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To cite this article: Carolyn W. Burns (1991) New Zealand lakes research, 1967–91, New Zealand Journal of Marine and Freshwater Research, 25:4, 359-379, DOI: [10.1080/00288330.1991.9516491](https://doi.org/10.1080/00288330.1991.9516491)

To link to this article: <http://dx.doi.org/10.1080/00288330.1991.9516491>



Published online: 30 Mar 2010.



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Silver jubilee review

New Zealand lakes research, 1967–91

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landscapes, and peatlands. Nearly 800 lakes exceed 0.5 km in length; the largest in area is 623 km² (Lake Taupo) and the deepest is 462 m (Lake Hauroko). They range widely in water chemistry, colour, clarity, and productivity, and include some extreme examples by international standards.

Abstract Research on New Zealand lakes over the past 25 years has focused mainly on eutrophication, measures of water quality, patterns, processes and production in plankton communities, and the spread and growth of submerged adventive macrophytes. Compared with most northern temperate lakes many New Zealand lakes show: low levels of inorganic nitrogen (N) and frequent N-limitation of phytoplankton growth; diffuse, rather than point source, nutrient inflows; a great diversity of optical properties; unusual and often variable timing of plankton growth (attributed to the pervasive influence of New Zealand's oceanic climate); low productivity and biomass of zooplankton, which appear to be limited by food rather than predators; and sensitivity to invasion by adventive macrophytes. Notable research developments include improved methods of measuring nutrients, empirical predictive models that relate indices of eutrophication to nutrient loading, and significant advancements in methods of quantifying and measuring water colour and clarity.

Keywords New Zealand lakes; limnology; eutrophication; phytoplankton; zooplankton; water transparency; aquatic plants; review

INTRODUCTION

For its size, New Zealand has a remarkable diversity of lake types. There are lakes formed by glaciers, earth movement, wind, rivers, landslides, and humans; lakes associated with volcanic activity, karst

HISTORICAL PERSPECTIVE

In the 150 years that have elapsed since the first Europeans settled in New Zealand, many species of plants and animals have been introduced, rivers have been dammed, and land has been cleared extensively for farming, forestry, roads, and urban development. The impact of these activities on New Zealand's lakes has directed much research. Before 1966 there had been scant investigation of New Zealand lakes. Some valuable taxonomic information on algae and invertebrates was available, but only a few general limnological studies had been carried out, and fewer still had been published (see reviews in Jolly & Brown 1975). Coastal dune lakes of Northland, New Zealand, had been studied (Cunningham et al. 1953), but the first paper on freshwater lakes to appear in the *New Zealand Journal of Marine and Freshwater Research* was Jolly's (1968) comparison of physical and chemical parameters of some of New Zealand's major lakes; it was also to provide valuable data against which to assess changes in some of these lakes over subsequent decades (e.g., McColl 1972; Vincent et al. 1984).

INSTITUTIONAL ARRANGEMENTS

Research on lakes gained momentum in New Zealand in the 1960s with the appointment of limnologists to the staff of universities; the formation of the New Zealand Limnological Society; and the establishment in 1969 of the Freshwater Section (currently within DSIR Marine and Freshwater) of the Department of Scientific and Industrial Research. The mandate of this section was to investigate eutrophication processes; the Ministry of Agriculture and Fisheries

M91061

Received 28 August 1991; accepted 11 December 1991

(MAF) had complementary studies on lake-front fisheries and eutrophication in Lake Rotorua. Problems related to the spread of exotic aquatic macrophytes prompted the creation of an Aquatic Plant Section within MAF, at Ruakura Agricultural Research Centre; some research on lakes was carried out by staff of Cawthron Institute in Nelson, a few Catchment Boards (now Regional Councils), New Zealand Electricity Department (now Electricorp), and Hydrology and Water Quality Centres of the Ministry of Works and Development (currently part of DSIR).

MAPS, KEYS, AND INVENTORIES

During the past 25 years most of New Zealand's lake basins have been surveyed, generally by J. Irwin and colleagues of New Zealand Oceanographic Institute. The resultant bathymetric maps, published as New Zealand Lake Chart Series (Irwin 1967, etc.) are a major asset to limnological studies in this country.

