

River function

Several studies have used measures of river metabolism and organic matter processing (see section 5.1.2 'Functional indicators') to infer resilience by focussing on ecosystem efficiency (Uehlinger & Naegeli 1998; Uehlinger 2000; Acuña et al. 2007). For example, Acuña et al. (2007) showed that streams were functionally more resilient to flood disturbances during summer because they were efficiently processing carbon entering the stream at this time. Ecosystem functions that occur in the hyporheic zone (e.g. hydrological exchange) have also been suggested as important indicators of river resilience (Valett et al. 1994), as they characterise the condition of an important refuge habitat. To assess functional resilience, knowledge of the pre-disturbance state (or of the functioning of reference sites) is also required, necessitating sampling of some reference sites. Some functional indices, such as the balance between rates of P and R, could also directly imply resilience, with a balanced system ($P/R = 1$) being more resilient than one relying entirely on external inputs of energy ($P/R \ll 1$). Thus, the use of functional attributes to infer ecosystem resilience has some attraction, and these are probably the best documented indicators related to resilience.

5.2 LAKES

Karr's (1996) definition of EI (see section 2.2) has influenced the development of the majority of current classification schemes for lakes that attempt in one form or another to measure EI (US EPA 1998; European Union 2000; Murphy et al. 2002; Solimni et al. 2006). The term 'integrity' has been criticised because it implies a definitive state rather than a gradient of states, with the ecosystem either having integrity or not (Westra et al. 2000). In response to this, the terms 'ecological condition' or 'ecological status' have been adopted by some freshwater lake classification schemes, notably in the European Water Framework Directive (WFD), where the ecological status of surface waters is defined as '... an expression of the quality of the structure and functioning of aquatic ecosystems associated with surface waters...' (European Union 2000). WFD uses primarily biological indicators to assign water bodies, including lakes, to one of five ecological classes ranging from high to low quality (European Union 2000). Our definition of EI also implies a gradient of condition or status.

Difficulties persist in how to define and determine the EI of specific lakes because integrity has often been defined in terms of deviation from a reference condition (Søndergaard et al. 2005), and it has been argued that the establishment of a realistic and appropriate reference condition is essential in lake ecological monitoring programmes (Moss et al. 1996; Wallin & Solheim 2005). Various approaches have been used to infer lake reference conditions, including palaeolimnological analyses (Laird & Cumming 2001), historical data combined with a modelling approach (Nielsen et al. 2003), survey data from existing reference sites, and expert judgement (US EPA 1998; Wallin & Solheim 2005).

In the reference condition guidance (REFCOND) produced by the European WFD, it was ultimately concluded that, for practicality's sake, reference conditions of

lakes need not necessarily equate to totally undisturbed, pristine conditions, but instead could include the condition of very minor disturbance, as long as there is no, or minimal, ecological effect (Anon. 2003). This is a practical compromise because of the difficulty in obtaining appropriate, pristine reference lakes (Leira et al. 2006). For example, historical and current datasets may be limited or of little relevance (Wallin & Solheim 2005), and palaeolimnological datasets with transfer functions capable of describing pre-human lake conditions are not yet common in New Zealand (but see Reid 2005; Cochrane et al. 2007).

It has been suggested that the use of data from limnological surveys is the most transparent, practical and defensible methodology for establishing reference conditions (US EPA 1998; Wallin & Solheim 2005). This approach usually takes one of two forms:

1. When a sufficient number of non- (or minimally) impacted lakes exist, a reference lake scheme approach can be used, whereby such lakes can define reference conditions
2. If there are insufficient minimally impacted reference lakes available, a lake population distribution approach can be used, whereby reference conditions are selected from the best quartile of the entire population of lakes.

Karr et al. (1986) developed the latter approach for the Index of Biotic Integrity (IBI) and it has been suggested that this approach may be useful for highly impacted areas, such as lowland agricultural areas, where unimpacted reference sites do not exist (US EPA 1998; Wallin & Solheim 2005). However, this approach is relativistic and substantially impacted lakes could be attributed with a high EI.

Reference conditions must reflect not only individual lake types but also regional variation, because lakes in different regions may respond differently to anthropogenic pressure (US EPA 1998; Søndergaard et al. 2005; Wallin & Solheim 2005). For example, lakes in different ecoregions of the USA have significantly different levels of total phosphorus and chlorophyll because of differences in soils, vegetation, land form and land use (US EPA 1998). Similarly, lakes of the Central Volcanic Plateau of New Zealand tend to have higher natural inputs of phosphorus than many other New Zealand lakes due to the higher phosphorus content of the underlying volcanic geology (Burns et al. 1997).

The use of ecological classification systems to define lake types and regions may assist in establishing appropriate reference conditions. However, type- and region-specific assessments of reference condition may be problematic because individual lakes may have unique communities and system dynamics influenced by lake-specific factors or conditions, which are not accounted for in the reference lake approach. Long hydraulic residence times in lakes dampens variability and strengthens biological interactions, which may promote stochastic dynamics driven by species interactions. Such systems with strong, specific biological interactions may respond uniquely to pressure gradients.

The above arguments indicate that the approach of establishing lake EI via the normalisation of current New Zealand lake conditions to appropriate reference conditions is problematic.

The literature on EI in lakes reflects the fact that the concept of EI, and indicators for assessing it, are relatively under-developed in lakes compared with rivers and

streams. Below, we present a number of potential indicators for measuring each of the four components of EI. Many of the indicators, excluding those relating to the measurement of nativeness, do not explicitly require a knowledge of reference conditions and have been previously used by researchers as indicators of the degree of degradation of aquatic ecosystems. Although the list of indicators we discuss is not exhaustive, our aim is to present and discuss some common and cost-effective indicators that may be useful for the determination of EI in New Zealand lakes.

5.2.1 Nativeness

Nativeness refers to the taxonomic makeup of the ecosystem as it existed in a reference state (Solheim 2005) and, therefore, high nativeness equates to high ecological condition or integrity (Harig & Bain 1998; Clayton & Edwards 2006b). New Zealand's aquatic macrophyte, fish and zooplankton communities have been impacted by introduced species, whereas the spread and impacts of introduced benthic macroinvertebrates in New Zealand are less well understood at present (Closs et al. 2004; Duggan et al. 2006). The scoring of separate nativeness indicators for lakes against the seven assessment criteria is included in Table 8 and a brief discussion of some of the key points for each of the indicators follows below.

Macrophyte community composition

Several European and North American schemes have used macrophyte community composition to monitor lake condition (e.g. Palmer et al. 1992; Melzer 1999; Nichols et al. 2000). In New Zealand, LakesPI or 'Lake submerged plant indicators' has been developed as a management tool, integrating three separate indices: a native condition index (extent and diversity of native macrophytes), an invasive condition index (extent and impact of invasive macrophytes), and an integrated LakesPI Index, derived from components of the previous two indices. Macrophyte community composition has been linked to various pressures in New Zealand lakes (Clayton & Edwards 2006a, b). Advantages of using macrophyte species composition as a measure of nativeness include their year-round presence, their

TABLE 8. EVALUATION OF NATIVENESS INDICES FOR LAKES AGAINST A SET OF ASSESSMENT CRITERIA. DETAILS OF THE ASSESSMENT CRITERIA ARE OUTLINED IN SECTION 4.5.

ASSESSMENT CRITERIA	MACROPHYTES	FISH	ZOOPLANKTON
Ease of sampling and analysis	Moderate (2)	Easy (3)	Moderate (2)
Potential geographic coverage	Moderate (2)	Wide (3)	Wide (3)
Relation to nativeness	Strong (3)	Strong (3)	Moderate (2)
Sensitivity to pressure gradients	High ^d (3)	Intermediate ^b (2)	Intermediate ^c (2)
Calibration to reference condition	Moderate (2)	Easy-Moderate ^d (3)	Difficult (1)
Temporal variability	Low (3)	Low (3)	High (1)
Use in New Zealand	Common (3)	Common (3)	Rare (1)
Use in other countries	Common (3)	Common (3)	Occasional (2)
Rank [points]	2 [21]	1 [23]	3 [14]

^a Unimodal.

^b Probably not unimodal.

^c Poorly known.

^d Probably non-linear.

relative longevity (allowing an integration of environmental impacts over time), and the moderate costs associated with macrophyte sampling, monitoring and identification. The nativeness of a lake can be assessed as the ratio of the number of native macrophyte species present to the number of macrophyte species expected to have inhabited the lake prior to human influence (observed/expected or O/E). However, this measure of nativeness requires robust predictions of the reference macrophyte community specific to each lake or lake type (Solheim 2005).

