recreation, food gathering and the functioning of freshwater ecosystems (Table 1). Some studies on contaminants and their impacts on freshwater ecosystem services in New Zealand are listed in Table 6. In general, geothermally influenced waters and biota living in those waters have elevated levels of heavy metals (Turner et al. 2005; Phillips et al. 2011b) and areas with intensive agriculture have elevated levels of microbial pathogens (Davies-Colley et al. 2004; Till et al. 2008), agricultural chemicals (Turner et al. 2005; Smith and Schallenberg 2013), and antimicrobial activity (Schallenberg and Armstrong 2004) and resistance (Winkworth 2013). Point sources of contaminants to lakes include treated sewage effluents, stormwater draining urbanised areas, and industrial effluents. These can also have substantial localised and downstream impacts on freshwater ecosystems and the services they provide. To our knowledge, the monetary costs of anthropogenic contaminants (not including nutrients and sediments) to New Zealand freshwater ecosystem services have not been assessed; however, a recent attempt has been made to assess the costs attributable to toxic cyanobacterial blooms in lakes (Hamilton et al. in press).

Cyanobacteria

High densities of planktonic cyanobacteria (commonly known as blue-green algae) can impair lake ecosystem services by affecting drinking water, recreational activity and biodiversity (MfE 2009). Many cyanobacteria have physiological adaptations that allow them to aggregate, producing surface (or occasionally

TABLE 6 Effects of some contaminants on freshwater ecosystem services in New Zealand

Contaminant	State and/or trends	Study
Organochlorines and heavy metals	●Reported levels of contaminants in eel/tuna, trout, smelt, flounder, watercress, mussels/kākahi, crayfish/kōura from South Island (Canterbury) and North Island (Bay of Plenty Region) ●Risk assessment showed contaminant levels high enough to limit consumption of many species in many locations	Phillips et al. (2011a, b); Stewart et al. (2011)
Contaminants and pathogens (organochlorines, pesticides, heavy metals, etc.)	●Range of contaminants and pathogens reported in freshwater fish (eel/tuna, trout, salmon, whitebait), invertebrates (crayfish/koura, mussels/kākahi) and macrophytes (watercress)	Turner et al. (2005)
Antibiotic residues	●Intermittent antimicrobial activity observed in surface water in agricultural catchment ●Risk of spread of antibiotic resistance to other microbes/pathogens	Schallenberg and Armstrong (2004); Winkworth (2013)
Agricultural nitrification inhibitor	●Presence of agricultural nitrification inhibitor in surface waters ●Presence of the inhibitor alters microbial nitrogen cycling in an experimental wetland system	Smith and Schallenberg (2013)
Microbiological pathogens	●*Campylobacter* and human adenoviruses most likely to be contracted by contact recreation ●*Campylobacter* is widespread in surface waters and 5% of cases of campylobacteriosis may be attributable to contact recreation in polluted waters	Till et al. (2008)
Coliform bacteria	●Dairy herds crossing streams caused elevated E. coli levels in stream waters	Davies-Colley et al. (2004)
Cyanotoxins	●Increasing incidents of toxic cyanobacterial blooms affect drinking water, recreation, food gathering and fisheries	Hamilton et al. (in press)

sub-surface) blooms and wind-blown 'scums'. The cyanobacterial cell has gas vacuoles to reduce cell density, rapidly regulates (typically daily) carbohydrates to assist in buoyancy control, and often forms multi-cellular filaments and colonies, which enhance movement through the water column (Oliver et al. 2012).

Of greatest concern in drinking water, contact recreation and food gathering is that some species or strains of cyanobacteria produce highly potent neurotoxins, hepatotoxins or dermatotoxins ('cyanotoxins'). Commencing in around the year 2000, there has been an apparent rapid increase in the incidence of potentially toxic cyanobacterial blooms in New Zealand (MfE 2009). Eutrophication due to increasing nutrient inputs appears to be a major driver of increasing dominance of cyanobacteria in lakes (e.g. lowland lakes in Waikato; Hamilton et al. 2010) and Paul et al. (2012) demonstrated a positive correlation between cyanobacterial densities in lakes and the percentage of a lake's catchment that is in pasture. However, it is often difficult in studies to distinguish effects of eutrophication on cyanobacteria from effects due to climate variations (MfE 2009; Carey et al. 2012). Regional and district councils in New Zealand have statutory obligations to protect the health and well-being of their constituent populations and so, when cyanobacteria biovolumes in a lake exceed defined threshold levels (MfE 2009), the lake (or the area within a lake where the threshold biovolume exceedance occurs) may be closed to contact recreation. Similarly, alternative drinking water supplies or specific additional treatment may be required when thresholds of potentially toxic cyanobacteria in drinking water are exceeded. Kouzminov et al. (2007) estimated that it cost NZ$50,000 over 3 months during 2002/03 to adequately monitor a bloom of *Anabaena planktonica* in the Waikato River. This bloom required expensive temporary treatment measures and was a precursor to a NZ$5 million upgrade of the water treatment plant for Hamilton City (population 125 000) in order to reduce the possibility of cyanotoxins entering the domestic water supply.