Accurate identification of the flora and fauna is critical to an interpretation of patterns and processes in most ecological systems. Although taxonomic keys for the identification of the biota of North American and European lakes have been available for most of this century, it is only in the past two decades that equivalent keys for New Zealand's lake biota have been compiled. Taxonomic keys and checklists are now available for larger invertebrates (Chapman & Lewis 1976; Winterbourn & Gregson 1981, 1989), some algae (Pridmore & Hewitt 1982; Cassie 1984a, 1984b; Croasdale & Flint 1986, 1988; Etheredge & Pridmore 1987), aquatic macrophytes (Johnson & Brooke 1989), and fish (McDowall 1978, 1990).

An inventory of the major lakes and catchment features of more than 81 lakes in each of the North and South Islands has been assembled (Livingstone et al. 1986). For each lake, the location, morphometric, and bathymetric features are listed; proportional vegetative cover of the catchment is described, and the available information on thermal regime, stratification, water chemistry, and biota is referenced.

SCOPE OF REVIEW

The broad extent of scientific understanding of New Zealand lakes in the last two decades is reviewed in three books (Jolly & Brown 1975; Viner 1987a; Vant 1987b) and two articles (Stout 1973, 1975). Lake Taupo, and biological aspects of the hydrolakes are

the subject of specialised books (Forsyth & Howard-Williams 1983; Henriques 1987). In the present review, areas of research emphasis over the past 25 years are identified, major findings are highlighted, and changes that have occurred in our understanding of New Zealand lakes during the period are noted. As lake fisheries are reviewed by McDowall (1991: this issue) they are not included in this review. Significant contributions have been made to limnological research in studies of lakes in the Ross Dependency, Antarctica, particularly in the last decade, but they are the subject of recent reviews (e.g., Vincent 1987a, 1988) and are not discussed here.

The total number of studies on lakes in New Zealand increased dramatically during the two decades, 1966–85 (Fig. 1). Although necessarily selective, the data illustrate that major areas of research emphasis in New Zealand during this period have been eutrophication and water quality, thermal and physical aspects of lakes, submerged macrophytes, and phytoplankton production and ecology. Fewer papers have been published on zooplankton production and ecology, benthos, and sediments. Studies published in each of these research areas during 1966–91, more than one-third of them in the *New Zealand Journal of Marine and Freshwater Research*, are reviewed below.

Eutrophication

Approaches The causes and consequences of increased nutrient loads in lakes provided the major focus for research in New Zealand from the early 1970s until the mid 1980s (Fig. 1). The deteriorating water quality of Lake Rotorua (Fish 1969a, 1970) and the occurrence of algal blooms and scums on lakes elsewhere in New Zealand (e.g., Burns & Mitchell 1974) coincided with heightened awareness of, and increased research on, accelerated eutrophication in North America and Europe. In New Zealand, the research was centred in the North Island on lakes of the Central Volcanic Plateau and in the South Island on lakes in Otago. The initial approach in the 1970s was to classify New Zealand lakes according to trophic state based on indices of eutrophication that had been developed in the Northern Hemisphere. For example, measurements of chlorophyll *a* (as an index of phytoplankton biomass), transparency (Secchi depth), various forms of phosphorus and nitrogen, and dissolved oxygen revealed a wide range of trophic states among lakes in the Rotorua area (McColl 1972). This study is notable in being the first to document the relation, in New Zealand, between increased land development