Invasive macrophytes are defined as a key ecosystem pressure in the LakeSPI system (Clayton & Edwards 2006a). Invasive condition assesses the invasiveness and relative abundances of invasive macrophytes, as well as their depth and coverage of the lake bed or shoreline. The proportion of the lake shoreline colonised by native or invasive macrophytes was selected by Moss (2007) as one of the most robust variables for assessing lake ecological condition. The major disadvantage of this system is that it is, by definition, indicative of only one pressure (plant invasion), although invasive species composition could in some circumstances also act as an indicator of oligotrophic or eutrophic conditions (e.g. *Lagarosiphon major* tends to colonise the former, while *Ceratophyllum demersum* tends to colonise the latter). In many freshwater lakes in New Zealand, Europe and North America, the geographical distribution of invasive macrophytes is spreading, indicating that many lakes have yet to be exposed to the colonists. Thus, mechanisms of spread, as well as biogeography, must be considered when using EI indicators that are based on the presence of exotic taxa.

Native fish species composition

Some advantages of using fish species composition as an indicator of nativeness include the relatively low number of species that must be considered, the relatively simple taxonomy involved and the high sensitivity of some fish taxa to human pressures (Søndergaard et al. 2005). Measurements of fish assemblage composition and abundance have been incorporated into the Index of Biotic Integrity (IBI) to assess pressures on river systems (Karr et al. 1986; Karr 1991) and attempts have been made to apply similar systems to lakes (Jeppesen et al. 2003). However, the high variability in lake morphology, bottom type and sampling efficiency (US EPA 1998) render the method costly. The sampling effort required to obtain representative samples of fish assemblages in lakes is high because thorough surveys usually necessitate using a combination of sampling methods, such as gillnetting, seining, trawling and electrofishing (Wanzenböck et al. 2002). Furthermore, some of these methods are unable to catch fish quantitatively, making it difficult to obtain useful abundance data. Carol et al. (2006) found that for fish assemblages with low richness, catch per unit effort (CPUE) and species composition were better indicators of pressures, including eutrophication, than commonly used species richness and diversity indices. Yonekura et al. (2004) found that the CPUE data showed clear impacts of two invasive species in 14 Japanese farm ponds, with negative relationships between the total abundances of native and exotic fish. However, both of these

studies cautioned against comparing abundances among species when standard fish sampling methods are used because most methods have different capture efficiencies for different species. Fish species can exhibit seasonal and diel changes in abundance and behaviour, and such temporal variability should be considered when planning fish sampling programmes. However, if carefully quantified, the relative contribution of native fish species to the fish community is a useful indicator of nativeness that can be applied directly and quantitatively to lakes regardless of their geographical locations.

Zooplankton

New Zealand is now home to at least three exotic crustacean zooplankters (C.W. Burns, University of Otago, unpubl. data). In addition, the exotic freshwater jellyfish *Craspedacusta sowerbyi* has been observed from numerous lakes (Boothroyd et al. 2004; M. Schallenberg, unpubl. data). While zooplankton are easily quantitatively sampled, the appearance of species in a lake and their abundances can be episodic, so that the absence of zooplankter species from a lake should be confirmed by repeated sampling over an annual cycle. Furthermore, it has been suggested that a number of native taxa may represent species complexes, indicating that taxonomic differentiation based on morphometry can be problematic. Thus, genetic taxonomic differentiation is increasingly used to identify certain species. Biogeographic patterns structure the distributions of some native zooplankters, as was shown by Jamieson (1998) for native copepod species. Thus, biogeography and dispersal should also be taken into account when interpreting the geographical distributions of some zooplankton taxa and when inferring potential reference conditions related to zooplankton abundance and distribution.

As exotic zooplankters appear to be relatively new invaders to New Zealand lakes, little is known about relationships between these new species and New Zealand ecological pressure gradients. However, anecdotal evidence suggests exotic *Daphnia* species may achieve higher densities than the native *D. carinata* and, thus, may improve water clarity in some lakes (M. Schallenberg, unpubl. data).

5.2.2 Pristineness

Pristineness may refer to various key components and processes of the ecosystem. Therefore, we have included structural, functional and physio-chemical elements for this component of EI. We discuss potentially useful indicators of New Zealand lake pristineness under the three elements below.

Structural indicators

Structural indicators relate either to taxonomic community structure or to the abundance and/or distribution of taxa within and among lakes. Here we will emphasise communities that are not covered under the nativeness component of EI. The scoring of separate structural indicators of pristineness for lakes against the seven assessment criteria is included in Table 9 and a brief discussion of some of the key points for each of the indicators follows below.

TABLE 9. EVALUATION OF STRUCTURAL INDICES OF PRISTINENESS FOR LAKES AGAINST A SET OF ASSESSMENT CRITERIA. DETAILS OF THE ASSESSMENT CRITERIA ARE OUTLINED IN SECTION 4.5.

ASSESSMENT CRITERIA	PHYTO- PLANKTON	ZOO- PLANKTON	MACRO- INVERTS	MACROPHYTES	EPIPHYTON/ PERIPHYTON
Ease of sampling and analysis	Difficult (1)	Difficult (1)	Moderate (2)	Easy (3)	Difficult (1)
Potential geographic coverage	Wide (3)	Wide (3)	Wide (3)	Moderate (2)	Moderate (2)
Relation to pristineness	Moderate (2)	Moderate (2)	Moderate (2)	Strong (3)	Limited (1)
Sensitivity to pressure gradients	Moderate ^a (2)	Moderate ^b (2)	Unknown ^c (1)	High ^d (3)	Unknown (1)
Normalisation to reference condition	Difficult (1)	Difficult (1)	Difficult (1)	Easy (3)	Difficult (1)
Temporal variability	High (1)	Moderate (2)	Low (3)	Low (3)	High (1)
Use in New Zealand	Common (3)	Occasional (2)	Rare (1)	Common (3)	Rare (1)
Use in other countries	Common (3)	Rare (1)	Common (3)	Common (3)	Occasional (2)
Rank [points]	2 [16]	4 [14]	2 [6]	1 [23]	5 [10]

^a Cyanobacteria.

^b Rotifers sensitive to trophic state.

^c Some sensitive taxa.

^d Some indices.

PLANKTON COMMUNITY COMPOSITION

Phytoplankters are important primary producers in lake food webs. The abundances of individual phytoplankton taxa may be positively or negatively correlated with nutrient inputs and, thus, the ratio of positive to negative species can be used as a metric of ecological status (Söndergaard et al. 2003). Algal community composition has been shown to be more sensitive to some pressure gradients than functional indicators such as primary productivity (Schindler 1987, 1990).

Zooplankton assemblage composition can be controlled by both higher (planktivores) and lower (phytoplankton) trophic levels and, therefore, provides a useful trophic link to fish predators. However, for this reason, interpretation of responses may be difficult and temporal variability in zooplankton community composition and abundance can be high (USEPA 1998). Chapman & Green (1999) found little seasonal regularity in crustacean zooplankton composition in Lake Rotorua/Te Rotorua nui ā Kahu-matamomoe and suggested that stochastic events such as storms may be the most important factor related to community structure. In contrast, a study examining the spatial and temporal variation of zooplankton community structure in a coastal lake/wetland showed that zooplankton community structure and biomass were highly sensitive to small changes in salinity and moderately sensitive to variables related to trophic state (Schallenberg & Burns 2003; Schallenberg et al. 2003). Ratios, such as the number of large species of cladocerans to total number of cladocerans, have sometimes proven more useful than measures of overall community composition for determining the ecological condition of lakes in Europe (Moss et al. 2003).

Jamieson (1998) showed that strong biogeographical drivers underpinned the distributions of native copepod species in New Zealand and, thus, restrictions on dispersal should also be taken into account when interpreting zooplankton community data and when inferring potential reference conditions of the zooplankton community.

In New Zealand (Duggan et al. 2001) and elsewhere (Gannon & Stemberger 1978), it has been shown that planktonic rotifer community composition is a good indicator of nutrient enrichment in lakes.

Malthus & Mitchell (1989) found that the ratio of phytoplankton biomass to zooplankton biomass was higher in a number of New Zealand lakes than the ratio typical of lakes elsewhere. Although the ratio was not suggested as a metric of pristineness, the authors did suggest that it could indicate the degree of balance between planktonic primary producers and grazers in lakes. This ratio has subsequently been used as an index of EI (Xu 2005).

It can be difficult to relate plankton community composition to pristineness when no appropriate reference lakes are available. Palaeolimnological methods may be used to reconstruct past plankton communities, and a transfer function has been developed linking diatom community structure with trophic state (Reid 2005), allowing the reconstruction of past trophic states in lakes. Fossil pigment analysis in sediment cores can also be used to reconstruct historical phytoplankton community structure (e.g. Leavitt et al. 1994), although problems of pigment preservation in older sediments cast some doubt on interpretations. Remains of body parts of zooplankters are sometimes well preserved in sediments, and work in other countries has resulted in the development of ecological transfer functions linking zooplankton community structure with lake trophic status and fish community structure (Jeppesen et al. 1996). Thus, it may be feasible and fruitful to determine linkages between plankton community structure and reference conditions via palaeolimnological approaches.