The effect of cyanotoxins on lake ecosystems and biodiversity appears to be difficult to demonstrate quantitatively, but Wood et al. (2006) noted an accumulation of cyanotoxins in trout and freshwater mussels in lakes that had persistent cyanobacteria blooms. Apart from direct negative effects on drinking water, recreation and food gathering, high levels of cyanotoxins can inhibit *Daphnia* grazing on phytoplankton (Lürling 2003), showing that cyanobacterial blooms may also impair other ecosystem processes and services derived from lakes.

Water level regulation

While dams provide significant benefits for flood control and protection of human infrastructure, they can also impact downstream species and habitats. Most dams moderate peaks and troughs of river discharge. This may be an unfavourable attribute of dams because floods can have a cleansing and renewing effect by scouring excessive growths of periphyton, organic matter, and fine sediment that may otherwise degrade aquatic habitat and ecosystem services (Quinn and Raaphurst 2009). When dams are filling, extended periods of low flows can result in proliferations of periphyton, including the toxin-producing cyanobacterium *Phormidium* sp. Dry mats of *Phormidium*, exposed at low flows, have caused the deaths of dogs that have consumed them (Heath et al. 2011).

Hydroelectric and irrigation reservoirs often have large variations in water level and unnatural variations in water level can have negative impacts on the diverse flora and fauna of the shoreline and littoral zone. For example, excessive water level variation and durations of low water levels beyond 30 days are correlated with reduced macrophyte diversity (Riis and Hawes 2002). In some cases hydro dams have resulted in only small changes to the water level regimes of natural lakes, such as for Lake Coleridge. In other cases, such as at Lake Hawea (Central Otago), the increase in lake level has been substantial (c. 14 m), flooding upland forest. In this lake, the water level operational range of the hydro dam results in water level fluctuations of up to 21.9 m (Thompson and Ryder 2008). This wide range in water levels severely restricts macrophyte growth and distributions, but it has had little effect on macroinvertebrate communities. At Lake Manapouri (Southland) the operating regime of the hydroelectric scheme exceeded natural water level fluctuations and rates of level rise and fall, resulting in slumping of beaches and erosion of shorelines. As a result, the operating range has been restricted to the natural water level range and rates of lake level change are also strictly controlled to minimise damage to aquatic macrophyte communities and shorelines.

Another form of hydrological regulation is employed in relation to some intermittently closed and open lagoons and lakes (ICOLLs). Some of these coastal systems have farmland on their margins and resource consents have been granted to regulate their water levels by excavating channels across their gravel barrier bars, which sometimes isolate these systems from the sea, to drain water from the ICOLLs to the ocean. Under natural conditions the ICOLLs were likely to have lost water by seepage through the barrier bar or by naturally breaching their bars when water levels became sufficiently high to overtop them. Several prominent ICOLLs in New Zealand, including Lake Ellesmere/Te Waihora (Canterbury) and Waituna Lagoon (Southland), have their bars excavated when agricultural land surrounding the lake becomes inundated by rising water levels (in the absence of a surface outflow). Schallenberg et al. (2010) found that there was little subsequent effect on water quality of the artificial opening in Lake Ellesmere/Te Waihora but there was considerable flushing of nutrients and phytoplankton when Waituna Lagoon was opened. This difference in flushing potential is due to greater tidal flushing in the smaller Waituna Lagoon (area 10–20 km^2) than in the larger Lake Ellesmere/Te Waihora (area 160–200 km^2). Under these circumstances and with rapid intensification of land use (mostly for dairy) in the Waituna Lagoon catchment, it is possible that openings may be able to provide some degree of protection from eutrophication by flushing nutrients and organic matter from both the water column and the bottom sediments of the lagoon. However, this type of water level regulation and flushing/mixing with seawater also has important implications for the macrophyte communities in such lakes because macrophyte distributions can be limited by water level operational ranges and macrophyte germination and growth may be limited by intrusions of saline water (Schallenberg and Tyrrell 2006).

DRIVERS OF CHANGE IN LAKES

Land use intensification and eutrophication

Nutrient enrichment is an anthropogenic pressure on lakes that impacts numerous ecosystem services (Table 1) and increasing nutrient loads are one of the most pervasive drivers of change in lake ecosystems (PCE 2012). However, the response of lake biota to increasing nutrient loads is mediated by complex interactions. Pristine lakes are often resilient to initial changes in nutrient loads, as changes in ecological condition are often not immediately apparent. This buffering capacity occurs because of their volume (e.g. diluting inputs), biogeochemical processes (e.g. denitrification), and biological interactions. In shallow lakes the aquatic macrophyte community plays a fundamental role in this resilience.

Positive ecological feedbacks create an 'inertia' that tends to maintain shallow lakes in either a macrophyte-dominated clear-water state or a de-vegetated, turbid state (Schallenberg and Sorrell 2009). However, these feedbacks can be broken by excessive pressures. For example, Lake Ellesmere/Te Waihora has not recovered from a loss of macrophytes as a result of a violent storm in 1968 because the lake has excessive nutrient loads and concentrations, which favour phytoplankton dominance (Schallenberg et al. 2010).