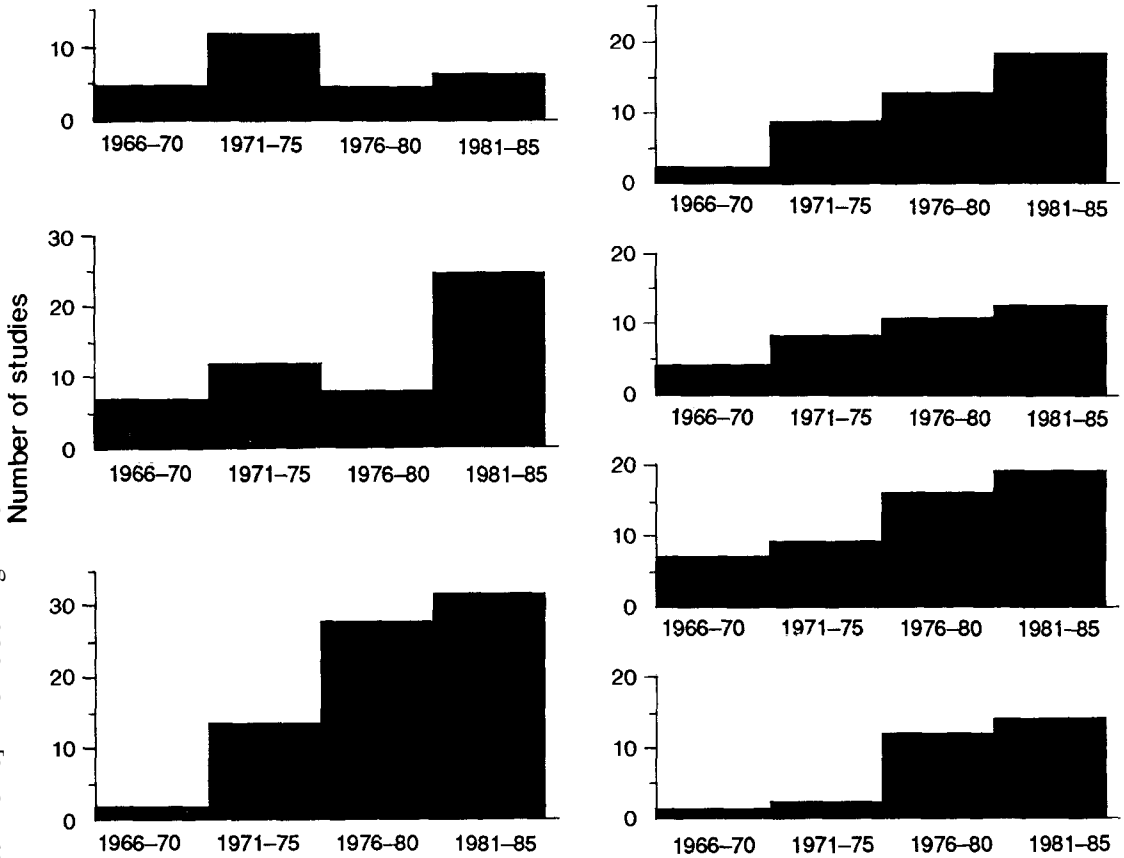


Fig. 1 Distribution of research in New Zealand lakes for the period 1966–85, based on citations in Viner (1987a) and Vant (1987b). Categories: **A**, General limnology (descriptive, rather than process-oriented research; includes physical and biological features of a lake, e.g., temperature, water transparency, plankton species composition, and biomass); **B**, Physico-chemical (includes water chemistry, thermal characteristics, mixing, optical properties, and groundwater studies; excludes bathymetric studies); **C**, Eutrophication (includes trophic indices, nutrient budgets, and oxygen deficits); **D**, Phytoplankton ecology and production (excludes taxonomy, new records, and inventories); **E**, Zooplankton ecology and production (excludes taxonomy, new records, and inventories); **F**, Submerged macrophytes; **G**, Sediments, benthos, and palaeolimnology. Some studies are listed in more than one category.

and lake trophic state (Fig. 2). This theme has been extended by White (1977, 1982, 1983) and others (e.g., McColl & Hughes 1981). White (1982) pointed out that New Zealand lakes differ from those in Europe and North America in that diffuse agricultural run-off, rather than point sources (e.g., feedlots, sewage), is a major source of nutrients in New Zealand; he also quantified the relationship between intensity of land use and trophic state. Descriptions of trophic state were soon augmented by predictive models and experimental approaches that were aimed at identifying the nutrients that were limiting algal growth. These techniques have been evaluated for use in New Zealand by Pridmore (1987). For lakes

with specific management problems, nutrient budgets have been developed (reviewed by Vant & Hoare 1987).