MACROINVERTEBRATE COMMUNITY COMPOSITION

Many macroinvertebrates have widespread geographical distributions, making them potentially good indicators of pristineness among lakes. For example, Timms (1982) showed that macrobenthic community composition changed along a gradient of lake trophic state. However, the community structure tended to respond more strongly at higher trophic states. Benthic macroinvertebrates are fed upon by fish and are, thus, important for the maintenance of energy transfer to higher trophic levels in lakes (Kelly & McDowall 2004; Rowe & Schallenberg 2004). While macrobenthos community composition is considered to exhibit moderate temporal variability in some countries (e.g. US EPA 1998), New Zealand's mild temperate climate results in low temporal variability (Talbot & Ward 1987). However, there are some disadvantages to their use as indicators of pristineness in lakes. Considerable within-lake spatial heterogeneity is common, necessitating considerable sampling effort (USEPA 1998; Carter & Griffiths 2001; MacNeil et al. 2001); for example, in New Zealand, depth preferences and substrate type strongly influence species composition (Forsyth & McCallum 1981; Weatherhead & James 2001). In addition, while extensively used in New Zealand streams and upland rivers, macroinvertebrate metrics are poorly developed for New Zealand lakes; however, macrobenthos communities are used as indicators of lake condition overseas (e.g. Anon. 1990; European Union 2000).

In Canterbury, reference conditions of Lakes Forsyth (Wairewa) (Woodward & Shulmeister 2006), Taylor (Schakau 1986) and Grasmere (Schakau 1991, 1993) have been reconstructed using chironomid (sub) fossils preserved in lake sediments, showing that the community structure of chironomids is a useful indicator of changes in trophic state and temperature in lakes.

MACROPHYTE DEPTH LIMITS

There is a strong relationship between the maximum depth to which macrophytes can grow and water clarity, across a wide range of lakes (Schwarz et al. 2000), indicating a strong sensitivity to pressure gradients affecting water clarity. The depth to which macrophytes can grow defines the littoral zone of lakes, which is generally the zone of highest productivity and biodiversity. Therefore, substantial reductions in macrophyte depth limits and water clarity have direct impacts on lake pristineness. Macrophyte depth limits are resilient to short-term variation in water clarity (Schwarz et al. 2000). Thus, this indicator may be preferable to more direct measures of water clarity, which may vary substantially over short time scales, particularly in shallow lakes (e.g. Schallenberg & Burns 2004). Macrophyte depth limits can be determined by SCUBA diving and should be assessed along a number of transects within a lake to account for potential spatial variability. In New Zealand, the maximum depth of submerged plants is used in the LakeSPI system as an indicator of ecological condition in lakes (Clayton & Edwards 2006b). In Europe, the depth limit of submerged plants has been found to be a better indicator of the ecological condition of small lakes than total percentage coverage of macrophytes (Mäemets & Freiberg 2007). However, macrophyte depth limits are not applicable to shallow lakes in which macrophytes either inhabit the entire lake bed or are completely absent from the lake.

EPIPHYTON AND PERIPHYTON COMPOSITION

Changes in the composition of epiphyton and periphyton have been shown to be useful indicators of eutrophication (Danilov & Ekelund 2000). The organisms that make up these communities generally have widespread geographical distributions, making them suitable for use as indicators of pristineness throughout New Zealand. Benthic diatoms can readily be referenced to pristine conditions using palaeolimnological techniques because their silicate frustules are generally well preserved in lake sediments (Battarbee et al. 2001). However, monitoring epiphyton and periphyton can be difficult and time consuming due to high spatial variability and the challenges of representative sampling and taxonomic identification (King et al. 2006). In addition, because light attenuation affects taxonomic composition, this should be taken into account when interpreting the composition of these groups as indicators of pristineness (Vis et al. 2006). The use of these groups as indicators is in its infancy in Europe (King et al. 2006), and has only been developed in New Zealand for subalpine pools (Kilroy et al. 2006).

Functional indicators

Functional indicators relate specifically to ecosystem processes that underpin ecosystem functionality. In response to increasing pressures, functional indicators such as rates of productivity or metabolism are generally conserved by species replacement within communities, where new species better adapted to new conditions replace species adapted to prior conditions (Schindler 1987, 1990). Therefore, while functional indicators may not be good early warning indicators of pressure changes, changes to ecosystem function can be catastrophic and, thus, indicators of ecosystem function should also be monitored. The scoring of separate functional indicators of pristineness for lakes against the seven assessment criteria is included in Table 10 and a brief discussion of some of the key points for each of the indicators follows below.

COMMUNITY METABOLISM

The metabolic rate of microbes in lake water and sediments has been studied for almost a century because of the strong link between this and higher level biological productivity. Between the 1950s and 1970s, there was great interest in these methods for assessing the ecological effects of nutrient enrichment in lakes. Phytoplankton primary productivity (PPr) is a key limnological variable for measurement because it represents a large proportion of the total energy available to the food webs of many lakes, particularly lakes in which macrophytes cover only a small proportion of the lake bed. PPr measurements of the water column are usually carried out in bottles filled with lake water, incubated for relatively short periods (e.g. hours to days). A variety of methods have been used to measure rates of phytoplankton production, including radio-labelled inorganic carbon uptake, oxygen production or changes in chlorophyll *a* (i.e. phytoplankton biomass) over time (Schallenberg 2004). Such bottle methods have also been used extensively to determine whether phytoplankton growth is limited by particular nutrients (e.g. nitrogen or phosphorus). While these methods can be relatively easily employed in any lake, studies indicate that rates of productivity can vary greatly on a seasonal basis and some lakes (e.g. Lake Taupo (Taupomoana), Lake Wakatipu) exhibit peaks in phytoplankton productivity in winter (Vincent 1983; Schallenberg & Burns 1997).

TABLE 10. EVALUATION OF FUNCTIONAL INDICES OF PRISTINENESS FOR LAKES AGAINST A SET OF ASSESSMENT CRITERIA. DETAILS OF THE ASSESSMENT CRITERIA ARE OUTLINED IN SECTION 4.5.

ASSESSMENT CRITERIA	METABOLISM	DECOMPOSITION	SEDIMENT ANOXIA	CONNECTEDNESS
Ease of sampling and analysis	Moderate (2)	Difficult (1)	Easy-moderate (2)	Easy (3)
Potential geographic coverage	Wide (3)	Wide (3)	Moderate (2)	Wide (3)
Relation to pristineness	Moderate (2)	Limited (1)	Moderate (2)	High (3)
Sensitivity to pressure gradients	Moderate ^a (2)	Unknown (1)	Moderate ^b (2)	Strong ^c (3)
Calibration to reference condition	Difficult (1)	Difficult (1)	Difficult (1)	Easy (3)
Temporal variability	Moderate (2)	High (1)	Moderate (2)	Low (3)
Use in New Zealand	Rare (1)	Rare (1)	Rare (1)	Occasional (2)
Use in other countries	Occasional (2)	Rare (1)	Rare (1)	Common (3)
Rank [points]	2 [15]	4 [10]	3 [13]	1 [23]

^a Probably non-unimodal.

^b In most cases, pristine sediments are aerobic.

^c For certain pressures, e.g. dams.

The assessment of whole lake rates of PPr and respiration (R) using inorganic carbon or oxygen budgets is difficult because of the equilibration of the gas molecules with the atmosphere, across the water-atmosphere interface. Consequently, the hypolimnion of stratified lakes has been a fruitful setting for research on carbon cycling because thermal stratification virtually prevents gases in this region from equilibrating with the atmosphere. Most research on hypolimnetic metabolism has focussed on oxygen depletion rates (Burns 1995; Schallenberg & Burns 1999), but some researchers have also examined carbon dioxide and methane ($\text{CO}_2 + \text{CH}_4$) accumulation rates, which is more appropriate if/when hypolimnia become anoxic (Carignan & Lean 1991). Rates of change of hypolimnetic gaseous carbon and oxygen have been expressed as volumetric and areal rates, and much debate has ensued as to which is more informative.