A shift from a clear to turbid state can be triggered by a number of factors including land use change, dominance of herbivorous (e.g. rudd, koi carp) and benthic-feeding fish (e.g. catfish), grazing of waterfowl, or storms. Schallenberg and Sorrell (2009) found that the shallow lakes are more likely to be in a turbid, phytoplankton-dominated state when the percentage of catchment in pasture is above 30% and especially once it increases above 70% (their study also found that the presence of invasive macrophytes and pest fish also stimulated such regime shifts).

Thus, the excessive loading of nitrogen, phosphorus, and sediment associated with land disturbance and land-use intensification can stimulate a series of non-linear responses in lake biota, break negative feedbacks, cause regime shifts, and create new feedbacks, which make it difficult to restore the system to its original state or condition (Scheffer 2004). The macrophyte community is a key factor in this dynamic, absorbing nutrient loads, usually until a threshold is reached. With the collapse of macrophyte beds, nutrients stored in plant material and in the sediments can be released into the water column fuelling a high biomass of macroalgae or phytoplankton, establishing a new set of feedbacks and ultimately resulting in inertia to change when the new regime is established (Verburg et al. 2012). As algae proliferate, more die, eventually decomposing on the lake bottom and causing the sediments to become anoxic. The roots of macrophytes can help oxygenate the sediments, so a reduction in macrophyte cover facilitates sediment anoxia and the release of dissolved phosphorus and ammonium, which can further stimulate algae growth. Strongly anoxic sediments may reduce denitrification rates by inhibiting nitrification, thus reducing the effectiveness of denitrification in removing reactive nitrogen from lakes.

Thus, macrophytes promote conditions allowing clear water (e.g. stabilisation of the lake bed, oxygenation of the sediments) creating a feedback that favours more macrophyte growth, while phytoplankton and macroalgae cause turbid water, creating a feedback that promotes further algal proliferation. Excessive nutrient supply reduces the ability of macrophyte communities to recover from disturbance (e.g. a storm event or lagoon opening). A sign that the macrophyte community is vulnerable to nutrient loading may be increased year-to-year variability in macrophyte biomass or cover. The shore zones occupied by macrophytes are biodiversity hotspots in lakes and impacts on these zones from land use practices and water level variations have a disproportionally large effect on biodiversity, and probable flow-on effects on ecosystem services.

Invasive species

Biological invasion is a key anthropogenic change to ecosystems, affecting the services they provide (MEA 2005; Table 1), with fresh waters considered ecosystems among the most impacted by species invasions in the world (Ricciardi and MacIsaac 2011). It has been suggested that biological invasions can be facilitated by other forms of environmental degradation (Didham et al. 2005; Strayer 2010).

Invasive species are almost exclusively non-native, and are usually defined as those that have negative economic, environmental, and/or ecological impacts when introduced. It is ironic that most invasive plants and fish were introduced to New Zealand lakes to provide resources or values (i.e. ecosystem services) that were deemed by settlers to be missing or under-represented amongst the native fauna and flora. So it was that ornamental plants (e.g. water lilies), forage grasses (e.g. *Glyceria maxima*), and food crops (water cress) were purposely established in and around lakes by acclimatisation societies. Likewise, widespread lake introductions of sports fish (e.g. salmonids) or 'coarse' fish (e.g. rudd) were made for food and angling opportunities and ornamental or aquarium stock (e.g. goldfish) were subsequently liberated. Other purposeful introductions were made misguidedly for mosquito control (e.g. mosquito fish), for improving habitat for fish and wildfowl (e.g. 'oxygen weeds'), or erosion control (e.g. willows). Rarely have the benefits from these introductions been compared with the unanticipated costs to ecosystems that have eventuated.

As a result of the introduction of salmonids to New Zealand lakes, several commonly occurring lentic fish species, such as kōaro and inanga, have been drastically reduced in their

TABLE 7 Alien submerged plants and fish recorded from lake surveys that are designated as Notifiable Organisms (NO), Unwanted Organisms (UO), included in the initiatives National Interest Pest Response (NIPR) or National Pest Plant Accord (NPPA), or managed under Regional Pest Management Strategies (RPMS). Scores are listed from the Aquatic Weed Risk Assessment Model (AWRAM) or Fish Risk Assessment Model (FRAM)

Species	NO	UO	NIPR	NPPA	RPMS	AWRAM	FRAM
Ceratophyllum demersum (hornwort)		✓	✓*	✓	✓	67	
Egeria densa (oxygen weed)		✓		✓	✓	64	
Hydrilla verticillata (oxygen weed)	✓	✓	✓	✓	✓	74	
Lagarosiphon major (oxygen weed)		✓		✓	✓	60	
Potamogeton crispus (curled pondweed)					✓	44	
Ranunculus trichophyllus (water buttercup)					✓	42	
Utricularia gibba (bladderwort)		✓		✓	✓	54	
Vallisneria australis (eelgrass)	✓	✓		✓	✓	51	
Ameiurus nebulosus (brown bullhead catfish)					✓		41
Carassius auratus (goldfish)					✓		31
Cyprinus carpio (koi carp)		✓			✓		45
Gambusia affinis (mosquito fish)		✓			✓		40
Oncorhynchus mykiss (rainbow trout)							36
Perca fluviatilis (perch)					✓		46
Salmo trutta (brown trout)							39
Scardinius erythrophthalmus (rudd)					✓		36
Tinca tinca (tench)					✓		31