Nutrient limitation and predictive models A major finding during the 1960s and early 1970s was that, by world standards, New Zealand lakes are generally low in total nitrogen (e.g., Jolly 1968; McColl 1972). Levels of inorganic nitrogen ($\text{NO}_3\text{-N}$) and ratios of nitrogen (N) and phosphorus (P) are generally much lower in New Zealand lakes than in most northern hemisphere lakes (White 1982, 1983; Fig. 3). Effects of these differences for the assessment, prediction, and management of eutrophication in New Zealand

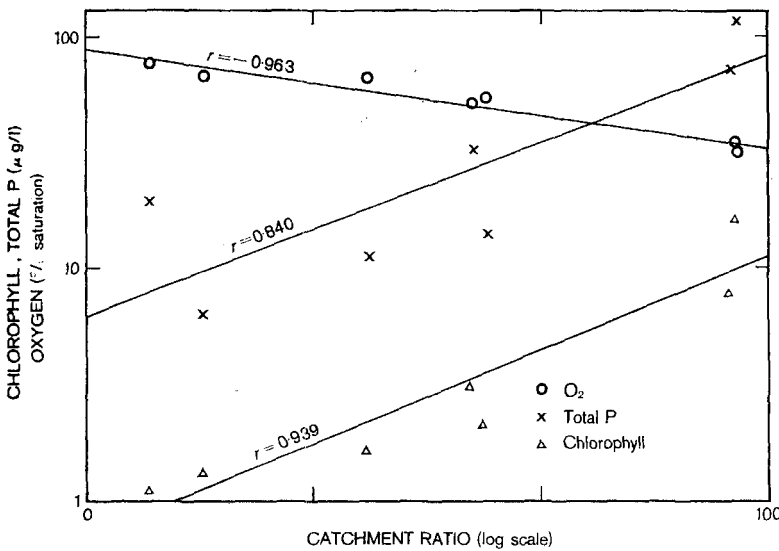


Fig. 2 Regression of catchment ratio (percentage of pasture, residential, and exotic pine forest plantation areas in the total land catchment) with mean percentage dissolved O₂ in bottom water and with mean total P and chlorophyll in surface waters of seven Rotorua lakes between April 1970 and April 1971 (r = correlation coefficient). From McColl (1972), with permission.

have been examined, particularly by White and his colleagues. Short-term nutrient enrichment experiments in a variety of lakes in both North and South Islands more than a decade ago implicated N as the nutrient most likely to limit algal growth in some New Zealand lakes (e.g., White & Payne 1977, 1978; Vincent 1981a, 1981b; Mitchell & Burns 1981). At the time, the prevailing view in North America and Europe was that algae were P-limited. Therefore, research in New Zealand helped draw to international attention the potential of phytoplankton growth to be limited by N rather than P (White et al. 1985, 1986).

The New Zealand research, described above, suggested that the findings of the Organisation for Economic Co-operation and Development Co-operative Programme on Eutrophication (OECD 1982), which were based largely on northern temperate lakes, are not directly applicable to lakes in New Zealand (White 1983). A general conclusion of the OECD report (1982) was that where the ratio of total nitrogen (TN) to total phosphorus (TP) in a lake was greater than 15, P would be the limiting nutrient and so would control algal biomass. Based on a series of studies in which N limitation was assessed by bioassays (see list above), White (1983) and White et al. (1985) suggested that 15 TN : 1 TP was inappropriate for New Zealand lakes because many contain a large proportion of their TN as dissolved organic nitrogen (DON)—a form that is largely unavailable to algae. If, however, the dissolved organic forms of N and P are subtracted first from the total

amounts, then the ratio above which P limits algal growth in New Zealand lakes approximates 15 N : 1 P. Accordingly, these authors advocated a more appropriate ratio, 15 (TN-DON) : 1 (TP-DOP).

Empirical models relating phytoplankton biomass (expressed as chlorophyll *a*) to TP levels that have been derived from northern hemisphere P-deficient lakes simply do not apply to New Zealand's N-deficient lakes (White 1983; Pridmore 1987). Nor are these models appropriate for shallow lakes with wind-induced resuspension of sediments (Hamilton & Mitchell 1988). In most New Zealand lakes in which nutrient limitation has been measured, however, phytoplankton associations are limited intermittently by both N and P, and some lakes appear to be P-deficient. In P-deficient New Zealand lakes, annual mean chlorophyll *a* concentrations appear to be positively correlated with TP (White 1982, 1983, but see White 1989; Pridmore et al. 1985) and regression models derived from New Zealand lakes lie between those from North America and OECD countries (Fig. 4).