As in river systems, the relative rates of PPr and R in lakes has been extensively studied (e.g. Del Giorgio & Peters 1993; Carignan et al. 2000), though not specifically as measures of pristineness. Whole lake PPr:R ratios provide an indication of the balance between primary productivity and respiration, which could theoretically be an important indicator of pristineness. For example, it can be argued that primary productivity and community respiration should be balanced in pristine ecosystems. However, PPr:R is also strongly driven by the amount of allochthonous organic matter input to lakes (that exported from the catchment mainly as dissolved organic matter), as well as by lake morphology and rates of organic carbon sequestration into the sediments. Therefore, the link between PPr:R and pristineness is also often correlated with other natural environmental gradients.

DECOMPOSITION RATES

The rate of decomposition of particulate organic matter (POC) is influenced by a wide range of environmental factors, which are themselves subject to natural and anthropogenic change (Allan 1995). Although studies on POC decomposition have been common in rivers and streams (e.g. Young et al. 2008), they are relatively rare in lakes. Pope et al. (1999) examined litter colonisation and leaf processing rates in the littoral zone of an oligotrophic lake in Canada and found that litter was used primarily as invertebrate habitat rather than a food source. Talbot & Ward (1987) found that benthic invertebrates specialised in shredding POC were relatively uncommon in Lake Alexandrina. Little is also known about how lake depth, substrate type, proximity to the shoreline and the slope of the lake bed influence POC processing rates in lakes (Pope et al. 1999). Lake sediments are highly spatially heterogeneous with respect to variables such as organic matter content, grain size and water content (Häkanson & Jansson 1983). Therefore, the assessment of sediment POC decomposition rates on a lake-wide basis would require a large number of sampling sites. Decomposition rates are also temperature dependent and, therefore, vary seasonally, not only in relation to thermal stratification.

Hoeniger (1985, 1986) and Ahn (1991) pioneered the use of dyed, regenerated cellulose strips to measure the decomposition rate of cellulose by bacteria in the water columns and sediments of lakes. When measuring the decomposition rates of any introduced substrates, it is important to note that the rates may be non-linear over time because the processing of new substrates integrates different processes, including microbial colonisation, growth and community

succession. Microbial enzyme activities on plant substrates (such as cellulose or lignocellulose) have been shown to be potentially useful indicators of organic matter processing rates in lentic environments (Jackson et al. 1995). Hill et al. (2006) found that sediment microbial enzyme activity in the Laurentian Great Lakes was directly related to nutrient availability and may be indicative of regional-scale anthropogenic stressors.

Perhaps the major disadvantages with the use of decomposition measures as indices of pristineness is that little is known about how decomposition relates to pristineness or to pressure gradients. On a broad scale, decomposition rates are positively related to rates of organic matter production and, hence, trophic state, but there can be time lags and spatial decoupling of organic matter production and decomposition within lakes (e.g. Viner 1989), and the magnitude and timing of allochthonous organic matter inputs may play a major role in the metabolism of some lakes (Wetzel 2001).

SEDIMENT ANOXIA

Anoxia (the depletion of dissolved oxygen) in lake sediments often accompanies eutrophication, especially in lakes that exhibit vertical thermal or density stratification of the water column. Anoxia can influence the abundance and composition of the sediment macroinvertebrate assemblage, the rate of organic matter decomposition, and the chemistry and bio-availability of phosphate in sediments. The oxygen status of the sediments can be determined directly using oxygen electrodes or indirectly by measuring either the sediment reduction-oxidation (redox) potential or the depth in the sediment below which an iron rod or wire is inhibited from rusting due to the lack of free oxygen (Schultz 1999). Redox measurements, though indicative of oxygen status, are also influenced by the concentrations of other redox couples (e.g. $\text{NO}_3^-/\text{NH}_4^+$, $\text{SO}_4^{2-}/\text{H}_2\text{S}$, CO_2/CH_4 , $\text{Fe}^{3+}/\text{Fe}^{2+}$) in the sediment. These methods can be applied generally across lakes, but the oxygen content of sediment is strongly influenced by a number of site-specific factors like temperature, substrate organic matter content, substrate porosity, the light climate at the lake bed and the presence of macrophytes. Therefore, the oxygen content of the sediment exhibits high spatial and temporal variability in lakes.

Under anoxic conditions, sulphate in the sediments can be microbially converted to hydrogen sulphide (H_2S), which may diffuse into the water column and reach toxic concentrations. When the rate of oxygen uptake in sediment is high, the oxic/anoxic boundary can migrate above the sediment into the water column facilitating the release of the plant nutrient phosphate into the water column. In addition, sediment and water column anoxia results in the loss of habitat for multicellular organisms except for those that are most tolerant of anoxia (e.g. many insect larvae of the Chironomidae).

There is no commonly used palaeolimnological method to establish reference sediment oxygen concentrations for a lake. However, the presence and/or abundance of some fossil benthic organisms such as chironomids, benthic diatoms or macrophytes may be used to infer the historical extent of oxygen conditions at the sediment surface at specific sites.

CONNECTEDNESS

The hydrological connectivity of a lake to the associated aquatic environments within its catchment is important for maintaining migrating organisms within lakes, as well as maintaining natural flows of water, energy and matter (e.g. nutrients, dissolved organic matter) through lakes. By definition, a lake with an intact hydrological regime should not receive water diverted from outside its catchment and it should not have its inflow discharges reduced by the diversion or abstraction of water (Moss et al. 2003). As such, the relationship between hydrological connectedness and pristineness is clearly defined and relatively easily determined for any lake. In coastal lakes, the lack of predicted or expected diadromous fish species provides an indication of barriers to hydrological connectedness. An example of managed connectivity in coastal lakes is the artificial opening of the seaward barrier bars of Lake Ellesmere (Te Waihora) and Waituna Lagoon to reduce flooding of surrounding farmland (Duggan & White 2010; Schallenberg et al. 2010). Given current elevated levels of nutrient and sediment loading to these systems, managed openings may now actively enhance EI. Such managed opening regimes highlight the fact that temporal variability may influence the connectivity of some systems. Many hydrological barriers (e.g. dams) and diversions can be assessed from maps and databases, but small-scale abstractions may be more difficult to account for. The New Zealand Water Bodies of National Importance (WONI) database currently contains information on dams and an additional spatial layer is being added for all consented abstractions; thus it may allow adequate assessment of hydrological connectedness/pristineness.

Physico-chemical indicators

Physico-chemical conditions of lakes can be indicators of pristineness. Below, we discuss three commonly used approaches for monitoring the physico-chemical condition of lakes. The scoring of separate physico-chemical indicators of pristineness for lakes against the seven assessment criteria is included in Table 11 and a brief discussion of some of the key points for each of the indicators follows below.

TABLE 11. EVALUATION OF PHYSICO-CHEMICAL INDICES OF PRISTINENESS FOR LAKES AGAINST A SET OF ASSESSMENT CRITERIA. DETAILS OF THE ASSESSMENT CRITERIA ARE OUTLINED IN SECTION 4.5.

ASSESSMENT CRITERIA	TLI AND COMPONENTS	DISSOLVED OXYGEN	NON-NUTRIENT CONTAMINANTS	DISSOLVED ORGANIC MATTER
Ease of sampling and analysis	Easy (3)	Moderate (2)	Moderate (2)	Easy (3)
Potential geographic coverage	Wide (3)	Wide (3)	Wide (3)	Wide (3)
Relation to pristineness	High (3)	High (3)	High (3)	Low (1)
Sensitivity to pressure gradients	High ^a (3)	Moderate ^b (2)	Moderate ^c (2)	Low ^d (1)
Normalisation to reference condition	Moderate (2)	Difficult (1)	Easy (3)	Difficult (1)
Temporal variability	Moderate (2)	Moderate (2)	High (1)	Moderate (2)
Use in New Zealand	Common (3)	Occasional (2)	Common (3)	Rare (1)
Use in other countries	Common (3)	Common (3)	Common (3)	Rare (1)
Rank [points]	1 [22]	3 [18]	2 [20]	4 [13]

^a Linear.

^b Complex.

^c Depends on contaminant.

^d Some relations with vegetation.

TROPHIC LEVEL INDEX (TLI) AND ITS COMPONENTS

The Trophic-Level Index (TLI) integrates measures of key nutrients, algal biomass and water clarity to indicate lake water quality (Burns et al. 2000). Partly because of its ease of measurement and widespread applicability, it has been widely used in New Zealand lakes, and has been linked to nutrient loading and catchment land use (Hamill 2006). Thus, it is related to the concept of pristineness. TLI has four component parts: total nitrogen (TN), total phosphorus (TP), Secchi depth and chlorophyll *a*.

TN and TP are used as indicators of nutrient availability in many lake quality assessment schemes (Moss 2007), and they are strong predictors of lake productivity in temperate northern hemisphere regions (Vollenweider 1975).

The Secchi depth (or Secchi disk transparency) is a measure of water clarity that integrates factors such as suspended sediment, phytoplankton biomass and water colour caused by dissolved organic matter (known as chromophoric dissolved organic matter or CDOM).