*South Island only

abundances in lakes (McDowall 1987; Howard Williams and Kelly 2003). These species would have dominated the pelagic open-water foodwebs of lakes and now remain only as diminished, remnant populations confined to refugia such as littoral vegetation. It is anticipated that the effects of salmonids on lake invertebrate communities is less pronounced (Wissinger et al. 2006), although less is known about possible effects on zooplankton, which can be highly impacted by fish in New Zealand lakes (Jeppesen et al. 1997), and which, themselves, provide ecosystem services discussed elsewhere in this chapter.

Currently 15% of the submerged plant species recorded during lake vegetation surveys are regarded as 'pests' based on legal definitions or inclusion under regional pest management strategies (Table 7). Most of the alien fish that have been introduced to lakes also have a pest management status. Invasive risk of species can be identified using assessment

TABLE 8 Cases of impacts of invasive, non-indigenous species on ecosystem services of New Zealand lakes. For key species, see Table 7

Invasive species	Impact
Macrophytes	●Weed drift impinging on hydro-station intake screens has caused shut-downs costing millions of dollars in repairs and lost generation (Closs et al. 2004), and has prompted large investments (NZ$3.2 million in one case) to retrofit mechanical weed clearing systems to screens. ●When native vegetation in the littoral zone of lakes is invaded by hornwort or 'oxygen weed' species it results in mostly monospecific beds of low floral diversity. Moreover, as these invading species do not produce seed, loss of viable seed banks in lake sediments over time results in a loss of stored genetic diversity and reduced potential for revegetation following disturbance (de Winton and Clayton 1996). ●A programme of invasive macrophyte management was undertaken in Lake Karapiro using the herbicide diquat to mitigate potential impacts on the 2010 World Rowing Championships (Matheson et al. 2010). Treatment of between 50 and 100 hectares per annum of surface-reaching weed beds to reduce sources of drift was estimated at a direct cost (herbicide and application only) of c. NZ$600,000. Co-benefits from the programme were reported for hydropower generation.
Salmonids	Lake-locked populations of kōaro (*Galaxias brevipinnis*) once provided a significant fishery for Māori in a number of lakes until they were decimated by predation from introduced trout (NIWA 2013).
Pest fish	Sediment and nutrient retention and processing have been altered by the introduction of alien fish, often illegally, for angling opportunities. The negative association between water clarity in North Island lakes and the presence of rudd, tench, perch, catfish, gold fish and/or koi carp indicated that water clarity was reduced by as much as one-third to one-half in lakes containing these fish compared with those without. The largest impacts occurred where multiple pest fish representing different functional groups (e.g. planktivorous, benthivorous, herbivorous) were present (Rowe 2007).
Daphnia dentifera	The introduction of an alien daphnia (*D. dentifera*) to a lake added a more efficient filter feeder of phytoplankton than was represented in the native zooplankton. This resulted in reductions in phytoplankton biomass and water clarity (Balvert et al. 2009). Such 'top down', grazer-mediated control of problematic phytoplankton could be a useful water quality management tool, but flow-on effects from these alien zooplankters to other biota are likely (Duggan et al. 2012) with possible unintentional consequences for ecosystem function.
Egeria densa, rudd, tench, catfish, koi carp	Significant correlations have been found between dominance by the macrophyte *Egeria densa,*, the presence of the fish species rudd, tench, catfish, koi carp, and sudden regime shifts in shallow lakes to a turbid state (Champion 2002; Schallenberg and Sorrell 2009)
Mosquito fish	The apparent local extirpation of native dwarf inanga (*Galaxias gracilis*) in a Northland lake followed introductions of mosquito fish (NIWA 2013), with similar native fish extinctions, or range restriction, reported after invasions by the closely related *Gambusia holbrooki* in Australia (Rowe et al. 2008). Local loss is significant in the case of these fish population units, which are often genetically differentiated from other lake populations.
Bladderwort	The recent spread of alien bladderwort (*Utricularia gibba*) through Northland and Auckland regions appears to be at the expense of the native bladderwort (*Utricularia australis*), which has subsequently been designated the conservation status of 'nationally critical' (de Lange et al. in press).

frameworks to score the pest potential of species out of a theoretical '100', under the aquatic weed risk assessment model (Champion and Clayton 2000) and out of 77 under the fish risk assessment model (Rowe and Wilding 2012). Although records of alien freshwater invertebrates have increased in the last decade (Balvert et al. 2009; Parkes and Duggan 2012; Duggan et al. 2012) their presence and impacts are less well known.

Invasive species impact indirectly on provisioning, cultural, regulating and supporting services, while having direct effects on biodiversity. Some examples of such impacts in New Zealand lakes are described in Table 8.