Sources of nutrients In the 1970s, there was considerable debate over whether soil erosion and run-off from fertilised catchments would accelerate the eutrophication of lakes by supplying P through desorption, and the extent to which P in lake sediments was available to sustain phytoplankton growth. The availability of both P and N from these sources, assessed by McColl (1975a) and McColl et al. (1977), showed that agricultural catchments can contribute

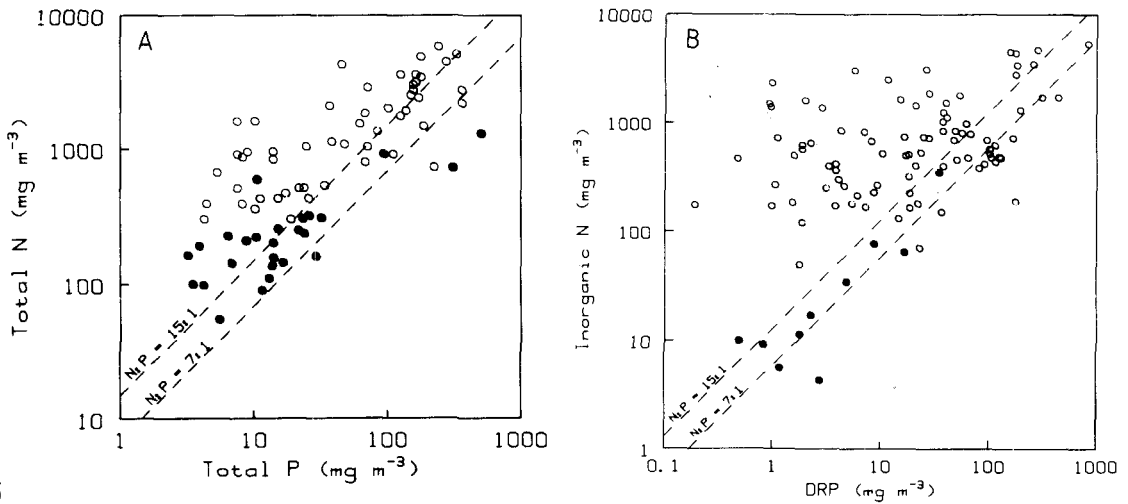


Fig. 3 Relative distribution of average annual values for nutrients in the, largely northern temperate, lakes of the OECD study (○) and New Zealand lakes (●). A, Total nitrogen and total phosphorus concentrations. B, Inorganic nitrogen and dissolved reactive phosphorus concentrations. The lines define a zone of N : P ratios that are typical of balanced algal growth (OECD 1982). From White (1983), with permission.

significant amounts of nitrate and phosphate to lakes compared with forested catchments.

Recognition of the pervasive influence of pumice soils on the nutrient chemistry of lakes in the Taupo volcanic zone, North Island, has aided understanding of their eutrophication (Timperley 1983). For example, in Lake Taupo where there is little evidence for geothermal influence, the weathering of rhyolitic pumice contributes 95% of the phosphate-P to this lake and thereby contributes also to the low N : P ratios in this lake. Gibbs (1979, 1987), however, drew attention to potentially high nutrient incomes caused by lakeshore development on pumice soils and showed that nutrients from septic tanks rapidly permeate such soils and free-flowing aquifers.

Nutrient budgets In the 1970s and 1980s considerable effort went into estimating nutrient loads of a few recreationally important lakes, particularly those that were experiencing algal blooms or massive growth of aquatic macrophytes (reviewed by Vant & Hoare 1987). Lakes Rotorua and Horowhenua (Vant & Gilliland 1991), the only two lakes in New Zealand to receive direct sewage inputs, and Lake Taupo were the focus of most attention. Detailed water and nutrient budgets were obtained for southern Lake Taupo (White & Downes 1977; Schouten et al. 1981;

Schouten 1983) and Lake Rotorua (e.g., Fish 1975a; Hoare 1980). To assist in evaluating the effects of nutrient reduction on Lake Rotorua, Rutherford et al. (1989) developed predictive models based on relationships between chlorophyll *a* and nutrients that had been developed in New Zealand, and a mass balance nutrient budget model that was calibrated for the lake.