Chlorophyll *a* concentration in the water is a measure of phytoplankton biomass and can be a robust indicator of nutrient enrichment (Moss 2007). However, variation in biomass-specific pigment content (e.g. chlorophyll *a* content per cell) and community composition may, to some extent, decouple chlorophyll *a* concentrations from phytoplankton biomass.

When using TLI as an indicator of pristineness, one must keep in mind that pristine lakes may exhibit high TLI scores due to high natural nutrient loads (shallow lakes situated on fertile plains, waterfowl nutrient loading, etc.) or naturally low water clarity (high levels of suspended sediments, peat staining of water, etc.). TLI variables often vary seasonally and, therefore, TLI measurements are often made on a monthly basis and then statistically adjusted for seasonality. Shallow lakes can exhibit high temporal variability in the components of TLI due to the entrainment of bottom sediment into the water column in windy conditions. Concentrations of inorganic suspended sediments can be used to correct TLI for sediment resuspension effects (Burns et al. 2000).

DISSOLVED OXYGEN

The dissolved oxygen (DO) content of water is a key component of water quality because of its metabolic importance to organisms and its important role in biogeochemical element cycling. DO measurements are particularly useful in lakes that undergo vertical thermal/density stratification because this virtually isolates the bottom waters (hypolimnion) from gas exchange with the atmosphere (reaeration). As a result, rates of DO consumption in the hypolimnion are more directly linked to metabolic processes than rates of change of DO in the mixed layer. Interannual changes in the DO content of the hypolimnion may indicate a trend in trophic state, as oxygen content may decline before other indicators of state (Carlson & Simpson 1996). It is generally considered that most fish cannot survive extended periods of time at oxygen levels below 2.0 mg/L (Wetzel 2001). If DO levels in the water column are below this threshold, it is highly likely that bottom sediments are anoxic, which has numerous implications for lake functioning (see section 5.2.2 'Sediment anoxia'). Thus, periods of anoxia in lake waters and surficial sediments would indicate an undesirable, and potentially non-pristine, state. However, the important influences of lake morphometry,

temperature and organic detritus can facilitate hypolimnetic anoxia in lakes, even if nutrient loading and phytoplankton biomass are at pristine levels.

In the mixed layer, single measurements of DO are usually not very indicative of water quality, due to typically large spatial, diel and seasonal variations (Moss et al. 2003). However, the use of data-logging DO sensors reduces the need for labour-intensive manual oxygen profiling and allows for measurements at high temporal resolution over long time scales. In shallow lakes, the degree of diel variation in DO concentration of the mixed layer can potentially indicate the level of metabolic activity occurring in lakes, although high-frequency measurements and corrections for oxygen equilibration with the atmosphere are required (Young & Huryn 1999).

NON-NUTRIENT CONTAMINANTS

Anthropogenic, non-nutrient contaminants often influence the public's perception about the ecological state of the environment (Mason 1997) and their presence in freshwater ecosystems is a clear indication of departure from a pristine condition. For example, in non-geothermal areas, heavy metal loading to freshwaters tends to be linked to point source contamination (e.g. mines, smelters) and trace element concentrations in lakes can be influenced by fertiliser use (Downs et al. 2008). The prevalence of organic pesticides in New Zealand freshwaters has not been assessed in detail. These contaminants tend to result from their applications on land by farmers, and by the horticultural and forestry industries. However, both heavy metals and organic pesticides are sometimes directly applied to freshwaters to manage nuisance growths of algae/cyanobacteria (e.g. CuSO_4 , chelated copper), macrophytes (e.g. Diquat) and riparian vegetation (e.g. glyphosate). Furthermore, alum (an aluminium-based, P-chelating chemical) has been added to lakes to attempt to reduce available phosphorus in the water column (e.g. Paul et al. 2008).

Faecal bacteria are routinely monitored as indicators of the presence of manure and sewage in freshwaters. Their occurrence in freshwaters either tends to be episodic and related to precipitation and resulting runoff from farms, or is related to sewage discharges.

The above indicators are often specific to certain anthropogenic activities and, therefore, their application is generally most useful when targeted to those specific activities or certain point sources of pollution. Contamination events are often episodic and, therefore, sampling to assess the degree of contamination can be difficult. For this reason, sampling sediment contaminant concentrations can be a useful way of determining time-integrated contaminant loads. Some of these indicators can be quite complex and costly to analyse (e.g. specific organic chemicals), whereas others are measured routinely and are not expensive to analyse (e.g. faecal bacteria).

For contaminants that naturally occur in low concentrations, determining pristine reference concentrations in lakes can be challenging and requires careful palaeolimnological procedures and exacting analytical methods.

DISSOLVED ORGANIC MATTER

Organic matter dissolved in lake waters is composed of a wide variety of organic solutes, from transparent, low-molecular-weight molecules to coloured, highly polymerised molecules. The latter are collectively referred to as chromophoric dissolved organic matter (CDOM), but have also been referred to as water colour, dissolved humic substances and gelbstoff. CDOM is responsible for a wide range of ecological functions in lakes, including chemical chelation (e.g. ions and a range of toxic contaminants; Steinberg 2004), the absorption of harmful UV radiation (Rae et al. 2001) and the provision of substrates for microbial food webs (Steinberg 2004). CDOM is typically supplied to lakes from soil organic matter and from wetland vegetation in the catchment (Rasmussen et al. 1989; Steinberg 2004). While CDOM is mainly sourced from the catchment, it is degraded in lakes by photo-oxidation and microbial degradation (Steinberg 2004) and, consequently, its concentration in lakes has been shown to decline with increasing water residence time (Rasmussen et al. 1989). Schindler et al. (1997) have also shown that the CDOM concentration of lakes in the Canadian boreal forest region is sensitive to climatic variations. Thus, while CDOM is an easily measured key physico-chemical component of lake water (Cuthbert & Del Giorgio 1992) reflecting the abundance and condition of soils and wetlands in the catchment, its concentration in lake water is also affected by *in situ* degradation processes and regional climate. Furthermore, little work has been done to characterise reference CDOM concentrations in lakes or CDOMs contribution to EI and, hence, its utility as an indicator of EI is questionable at this time.

5.2.3 Diversity

Biological diversity is usually a community-specific indicator that refers simply to species richness (number of species) or to any of a wide range of diversity indices that incorporate other data to account for the distribution of biomass across the taxa that make up the community (see section 5.1.3 for discussion about diversity indices). For example, a variety of diversity indices have been commonly used to summarise New Zealand stream invertebrate and fish community structure (e.g. Death & Winterbourn 1995). However, less work has been done on lake biodiversity in New Zealand. It has been suggested that diversity in ecosystems should impart ecological resilience (McCann 2000). The scoring of separate community diversity indicators for lakes against the seven assessment criteria is included in Table 12 and a brief discussion of some of the key points for each of the indicators follows below.

Native aquatic macrophyte diversity is probably the best-documented indicator, and is included as a component of the commonly used LakeSPI methodology of lake condition assessment (e.g. Clayton & Edwards 2006b). The diversity of low-growing aquatic plants was found to be positively correlated to intra-annual water level variation, while negatively correlated to inter-annual water level variation in 21 New Zealand lakes (Riis & Hawes 2002). This work indicates that macrophyte diversity is sensitive to lake condition, the presence of certain invasive aquatic macrophytes and physical disturbance regimes. While macrophyte biomass can vary greatly depending on season, macrophyte species richness is relatively unaffected by seasonal variation (De Winton & Schwarz 2004).

TABLE 12. EVALUATION OF DIVERSITY OF DIFFERENT TAXONOMIC GROUPS FOR LAKES AGAINST A SET OF ASSESSMENT CRITERIA. DETAILS OF THE ASSESSMENT CRITERIA ARE OUTLINED IN SECTION 4.5.

ASSESSMENT CRITERIA	PHYTO- PLANKTON	ZOO- PLANKTON	MACRO- INVERTS	FISH	MACRO- PHYTES	EPIPHYTON/ PERIPHYTON
Ease of sampling and analysis	Difficult (1)	Difficult (1)	Moderate (2)	Moderate (2)	Moderate (2)	Difficult (1)
Potential geographic coverage	Wide (3)	Wide (3)	Wide (3)	Moderate (2)	Moderate (2)	Moderate (2)
Relation to diversity	N/A	N/A	N/A	N/A	N/A	N/A
Sensitivity to pressure gradients	Low ^a (1)	Low ^a (1)	Moderate ^b (2)	Moderate ^c (2)	High ^d (3)	Low ^a (1)
Normalisation to reference condition	Difficult (1)	Difficult (1)	Difficult (1)	Moderate (2)	Moderate (2)	Difficult (1)
Temporal variability	High (1)	Moderate (2)	Low (3)	Moderate (2)	Low (3)	High (1)
Use in New Zealand	Rare (1)	Occasional (2)	Rare (1)	Rare (1)	Common (3)	Rare (1)
Use in other countries	Rare (1)	Rare (2)	Rare (1)	Occasional (2)	Common (3)	Occasional (2)
Rank [points]	5 [9]	4 [12]	2 [13]	2 [13]	1 [18]	6 [9]

^a Poorly known.