Globally, the impact on inland waters of invasion is projected to increase in the future (MEA 2005). While New Zealand's borders are protected via import regulations and inspection procedures, avenues exist for illegal (or possibly malicious) importation of alien aquatic flora and fauna (Champion and Clayton 2000), and are poised to increase with enhanced world trade and human immigration. The planned creation in New Zealand of numerous reservoirs for agricultural water storage will likely increase the opportunities for spread and establishment of alien aquatic species, which increases invasion risk to natural lakes (Johnson et al. 2008). Nevertheless, how future invasions will interact with other natural and anthropogenic drivers of lake change is as yet poorly understood.

Harvesting and food web interactions

The main direct driver of sustainability in fisheries is the management of the harvesting so that the annual harvest and wild populations are maintained at stable, sustainable levels. However, discussion of quota management and harvesting policy is beyond the scope of this chapter.

The sustainability of the harvests from lakes may be indirectly affected by foodweb interactions. For example, eels are the dominant native top-predator in New Zealand lakes. Introductions of other predatory sport fish such as salmonids and perch have very likely changed the foodweb dynamics of many lakes (Closs et al 2003; McDowall 2006). The combination of changes in eel biomass (due to harvesting) with the introductions of salmonids and perch is likely to have altered the community composition and foodweb dynamics of these systems. Such ecological changes are also expected to influence the level of biomass that can be sustainably harvested from lakes.

Modification of hydrological regimes

The main modifications to natural hydrological regimes that affect lakes are the damming of lake outflows, the diversion of water flowing into lakes, and the abstraction of water upstream of lakes. Recently, consideration has been given to the commissioning of new hydro dams on both unregulated rivers (e.g. Mokihinui River, West Coast, South Island) and regulated rivers (e.g. Clutha River, Otago), as well as on canal networks (Waitaki River catchment, Canterbury), which could collectively add up to around 2500 MW of power to the existing grid network. Many dams that have reached the formal proposal stage have been strongly contested on scenic and ecological considerations including the flooding of native forest (Mokihinui River), threats to isolated populations of native fish (Beaumont Dam on the Clutha River), and barriers to migration of populations of diadramous fish.

A major additional drive for dam construction relates to irrigation for agriculture, either as part of an integrated system that includes hydroelectricity generation or solely for irrigation purposes. New Zealand has the highest rate of growth of irrigation amongst 25 countries of the Organisation for Economic and Co-operative Development (5.6% from 2007 to 2012); a situation underpinned by a lack of charges on a volumetric basis for irrigation water used for agriculture and a rapidly expanding dairy sector. Many new farms have arisen in arid areas (e.g. Canterbury) where irrigation is essential to support economically viable operations. Estimates have been made that by 2035, irrigation will have resulted in an increase in agricultural exports by NZ$4 billion; for context the revenue for all agricultural and horticultural exports from New Zealand was NZ$23 billion in 2008/09. In light of this, in 2011 the New Zealand Government indicated that it would commit NZ$400 million over several years to support additional irrigation development. Some of this funding is intended to support construction of new irrigation dams for water storage purposes. The size of the proposed dams varies; from the Ruataniwha Dam (dam height 83 m, reservoir area 372 ha) on the upper Makaroro River in Hawke's Bay (North Island) to smaller dams limited to supplying one or a few farms. An existing example of a moderate-sized irrigation dam that also has hydroelectric generation capacity (7.7 MW) is the Opuha Dam (dam height 50 m, reservoir area 710 ha) in South Canterbury.

Until recent times, artificial opening of barrier bars to regulate water levels of ICOLLs had been carried out with little regard to the ecology of the ICOLLs and ecosystem services that they provide. However, recent concerns over the ongoing degradation of some ICOLLs have focused attention on the potential to utilise artificial openings to enhance the ecology and ecosystems services. For example, artificial openings can enhance the flushing of nutrients, sediments and phytoplankton from ICOLLS. Such proposals are being considered for both Lake Ellesmere/Te Waihora and Waituna Lagoon, and, if successful, will improve the ecological functioning of these systems.

Climate change

Air temperatures in New Zealand have increased by about 1°C over the past century (Mullan et al. 2008). The climate in New Zealand results from a combination of natural variability, mainly explained by cycles in the El Niño-Southern Oscillation (ENSO; Mullan 1996) and the Interdecadal Pacific Oscillation (IPO; Salinger et al. 2001), and the climate change caused by anthropogenic activity. These components of the climate system can interact synergistically or antagonistically with regard to their effects on climate. For example, the negative phase of the IPO, which began around 1999–2000, is associated with changes opposite to what is expected from anthropogenic climate change, resulting in relatively stable annual mean air temperatures over the past decade and the absence of a clear trend. A phase change to the positive IPO, expected in a decade or so, is likely to enhance anthropogenic climate change trends (Salinger et al. 2001).

In view of the fact that air temperatures have increased by 1°C over the past century, and are expected to increase by 2°C during the present century (Mullan et al. 2008), there is little doubt that lake water temperatures have increased as well and will continue to do so in the present century. However, because of the counteracting effects of climate change and the negative phase of the IPO, and because the best long-term records of water temperatures in New Zealand lakes are no longer than a decade or two (Gibbs 2011; Verburg et al. 2013), the evidence for long-term warming in New Zealand lakes is ambiguous (Hamilton et al. 2013). Better data exist for streams, where the average temperature at 77 sites in 35 rivers in the North and South Island has increased by about 0.4°C since 1989 (Ballantine and Davies-Colley 2009). Little is known about how the changing climate has so far affected the aquatic environment in New Zealand. The expected change in lake ecosystems is therefore mainly derived from modelling results (Trolle et al. 2011) and from changes found elsewhere in the world.