Measuring nutrients and nutrient limitation

Accurate, reliable methods of measuring nutrients are essential for constructing nutrient budgets and evaluating nutrient limitation. In some lakes of the Central Volcanic Plateau, North Island, low levels of inorganic P are coupled with high levels of arsenate, silica, and mercuric chloride which interfere with standard techniques for the analysis of phosphate-P. Also, low concentrations of nitrate-N could not reliably be measured by some automated methods. By modifying existing techniques, Downes (1978a) reduced considerably the effects of interference on phosphate-P determination and developed a sensitive interference-free automated technique for the measurement of nitrate-N (Downes 1978b). Studies of nutrient limitation in New Zealand lakes have evaluated, modified, and developed new assays. For example, Vincent (1981a, 1981b) evaluated several

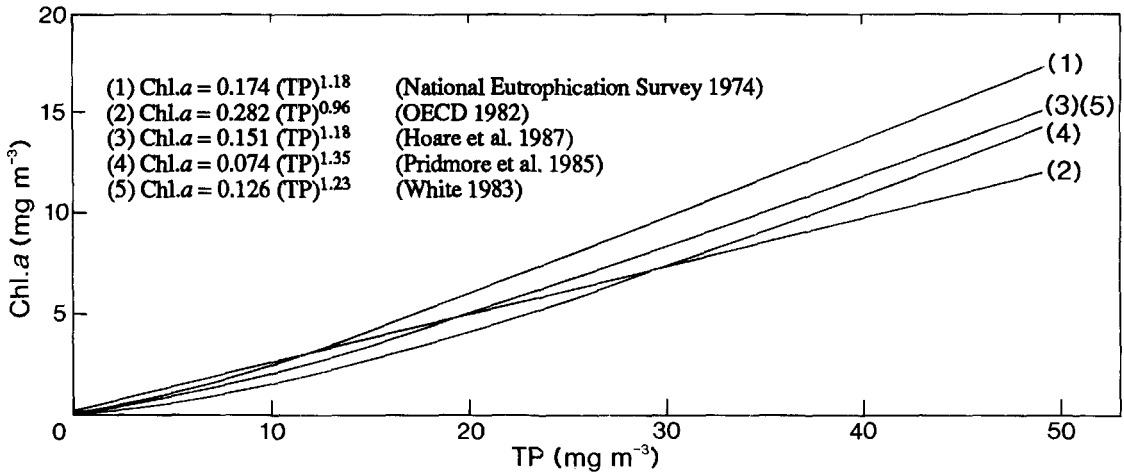


Fig. 4 Comparison of the chloro-phyll-phosphorus relationships derived for New Zealand lakes (lines 3, 4 and 5) with published northern hemisphere models (lines 1 and 2). Annual means or median concentrations of chlorophyll *a* (Chl.a) and total phosphorus (TP) are used in all relations. From Pridmore (1987) with permission, modified.

physiological assays to assess the demand by phytoplankton for N and P. Subsequently, one of these assays, ammonium enhancement, has been used and re-evaluated several times in New Zealand as a method of detecting N-deficiency in algae (e.g., Mitchell & Malthus 1984; White et al. 1985; Mitchell 1989).

Dissolved oxygen Changes in levels of dissolved oxygen in lakes are often associated with change in trophic condition. During the late 1950s and early 1960s, Jolly (1968) and Fish (1969b, 1970) measured oxygen levels at depth in several Rotorua lakes providing, thereby, valuable baselines against which to assess subsequent changes. By comparing dissolved oxygen profiles of seven Rotorua lakes in 1970–71 with earlier data, McColl (1972) showed that oxygen had decreased in at least six of the seven lakes during the previous 15 years and that the decreases were correlated with increased agricultural, forestry, or urban development in the catchments (Fig. 2). Subsequent studies focused further on the relation between levels of dissolved oxygen, and rates of oxygen depletion, and indices of lake productivity with the aim of deriving empirical models. White (1976) showed that the hypolimnetic oxygen content of 35 stably stratifying lakes was correlated with lake productivity. However, rates at which oxygen was

depleted were poorly correlated with productivity (Rutherford 1982) and so it is still not possible to make general predictions for New Zealand lakes about the rates of areal hypolimnetic oxygen depletion that might occur as a result of changes in lake productivity (Vant 1987a). In individual lakes where changes in rate of oxygen depletion and productivity have been measured with time (Fish 1969b; Mitchell & Burns 1979; Vincent et al. 1984; Vant 1987a; Viner 1989a), useful predictions can be made.