^b Some sensitive taxa.

^c Sensitivity to invasive species.

^d Some indices.

The negative impacts of introduced trout on native fish diversity have been clearly demonstrated in streams (Townsend 1996). However, evidence for similar effects in lakes remains largely circumstantial (Deans et al. 2004; Wissinger et al. 2006). It has also been suggested that, due to the generally low freshwater fish diversity in New Zealand, fish species diversity is a poor indicator of lake condition, despite its popularity as an indicator of lake condition in other countries (Rowe & Graynoth 2002). Freshwater fish diversity can vary seasonally due to migrations.

Macroinvertebrate diversity has been shown to relate to the nutrient status of lakes, but the relationship was quite non-linear, with the main response occurring at the super-eutrophic end of the nutrient gradient (Timms 1982). Weatherhead & James (2001) also showed that littoral invertebrates were strongly influenced by physical gradients of depth and exposure, and Kelly & Hawes (2005) demonstrated that the community composition of macroinvertebrates was related to invasive macrophytes. Generally, the diversity of sub-littoral and littoral zone macroinvertebrates remains quite stable throughout the year (Talbot & Ward 1987; Kelly & McDowall 2004).

Zooplankton exhibit sufficient levels of diversity in New Zealand lakes to indicate that zooplankton diversity could be a useful indicator of EI. This has not been extensively explored in New Zealand, but Drake et al. (2010) showed that rotifer diversity was negatively correlated with land-use pressures in shallow lakes.

The measurement of diversity is sensitive to sampling effort because the ability to collect rare species in a sample can be strongly dependent on sampling effort (Hughes 1978). Thus, when comparing diversity measures among samples, the diversity values should be standardised for sampling effort, although there is no universally accepted method for doing this. One approach may be to count an equal number of individuals in each sample. Thus, a large number of samples are required to effectively quantify the diversity in habitats with high diversity density (e.g. littoral zones of lakes; MacNeil et al. 2001). The taxonomic acuity

of the researcher identifying the organisms also influences diversity assessments, making it difficult to compare diversity assessments made by different researchers. The ability to resolve taxa to genus or species varies among groups of taxa (e.g. fish are easier to identify than phytoplankton). Therefore, diversity is more likely to be quantified in communities in which accurate taxonomic identification and discrimination is easier.

Across wide geographical scales, the diversity of communities is related to a number of natural gradients such as altitude, latitude, evapotranspiration, and spatial and temporal habitat variability (Mason 1997). Furthermore, biogeographical influences related to immigration rates (especially on islands), extinction rates and species refugia influence the diversity of communities in ways that do not reflect anthropogenic pressures. The human-assisted introduction of non-indigenous species into ecosystems compromises the nativeness and pristineness components of EI. Therefore, the measurement of the diversity of native species aligns more closely to our definition of EI than does the total species diversity of a given freshwater community.

Currently, little is known about how levels of native diversity under pristine conditions compares with diversity in lakes experiencing various levels and types of anthropogenic pressures.

5.2.4 Resilience

Ecological resilience can be assessed by measuring the amount of perturbation required to modify the set of mutually reinforcing processes and structures that characterise a lake ecosystem (Petersen et al. 1998). Thus, the concept of ecological resilience relates to factors affecting stability and vulnerability to change in lake ecosystems. Below, we discuss how light limitation and macrophyte collapse, nutrient limitation and cyanobacterial blooms, and food web complexity may be potentially useful indicators of ecological resilience of lakes. In Table 13, we assess the utility of these resilience indicators against the seven assessment criteria for assessing lake EI.

TABLE 13. EVALUATION OF INDICES OF RESILIENCE FOR LAKES AGAINST A SET OF ASSESSMENT CRITERIA. DETAILS OF THE ASSESSMENT CRITERIA ARE OUTLINED IN SECTION 4.5.

ASSESSMENT CRITERIA	LIGHT LIMITATION	NUTRIENT LIMITATION	FOOD WEBS
Ease of sampling and analysis	Easy-moderate (3)	Moderate (2)	Difficult (1)
Potential geographic coverage	Wide (3)	Wide (3)	Wide (3)
Relation to resilience	Complex (1)	Complex (1)	Complex (1)
Sensitivity to pressure gradients	Low ^a (1)	Low ^a (1)	Low ^a (1)
Normalisation to reference condition	Difficult (1)	Difficult (1)	Difficult (1)
Temporal variability	High (1)	High (1)	Low (3)
Use in New Zealand	Common (3)	Common (3)	Occasional (2)
Use in other countries	Common (3)	Common (3)	Common (3)
Rank [points]	2 [16]	3 [15]	1 [17]

^a Poorly known.

Light limitation and macrophyte collapse

The growth of aquatic macrophytes is strongly linked to water quality in lakes. Jeppesen et al. (1990) found significantly higher water transparencies in lakes with a large coverage of macrophytes compared with lakes where macrophytes were absent. In addition, Scheffer et al. (1993) argued that macrophyte growth leads to self-stabilisation of a clear water, macrophyte-dominated state that is ecologically valuable because macrophytes increase water clarity by reducing algal biomass and the resuspension of sediments. Scheffer (1998) described a theory of alternative stable states in shallow lakes, whereby either a macrophyte-dominated clear water state or a plankton-dominated turbid state can be maintained by ecological feedbacks, despite pressures to change from these states. If pressures exceed a resilience threshold, a lake can undergo rapid change to the alternate stable state.

Light limitation of macrophytes can be caused by increased turbidity and excessive growth of periphyton and/or deposition of fine particulate material on macrophyte fronds. The euphotic depth (depth in the lake to which 1% of surface irradiance can penetrate) is indicative of the maximum depth to which macrophytes can grow. Euphotic depth is assessed by measuring depth profiles of PAR (photosynthetically active radiation) with an underwater PAR sensor. The euphotic depth can be assessed in any lake but can vary markedly over time in response to seasonality, floods, algal blooms and wind. Excessive variation in, or consistent reductions in, the euphotic depth over time can indicate that any macrophyte communities that are present may become light-limited, leading to the collapse of these communities. Thus, where historical water clarity data are lacking, the ratio of the euphotic depth to the maximum depth of macrophyte growth is likely to be a useful indicator of recent change in water clarity. Water level variations and the effect of the wave wash zone also help determine the potential area of lake bed available for macrophyte growth.

The collapse of macrophytes has been found to accompany declines in water quality in many New Zealand lakes (Hayes & Rutledge 1991; Hamill 2006; Kelly & Jellyman 2007; Schallenberg & Sorrell 2009). While the consumption of macrophytes by birds, fish or freshwater crayfish can contribute to macrophyte collapse (Hamill 2006), the reduction in light penetration as a result of excessive algal growth (usually the result of nutrient enrichment from the catchment) and the introduction of the invasive exotic macrophyte *Egeria densa* may also be important drivers (Schallenberg & Sorrell 2009). Other factors include the erosion of lake margins due to water level fluctuation, increased levels of suspended solids contributed from tributaries and the introduction of bottom-feeding exotic fish (Rowe 2004; Schallenberg & Sorrell 2009). Therefore, regime shifts from clear water to turbid states and the past frequency of such shifts are strong indicators of vulnerability to abrupt changes in EI. Furthermore, the determination of the proximity of a lake's condition to its resilience threshold (demarcating the onset of macrophyte collapse) is a key indicator of the resilience of a lake to macrophyte collapse and the potential to switch states (Schallenberg & Sorrell 2009). To assess whether specific lakes exhibited regime shifts prior to anthropogenic influence necessitates the use of palaeolimnological techniques, but these rarely provide the high temporal resolution required to determine the historical frequencies and/or durations of regime shifts.

Nutrient limitation and cyanobacteria blooms

Phytoplankton blooms are generally related to lower water quality and they often have serious consequences for lake ecosystems. The growth of phytoplankton can be limited by the availability of a number of factors in lakes. While it is often assumed that phytoplankton will respond positively to nutrient additions, this may not be true if they are nutrient saturated and are limited by other factors such as light (Schallenberg 2004). On the other hand, where the availability of nutrients does limit phytoplankton growth, nutrient management may be a useful tool for controlling algal proliferation. Therefore, understanding the factor(s) limiting algal proliferation in lakes is important if we are to understand the potential resilience of lakes to anthropogenic pressures such as nutrient loading.