The effect on lakes of warming depends on lake morphology, mixing regimes and climatic conditions (e.g. Quayle et al. 2002; Verburg et al. 2003). Deep permanently stratified lakes may experience reduced productivity due to reduced vertical mixing and reduced internal renewal rates of nutrients from deep water (Verburg et al. 2003), while other lakes may experience enhanced productivity due to longer ice-off times, reduced light limitation, increased nutrient loading by melt-water runoff (Quayle et al. 2002) and enhanced internal nutrient loading.

As a result of climate warming, the duration and strength of stratification in New Zealand lakes are expected to increase because surface water usually heats more than deeper water (Verburg et al. 2003; Winder and Schindler 2004). Stratification of the water column limits the amount of vertical mixing that can occur. Reduced vertical mixing tends to reduce the replenishment of oxygen in bottom water and anoxia may occur or become more frequent. Furthermore, increased runoff and external nutrient loading in New Zealand lakes, where water quality is already deteriorating as a result of land use practices (Verburg et al. 2010), will compound such problems by increasing productivity (Trolle et al. 2011) resulting in increased oxygen consumption in bottom water (Nürnberg 1995).

Oxygen depletion in bottom water generally results in a higher trophic state and the potential for blooms of algae, in particular of blue-green algae (i.e. cyanobacteria), by enhancing internal loading of nutrients from the lake bottom sediments. A portion of the nutrients that enter lakes from their catchment is buried in the sediment that builds up on the bottom of lakes and, thereby, removed (sequestered) from the ecosystem. When hypolimnetic oxygen consumption results in anoxia, the efficiency of burial of nutrients in the sediment in lakes is reduced (Nürnberg 1984; Vant 1987) and the release of nutrients from the sediment to the water column is enhanced (Nürnberg 1984). The internal loading of nutrients, in particular phosphorus, becomes progressively more important than external nutrient loading in fuelling eutrophication when hypolimnetic oxygen concentrations decline towards anoxia. Thus, warming and stratification in a productive lake can result in rates of bottom-water oxygen consumption sufficient to diminish the availability of oxygen, causing sediment nutrient release, which accelerates eutrophication through a positive feedback loop. In addition, by enhancing rates of phosphorus (P) release relative to nitrogen (N) release from the sediments, such effects can also reduce the N:P ratio of the water column, which may favour a change in algal species composition, with low N:P ratios tending to favour blooms by nitrogen-fixing blue-green algae (Smith 1983). Blue-green algal blooms are also expected to become more frequent as their temperature optima tend to be higher than that of other algal species and because stronger stratification favours the more buoyant algae species (Carey et al. 2012).

In summary, in a warmer climate New Zealand lakes are expected to become more enriched with nutrients, more productive, and algal blooms are expected to be both more frequent and more frequently represented by nuisance species such as blue-green algae. To maintain lakes in a low-nutrient state, the reduction of external nutrient loads will become even more important because as the climate warms, internal nutrient loading will be exacerbated in many lakes.

ECONOMIC VALUATION OF LAKE ECOSYSTEM SERVICES

An economic valuation of ecosystem services compares competing demands on lakes by reducing a multi-dimensional problem into a single dimension. While attempts have been made to view nature and ecosystems as 'natural capital' and their productivity and processes as 'ecosystem services', it is often difficult to establish a monetary value for many of these concepts (Fenech et al. 2003), such as those listed in Table 1. Furthermore, economic valuation is neither neutral nor objective because its framework is based on normative, contestable assumptions. For example, Pemberton (2013) noted that a cost–benefit framework gives more weight to the preferences of the wealthy than the poor and does not necessarily give any weight to the preferences to future generations. Furthermore, cost-benefit analyses do not often account for the intrinsic value of ecosystems or for the incommensurability of the values that can be ascribed to ecosystems.

Costanza et al. (1997) attempted to attribute a dollar value to the ecosystem services provided by 17 ecosystem types on a global basis. Of these, an average monetary value of US$8,498 per hectare per year was attributed to river and lake ecosystems. While there has not been an attempt to value New Zealand's lake ecosystem services so far, Patterson and Cole (1999) estimated the total value of ecosystem services in the Waikato, of which lakes contributed NZ$1,513 million (or 16%) per annum (in 1997 dollars), placing them second only to forests with regard to total value of services. On a per hectare basis, Waikato lakes contributed NZ$20,300 per hectare per year to the local economy, a value similar to that calculated by Costanza et al. (1997) for lakes and rivers on a global basis.

A number of notable attempts have been made to evaluate the monetary costs (externalities) of the loss of lake ecosystem services under specific scenarios. For example, Tait and Cullen (2006) estimated the loss of ecosystem services due to the effects of dairying in Canterbury. Effects on some aquatic ecosystem services were quantified and these included loss of surface water quality, loss of angler values and loss of biodiversity due to sediment in surface waters.