Water quality of lakes

Optical properties Although "Secchi depth" measurements of visual clarity have routinely been made in most studies of New Zealand lakes, it is only in the past decade that the remarkably diverse properties of the country's lakes have received close scrutiny. Since the colour and clarity of water are indicative of water quality, much research has been carried out either to provide predictive relationships between optical indices of water quality and indices of lake productivity or catchment development, or to improve methods of measuring colour and clarity (reviewed by Davies-Colley 1987). Based on measurements of quantum irradiance and a range of factors known to influence water quality (e.g., pigment, suspended solids) in 27 optically diverse lakes, Vant & Davies-Colley (1984) developed a

model of lakewater clarity that can be used to classify lakes into optical types and to partition clarity into proportional contributions from phytoplankton pigment, yellow substance, non-volatile suspended sediments, and detritus. Therefore, it offers a means of predicting the clarity of new impoundments and effects of changes in nutrient loading.

Studies have also focused on the underwater light climate for algae. Howard-Williams & Vincent (1985) examined the light available for photosynthesis (photosynthetically active radiation, PAR) in a wide range of New Zealand lakes. They showed how the rate of attenuation changes with depth, and quantified the influence of seston on this rate. In the same study, they examined the extent to which downward irradiance differs from scalar irradiance (i.e., total PAR) and showed that, in turbid lakes, measurements of downward irradiance alone can underestimate the number of quanta available to phytoplankton by as much as 60% (Howard-Williams & Vincent 1984).

Optical methods These and other studies of the underwater light climate of New Zealand lakes have stimulated appraisals of standard methods and techniques. For example, a method of measuring PAR under the changing ambient light conditions caused by drifting cloud patches was developed by Davies-Colley et al. (1984). The relation between scalar irradiance (measured by a 4π irradiation meter) and downward and upward irradiance (measured by a flatplate cosine-corrected irradiance meter) was examined by Spigel & Howard-Williams (1984) who provided a potentially useful conversion of measurements based on one method to those based on the other. Standard methods of measuring colour and clarity of water have been evaluated and improved by Davies-Colley (1983) who developed an integrating sphere attachment for a spectrophotometer to provide estimates of intrinsic optical properties of natural waters, especially turbid waters. An innovative procedure, that has attracted international interest, makes use of a wholly black Secchi disc, oriented vertically, to measure water clarity in rivers and reservoirs (Davies-Colley 1988a). Through the studies of the optical properties of New Zealand lakes, their authors have made significant contributions internationally to basic understanding and measurement of the underwater light environment of lakes in general.

Water chemistry The diverse pattern of lithology, soils, vegetation, and climate of New Zealand has resulted in equally diverse patterns of water chemistry

which are reviewed by Timperley (1987). Particularly unusual are lakes in the Taupo volcanic zone where geothermal and lithological influences may occur. Here, the range of ionic composition is probably unique among lakes of the world (Timperley & Vigor-Brown 1986). For example, in some of these lakes geothermal fluids (water, steam) may contribute high concentrations of chloride, sulphate, and potentially toxic elements (e.g., As, Hg, B), and there may be high ratios of monovalent to divalent cations (McCull 1975b). The physical and chemical properties of the pumice soils can also have important consequences for water chemistry (see above).