In shallow lakes that do not thermally stratify, phytoplankton light limitation is related to the ambient light levels, the euphotic depth, the maximum lake depth and physiological characteristics of the phytoplankton community. In thermally stratified lakes, light limitation is also related to the mixed layer depth. Some phytoplankters are able to overcome light stress passively by regulating their buoyancy using gas vesicles (e.g. cyanobacteria) or by active movement (e.g. dinoflagellates).

In lakes in which phytoplankton receive sufficient light, nutrient availability may limit the growth of phytoplankton at times (Schallenberg 2004). Nutrient limitation can be determined by carrying out nutrient enhancement bioassays, and may be inferred by examining nutrient concentrations (i.e. availability) in the mixed layer (White et al. 1985). Nutrients that commonly regulate phytoplankton growth in lakes include inorganic nitrogen, inorganic phosphorus and trace elements (Schallenberg 2004; Downs et al. 2008). Phytoplankters that can utilise alternative sources of nutrients, either by fixing atmospheric nitrogen (e.g. some cyanobacteria) or by consuming bacteria (e.g. some dinoflagellates), are able to overcome a lack of inorganic nutrient availability that can limit the growth of other phytoplankters. Thus, nitrogen fixing cyanobacteria often dominate the phytoplankton in lakes in which other phytoplankters are nitrogen limited. Such conditions may be inferred by examining the ratios of dissolved inorganic nitrogen to total phosphorus in the mixed layer (Morris & Lewis 1988).

Under certain conditions, some cyanobacteria can achieve very high biomasses. Such 'blooms' can trigger anoxia in bottom waters as the blooms decompose, facilitating the anaerobic release of phosphate previously bound in the lake sediments. This can then fuel further phytoplankton growth, establishing a positive ecological feedback. Furthermore, some cyanobacteria taxa can produce toxins that can injure or kill wildlife, pets and humans that come into contact with lake water (Wood et al. 2006). The frequency of occurrence of visible cyanobacterial blooms has been suggested as one of the few variables that can be used robustly and inexpensively to assess the ecological condition of European lakes (Moss 2007). Blooms and periods of toxin production can be highly episodic and, therefore, monitoring should be undertaken at a relatively high frequency to determine whether cyanobacteria occur and produce toxins in a given lake.

As light and nutrients are often the main drivers of phytoplankton biomass and growth in lakes, knowledge of light and nutrient conditions in lakes is important for assessing the potential for phytoplankton blooms to occur, particularly cyanobacterial blooms. Whether New Zealand lakes in their pristine condition experienced cyanobacterial blooms is not yet understood; however, the resting stages (akinetes) produced by some cyanobacteria have been recovered from lake sediments up to 100 years old (Wood et al. 2009). Thus, palaeolimnological methods appear to be able to provide information on the historical presence of cyanobacteria in lakes. Determining both the resilience of lakes to phytoplankton blooms and the relationships between resilience and anthropogenic pressures are important in assessing EI.

Food web analysis

Studies investigating the impact of biodiversity loss on ecosystem function have become widespread as a result of concern over species extinctions (Loreau et al. 2001; Duffy 2002). Examination of food web complexity or food chain length is a useful means of integrating information on potential changes to the functioning of aquatic ecosystems (Vander Zanden et al. 1999b). Sampling of food web components can be time consuming and costly, especially if whole food webs are examined. However, costs can be reduced by focusing on portions of the food web (e.g. top trophic levels). Food web studies can be conducted in any system; however, biogeography and lake ecotype considerations may be relevant when comparing results between lakes or regions, or calibrating results to reference lakes. Food web studies can help develop an understanding of the complex effects of introduced species (Vander Zanden et al. 1999a; Rowe & Schallenberg 2004; Kelly & Hawes 2005) and eutrophication (Fry 1991; Jones et al. 2004) on aquatic systems. Stable isotopes of carbon and nitrogen have often been used to provide time-integrated information about food web dynamics and energy flow through the food web (Vander Zanden et al. 1999b; James et al. 2000; Kelly & Jellyman 2007; Pace et al. 2007). Stable isotope data have been collected in a variety of New Zealand lakes and may provide insights into how lake food webs respond to disturbance, serving as a suitable structural indicator of ecosystem resilience.

6. Discussion

Ecological integrity continues to be a controversial concept, both in definition and measurement. Our working definition follows a long line of previous attempts worldwide. Although the precise definition may vary, EI is generally considered to be a composite of at least some aspects of nativeness, pristineness, diversity and resilience. To exhibit maximum integrity, a river or lake would maintain itself independently of any human influence, exhibiting resilience to natural changes.

Problems persist in defining appropriate reference conditions against which to assess the current EI of New Zealand's rivers and lakes. Many water quality classification systems have opted for using minimally impacted sites to represent reference conditions. Around the world, classification systems are increasingly being used to classify lakes and streams into types and type-specific biological targets, as a result of many government agencies adopting a holistic, ecoregion approach. Such geographical classifications are useful for dealing with natural geographical variability, as they acknowledge that differences between regions may influence how pressures impact on biota (Hawkins et al. 2000; Sandin & Verdonschot 2006). The European Water Framework Directive (WFD) uses abiotic variables to classify streams and rivers into types, defined by ecoregions, catchment area, geology and altitude, whereas the UK RIVPACS predictive model and its many derivatives use biotic variables. Sandin & Verdonschot (2006) suggested that multivariate models were more effective at predicting reference conditions for macroinvertebrates than WFD physical typology categories, as they made use of continuous rather than categorical variables. However, FWENZ (Freshwater Environments Classification of New Zealand rivers), the GIS-based multivariate environmental classification of the New Zealand river network, seems to be an advance on the WFD methodology. It uses a unique combination of biological (fish and macroinvertebrate) and environmental inputs to classify New Zealand's rivers and streams into general habitat groups at a range of scales, from national to local (Leathwick et al. 2008b). The detailed nature of local and regional type classes offers great potential for EI assessment in specific river habitats or ecotypes, allowing focussed use of metrics (especially if major pollution threats have already been identified) and providing environmental contexts for interpretation.

Rivers and lakes have some key differences with regard to the factors governing their physico-chemical conditions and structuring their biotic communities. However, both are subject to an array of anthropogenic pressures, impacting at a variety of spatial and temporal scales (Allan et al. 1997; Danz et al. 2007). In general, analytical tools for the evaluation of EI in lakes are less developed than those for rivers. This may be a reflection of the great ecological variability that seems to exist within lake ecotypes, necessitating the establishment of reference conditions on a case-by-case basis. Useful indicators of EI should be relatively robust to natural spatio-temporal variability, but must be sensitive to the anthropogenic pressures they attempt to assess. We have discussed some of the sources of variability and uncertainty related to many potential EI indicators and, ideally, sampling error, variability in taxonomic resolution and other extraneous sources of variability must be accounted for when using them. This has also been highlighted as a concern in a number of current European and North American indicator schemes.

6.1 RECOMMENDED INDICATORS

The careful selection of structural and functional indicators is important when developing a practical scheme for assessing EI. We have evaluated a range of common indices that can be used to measure the four core components of EI: nativeness, pristineness, diversity and resilience. In Tables 14 & 15, we present a list of the indicators for rivers and lakes that we determined as being the most useful and robust for measuring the components of EI. Our assessment was guided by seven assessment criteria.

For the purpose of this review, there was no weighting of the assessment criteria, so each contributed equally to the indicator's rank. If the objectives of the monitoring programme were focussed around specific criteria, such as sensitivity to particular pressure gradients, the assessment criteria could be weighted accordingly. Within the tables, we have also cited the predominant pressure gradients associated with each of the indicators; thus, a suite of indicators could be selected to align with known pressures. Because there is some redundancy in the indicators identified in the tables (typically three indicators per EI component), the use of all the suggested indicators is not essential to obtaining a robust assessment of EI. Thus, ideally, the combination of indicators selected should reflect the range of pressures expected over the monitoring network and should cover the four EI components.

TABLE 14. SUGGESTED LIST OF INDICATORS FOR THE ASSESSMENT OF ECOLOGICAL INTEGRITY IN RIVERS AND STREAMS.

The indicators identified under each category were taken from the highest ranking indicators as tested against the seven assessment criteria (Tables 1-7). Indicators are thereby thought to be universally applicable, robust, relatively inexpensive, require minimal taxonomic skill and are likely to be the most responsive to anthropogenic stressors. The main stressors that can be detected by the indicators are also reported.