While economic analysis was done to support the decision to protect Lake Tāupo from increasing nutrient loading due to agricultural intensification, this did not involve a valuation of lake services. Instead it started from a position that the existing high water quality in the lake was critical to the success of local tourism. Tourism was identified as by far the most important economic activity in the district and the benefits of protecting a threat to tourism from reduced water quality in the lake far outweighed the costs from reduced farming activity (McDermott Fairgray 2001; Hickman 2002).

A different approach to assessing the value of ecosystem services attempts to determine the public stated preferences and willingness to pay for competing scenarios. For example, Bell et al. (2009) estimated the dollar value for indigenous biodiversity that might be lost in Lake Rotoroa if there was a hypothetical incursion of the invasive non-indigenous macrophyte *Hydrilla verticillata*. Based on the amount people were willing to pay, a

CASE STUDY: ***Lake Ōmāpere***

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Here we compare the ecosystem services provided by Lake Ōmāpere under different states of ecological impairment, with what they would be under a desired state (Table 9), by providing a historical and lake management context to changes in this waterbody.

The largest lake in Northland, Lake Ōmāpere (1197 ha) is shallow (maximum depth is approximately 2.6 m) and was once a forested wetland (Newnham et al. 2004). The lake feeds the Utakura River, flowing through the Utakura Valley to the Hokianga Harbour.

Ōmāpere is a lake of great significance (a taonga) to Ngāpuhi, who maintain manawhenua (ownership) and kaitiaki (guardian) rights and responsibilities particularly via the leadership of the Lake Ōmāpere Project Management Group and Te Roopu Taiao o Utakura. Manawhenua have continually lobbied for protection of Lake Ōmāpere and environs, and are determined to reverse the state of degradation. They have articulated the significance of the integrity of this ecosystem thus: 'use of the lake is determined by the health of the lake, the health of the lake and the health and of the people are intertwined' (Henwood and Henwood 2011).

In 2004, manawhenua leadership brought together community stakeholders and agencies with responsibilities in the area to identify a restoration and management strategy. The approach adopted – ma uta ki tai (catchment-wide) – emphasises interconnectedness and inclusion, both spatially and socially (Lake Ōmāpere Project Management Group 2006). To date, the extensive fencing, riparian planting and development of farm environmental plans have likely reduced external nutrient loads to the lake (Grey 2012). The manawhenua group of the downstream Utakura catchment, Te Roopū Taiao, have adapted culturally specific assessment and monitoring tools (Henwood and Henwood 2011), which complement and direct continuing restoration initiatives.

Historically Lake Ōmāpere has been a 'food basket' that supplied tuna (eel), torewai (freshwater mussels), raupō (bulrush, *Typha orientalis*), kāpūngāwhā (clubrush, *Schoenoplectus tabernaemontani*) and harakeke (flax, *Phormium tenax*) (White 1998). In the 1920s, the lake was partially drained reducing the depth by about 1.2 m (White 1998). Eel-fishing methods included using spears and torches from canoes (White 1998) suggesting the lake waters were clear.

In the 1970s the lake was used for recreational boating, and water quality was satisfactory to supply domestic water for the nearby township of Kaikohe (NRC 2001). Since that time, further development of the surrounding catchment for pastoral farming contributed to additional nutrient loads to the lake. In 1984 'dense growths and drift accumulations' of the invasive weed *Egeria densa* were first documented (Tanner et al. 1986) but the weed beds collapsed, leaving Lake Ōmāpere in a turbid, de-vegetated state for years (Champion and Burns 2001). In 1985, the Northland Area Health Board prohibited water takes from the lake for domestic supply due to a severe cyanobacterial bloom (NRC 2001). In the Utakura River and upper reaches of the Hokianga Harbour, fish and shellfish became unsafe to eat (Grey 2012).

Monitoring from 1992 captured a step-wise shift in water quality to higher water clarity, lower chlorophyll a levels, and a return by submerged plants in late 1993 (Champion and Burns 2001). The trigger appeared to be the recovery of freshwater mussel/torewai populations to densities where they could theoretically filter a volume equivalent to that of the lake in 20 hours (Champion and Burns 2001). However Egeria beds increased from 1994 to 2000, and again grew over most of the lake.

In 2001 a ministerial enquiry accepted scientific evidence suggesting an imminent weedbed collapse and further toxic algal blooms (Māori Law Review 2001). Benthic deoxygenation (DO < 1 mg L^{-1}) within the weedbeds caused large-scale die-off in freshwater mussel/torewai (5-fold density reduction), collapse of the weed beds, and led to another persistent algal-dominated state (Champion 2004). This was the catalyst for the introduction of 60 000 diploid grass carp between 2000 and 2002. Although stocking of grass carp was too late to avoid the collapse of Egeria in late 2001, the effective eradication of this weed has interrupted its boom–bust cycle of invasion alternating with an algal-dominated state.

Commercial eeling in the lake began in 1982 (Champion and Burns 2001), with reported catches of 72 tonnes between 1999 and 2001, and 73 tonnes between 2003 and 2008 (Williams et al. 2009). A 2008 fishery assessment in Lake Ōmāpere showed a high proportion of commercial-sized eels/tuna (i.e. > 220 g), with shortfin tuna (*Anguilla australis*) having amongst the highest growth rates recorded in New Zealand (Williams et al. 2009). However, few shortfin and longfin tuna (*A. dieffenbachii*) in the catchment were of the large size preferred for customary take and the size required to migrate out of the catchment to breed (Williams et al. 2009). On the basis of this commissioned research the Lake Ōmāpere Trust placed a rāhui (prohibition) on the commercial harvest of lake eel/tuna populations in 2010.

A nutrient budget for Lake Ōmāpere (Verburg et al. 2012), again commissioned by Te Roopu Taiao, showed that during the algal-dominated phase a nutrient legacy in the sediments fuelled internal high regeneration rates of nitrogen and phosphorus levels. These greatly exceeded loads from the catchment, with eventual export from the lake via the Utakura River and denitrification (microbial transformation of nitrate to atmospheric gas). In contrast, during the weed bed-dominated state, nutrients accumulated in the sediments (Verburg et al. 2012). A recent improvement in water quality (hypertrophic to eutrophic) may have been assisted by increased torewai populations (Grey 2012).

There have been no algal blooms in the lake since 2007 and many of the ordinary practices of water use in the catchment have resumed. In 2011 tuna were returned to the tables of Mokonuiarangi Marae, welcoming guests with this traditional kai (food) for the first time in more than a decade.

Collectively, the management interventions are moving Lake Ōmāpere and the Utakura catchment towards a desired state where a wider range of more consistent and sustainable ecosystem services are available (Table 9) to all sectors of the community.

special tax was levied with the rates, for maintaining or limiting deterioration of indigenous biodiversity in the lake. The existing environmental attributes of Lake Rotoroa that rated highest were the native charophytes, birds, fish, and freshwater mussel/kākahi.

Marsh (2012) similarly developed a 'choice experiment' by assessing public opinion in a dairy catchment in the Waikato Region on the preference for more local jobs in the agricultural sector or improved water quality. He found that the community was willing to pay for water that was safer for swimming, with improved water clarity and ecological health, but that the level of support declined if these improvements were accompanied by job losses.

There is disagreement on how accurate stated-preference techniques are at revealing preferences. Willingness to pay is also likely to be specific for each lake considered because actual costs and benefits vary from lake to lake. For example, people may be willing to pay more for initial biosecurity incursions with the expectation that preventing the colonisation of a given lake by a pest species will help prevent the spread of that species to other nearby lakes.

Attempts to place monetary values on lake ecosystem services date back at least as far as the 1970s and a number of different approaches have been trialled (Wilson and Carpenter 1999). The ability to place monetary value on different ecosystem services varies greatly and, generally, many ecosystem services have been omitted from these assessments. In this chapter we have attempted to raise awareness of the breadth of ecosystem services provided by lakes and the numerous anthropogenic pressures that reduce not only ecosystem services but also natural capital. Beyond this economic paradigm are the intrinsic, spiritual, cultural, and scenic values, which we have not discussed, but which are nevertheless important to human well-being.

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TABLE 9 Ecosystem services identified for Lake Ōmāpere under different states

Ecosystem service	Desired state	*Egeria* dominated	Algal dominated
Provisioning	●Domestic and rural water supply ●Sustainable commercial tuna fishing ●Sustainable customary tuna harvesting ●Shellfish gathering ●Swan shooting ●Natural fibres ●Recreation	●Domestic and rural water supply ●Commercial tuna fishing ●Restricted customary tuna harvesting ●Shellfish gathering ●Swan shooting ●Natural fibres	●Rāhui (ban) on commercial tuna fishing ●Restricted customary tuna harvesting ●Restrictions on shellfish harvest in Hokianga harbour
Supporting & regulating	●Water filtering (torewai & plants) ●Nutrient lock-up (sediments/plants) ●Denitrification ●Drainage ●Water storage ●Flood buffering ●Native biodiversity & rare species (mudfish, *Isoetes*, longfin)	●Water filtering (torewai & plants) ●Nutrient lock-up (sediments/plants) ●Denitrification ●Drainage ●Reduced water storage (weed-beds) ●Flood buffering ●Reduced native biodiversity & rare species (mudfish, longfin)	●Denitrification ●Drainage ●Water storage ●Flood buffering ●Reduced native biodiversity & rare species (mudfish, longfin)
Cultural[1]	●Kaitiakitanga actively practiced by manawhenua ●Spiritual wellbeing (e.g. sites of importance for spiritual practise protected and enhanced) ●Preservation of cultural heritage/landscapes and practise of whakapapa, taonga and mātauranga related activities (e.g. intergenerational knowledge transfer occurring) ●Cultural events and activities ●Eco-tourism	●Kaitiakitanga actively practiced by manawhenua ●Reduced spiritual well being ●Impacted intergenerational knowledge transfer opportunities	●Kaitiakitanga actively practiced by manawhenua ●Reduced spiritual well being ●Impacted intergenerational knowledge transfer opportunities

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