GENERAL PROPERTY OF EI	INDICATOR	EXAMPLES OF MAIN STRESSORS THAT MAY BE DETECTED	
Nativeness	Native fish (% native, no. of introduced species, O/E)	Invasion and introduction	
	Presence of invasive macrophytes/algae	Invasion and introduction	
Pristineness	Structural	Macroinvertebrate community composition (MCI, %EPT)	Multiple disturbances
		Fish IBI	Invasion and introduction
	Functional	Ecosystem metabolism	Eutrophication, habitat degradation, flow abstraction
		Wood decomposition rates	Eutrophication, change in land use
		BOD	Organic enrichment
	Physico-chemical	$\delta^{15}\text{N}$ of primary consumers	Specific N and P enrichment
		Water clarity, turbidity	Eutrophication, sedimentation
		Nutrient concentrations	Eutrophication, sedimentation
		Water temperature, dissolved oxygen	Riparian and catchment clearance, abstraction
	Diversity	Macroinvertebrate taxonomic richness, diversity, O/E richness	Multiple disturbances
Abiotic structure (habitat template)		Change in physical template, abstraction, irrigation	
Resilience	Presence/absence of key indicator taxa	Multiple disturbances	
	Ecosystem function	Change in physical template	

TABLE 15. SUGGESTED LIST OF INDICATORS FOR THE ASSESSMENT OF ECOLOGICAL INTEGRITY IN LAKES.

The indicators identified under each category were taken from the highest ranking indicators as tested against the seven assessment criteria (Tables 8-13). Indicators are thereby thought to be universally applicable, robust, relatively inexpensive, require minimal taxonomic skill and are likely to be the most responsive to anthropogenic stressors. The main stressors that can be detected by the indicators are also reported.

GENERAL PROPERTY OF EI	INDICATOR	EXAMPLES OF MAIN STRESSORS THAT MAY BE DETECTED	
Nativeness	Catch per unit effort (CPUE) of native fish	Invasion by/introduction of exotic species	
	Percentage of species native (macrophytes, fish)	Invasion by/introduction of exotic species	
	Absence of invasive fish and macrophytes	Invasion by/introduction of exotic species	
	Proportion of shoreline occupied by native macrophytes	Invasion by/introduction of exotic species	
Pristineness	Structural	Depth of lower limit of macrophyte distribution	Eutrophication (benthic effects)
		Phytoplankton community composition	Eutrophication
	Functional	Intactness of hydrological regime	Connectedness, abstraction, irrigation, artificial human barriers
		Continuity of passage to sea for migrating fish (potentially indicated by diadromous fish)	Connectedness, artificial human barriers
		Water column DO fluctuation	Eutrophication
		Sediment anoxia (rate of redox potential change in sediments)	Anoxia, eutrophication (benthic effects)
	Physico-chemical	TLI (or its components)	Eutrophication
		Non-nutrient contaminants	Depends on pressures
	Diversity	Macrophyte, fish, invertebrate diversity indices	Loss of biodiversity
	Resilience	Number of trophic levels	Loss of top predators
Euphotic depth compared to macrophyte depth limit		Macrophyte collapse	
Instance/frequency of macrophyte collapse or recorded regime shifts between clear water and turbid states		Macrophyte collapse	
Compensation depth compared to depth of mixed layer		Potential for light or nutrient limitation of phytoplankton growth	
DIN:TP ratio		Risk of cyanobacterial blooms	
	Presence of potentially bloom-forming cyanobacteria	Risk of cyanobacterial blooms	

EI indicators could also be used to assess the outcomes of restoration or site rehabilitation. In such cases, the selection of indicators would reflect the management actions employed at the site. For example, if nutrient attenuation (e.g. riparian enhancement) was the primary focus of the restoration, indicators could reflect the physico-chemical components of pristineness, such as nutrient concentrations, and the structural and functional components of the ecosystem that could respond to such changes in physico-chemistry, such as native plants and macroinvertebrates, and ecosystem metabolism.

6.2 COMBINING METRICS TO MEASURE ECOLOGICAL INTEGRITY

Diverse anthropogenic pressures, such as agriculture, point source pollution and changes in land use, overlap in space and time, and can have independent, synergistic or antagonistic effects on ecosystems (Niemi & McDonald 2004). This review has evaluated a range of potentially useful indicators of EI and grouped them into the four components of EI. From a management perspective, it would be useful to combine these individual component metrics into a single, comprehensive measure of EI. This has previously been attempted in different ways, but predominantly by either combining or averaging indicator values, informed by expert opinion, into a single multimetric index, or by developing a multimetric model from a range of indicators using multivariate statistical methods.

Karr (1981) was the first to suggest combining fish metrics to create an index of biological integrity (IBI). His approach formed the cornerstone of multi-metric index (MMI) development and has been widely adopted in river assessment (e.g. Lyons 1992; Hering et al. 2006) and to some degree in lakes (Reavie et al. 2008). When they work, these can be powerful tools for making informed management decisions about EI. However, they can also be oversimplistic and misleading if insufficient attention is paid to assumptions, or if it is difficult to measure or evaluate the present departure of the system from expected reference conditions (Niemi & McDonald 2004). Recent comparative studies of multiple indicators have shown how different groups of organisms provide complementary information about ecological condition. For example, a parallel investigation of fish, macroinvertebrates and diatom assemblages showed that assessments based on one group were less likely to indicate degraded conditions than assessments based on several groups. Individual component metrics should be carefully weighted, as the discriminatory power and relative importance of different metrics have been shown to vary markedly in rivers and streams. For example, in a study of over 150 streams, Johnson et al. (2006) found that benthic diatom and macroinvertebrate metrics showed high discriminatory power and low error for a pressure gradient describing nutrient enrichment, but performed poorly for a gradient describing habitat alteration and hydromorphology; the converse was true for fish and macrophyte metrics. Snelder et al. (2006) highlighted the problems of weighting and transforming variables when designing multivariate environmental classifications. Similarly, Leathwick et al. (2008b) recognised the problems in the development of FWENZ, which used environmental variables for which selection, weighting and transformation had been defined via analysis of fish and macroinvertebrate distribution data.

Multivariate statistical methods such as canonical correspondence analysis (CCA) and redundancy analysis (RA) (Ter Braak & Verdonschot 1995) have been used to derive statistical models for estimating and predicting ecological condition (e.g. Danz et al. 2007), and informative comparisons have been made between these methods and multimetric methods (e.g. Reynoldson et al. 1997; Karr 2000). Such methods include axis reduction procedures, which can help simplify and focus models on key variables and relationships. Other advantages include objective model selection, statistical optimisation and validation, and the modelling of multivariate response variables (e.g. EI).

Multivariate regression tree modelling is a type of multivariate analysis related to RA and CCA. However, rather than analysing environmental gradients as RA and CCA do, the regression tree approach produces a classification of discreet environment types (De'Ath 2002). Boosted regression tree modelling (BRT; Elith et al. 2008) was applied to a national New Zealand dataset to examine the responses of multiple ecological indicators to a range of environmental stressors (e.g. agricultural land use, urbanisation), yielding some useful information on the performance of various ecological indicators against known stressor gradients (Clapcott et al. 2010; J. Clapcott, unpubl. data). The BRT models provided a comparative measure of strength of association (% deviance explained) and predictive error (cross validation coefficient), as well as an indication of the form of the relationship (i.e. linear, curvilinear, unimodal). The strongest indicators, based on model sensitivity and precision, were NO_x, the $\delta^{15}\text{N}$ of primary consumers and the macroinvertebrate community index, while the weakest overall were gross primary productivity, fish taxon richness and invertebrate taxon richness. This information was then used in a multimetric indicator of EI, with individual metrics weighted based on their contribution to the model (% deviance explained) and the proportion of the river network for which the indicator data were available (i.e. certainty). Similarly, Drake et al. (2010) used BRT modelling to examine a range of lake metrics to land-use stressor gradients, but due to the limited sample size (45 shallow lowland lakes), were unable to develop a multimetric lake EI index from the dataset.

The next stage of this project will quantitatively examine the performance of indicators against a number of human pressure gradients as defined in the Waterbodies of National Importance (WONI) model (Leathwick & Julian 2007). This work, which is partially underway, will provide a quantitative evaluation of the recommended EI indicators for lakes (Drake et al. 2010) and rivers (Clapcott et al. 2010), and will also provide further guidance on measuring the EI of freshwaters.

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How can ecological integrity be used to manage New Zealand freshwaters?

Ecological integrity (EI) can be used to quantify ecosystem structure and function. However, there are many definitions of EI and, consequently, several different methods are used to measure it. In this report, we arrive at a working definition of EI, which includes four components: nativeness, pristineness, diversity and resilience. We then develop a methodology for assessing EI based on quantification of these components. We conclude with a list of suitable indicators for determining EI in New Zealand rivers and lakes.

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