Physical and hydrological properties of lakes

Thermal stability and mixing Early studies of physical attributes of New Zealand lakes concentrated on heat budgets, seiches, and reasons for the apparently deep thermoclines of many New Zealand lakes (reviewed by Green et al. 1987). As temperature profiles were obtained for an increasing number of lakes during the 1960s (Jolly & Irwin 1975), it became apparent that New Zealand lakes either do not stratify thermally for sustained periods or stratify only in summer. It became apparent too that some small wind-exposed South Island lakes that mix in summer and often freeze in winter do not fit into the internationally widely accepted classification of lakes that requires warm monomictic lakes always to exceed 4°C (Hutchinson & Löffler 1956). Therefore, a modification of this classification that subdivides warm monomictic lakes into those that do and do not exceed 4°C in winter (Bayly & Williams 1973), or an alternative classification based on frequency and duration of mixing (Lewis 1983) is more appropriate for New Zealand lakes. Thermal data from a range of New Zealand lakes, when compared with an empirical model developed for mid-latitude European lakes (Straskraba 1980), confirm that the surface waters of New Zealand lakes are generally warmer in winter and cooler in summer than those of European lakes. The importance of seiches in generating turbulence in New Zealand lakes is reflected in mean epilimnetic depths that are 25 to 90% deeper and temperature gradients in the metalimnion that are relatively low compared to their European counterparts (Green et al. 1987).

At a time when much current research focused on the role of nutrient availability in determining algal succession and biomass, Viner & Kemp (1983) and Viner (1984) drew attention to the importance of lake stability (that is, resistance to mixing) and the underwater light climate in these processes. Based on

analyses of the bathymetric and mixing patterns of 20 New Zealand lakes, Viner (1984) developed a predictive equation that related seasonal maximum stability to mean depth. Subsequently, Davies-Colley (1987, 1988b) quantified the relation between epilimnetic depth and fetch and provided guidelines for predicting the stability of stratification. The equations developed by these authors are useful in allowing better predictions of the potential susceptibility of lakes to the formation of cyanobacterial scums, and of the scale and cost of mixing a lake artificially to combat consequences of an anoxic hypolimnion. More recently, attention has turned to microscale measurements of water movements in an attempt to understand better the local environment of the biota (e.g., Imberger & Spigel 1987; Spigel & Imberger 1987).

These, and other studies that have sought to relate biological responses to mixing events in lakes, highlight the potential value of Wedderburn numbers (a dimensionless index that can be used to predict the general pattern of wind-induced movements in stratified lakes). This number has been defined (Imberger & Hamblin 1982) and promoted for use in New Zealand (e.g., Davies-Colley 1987; Green et al. 1987; Hoare & Spigel 1987); its use is likely to increase in future as limnologists seek to predict the ecological effects of climate change in lakes.

Waves and currents A knowledge of hydrological properties of lakes is necessary for the development of nutrient budgets and to understand aspects of water quality (reviewed by Hoare & Spigel 1987). Seiches were measured in Lake Wakatipu more than 30 years ago (Bottomley 1956). Since then, seiches and other waves have continued to be measured sporadically, particularly in New Zealand's large lakes (e.g., Ridgway 1974; Heath 1975; Gilmour & Heath 1989; Gilmour 1991). Effects of turbid river inflows on circulation and sedimentation have been examined in several studies. For example, in Lakes Wakatipu and Tekapo the inflowing rivers continue as subsurface flows that can be traced for several kilometres; in Lake Wakatipu, diel and seasonal cycles of interflow (summer) and underflow (spring) have been detected (Pickrill & Irwin 1982; Irwin & Pickrill 1982).

Sediments There have been relatively few studies of the sediments of New Zealand lakes (reviewed by Lowe & Green 1987). Sediments have been evaluated as a source of nutrients for phytoplankton (McColl 1977; White et al. 1978; Viner 1989b), and Vant & Davies-Colley (1984, 1986) have quantified the effect

of suspended sediments on optical properties of lakes. Some Waikato lakes have provided palaeolimnological information that contributes to international understanding of post-glacial climatic and ecological changes (Green 1979; Green & Lowe 1985), whereas Glasby et al. (1991) suggested that Lake Te Anau could serve as a baseline for future studies of global pollution because of its remoteness and the composition and origin of its sediments.

Phytoplankton

Production and biomass Algal production in open waters of a New Zealand lake was first measured by Mitchell (1971) who compared phytoplankton biomass and production in three coastal South Island lakes. Burnet & Wallace (1973) also examined the relation between phytoplankton productivity, nutrients, and the environment for trout in several lakes. Their results, plus those of studies on lakes elsewhere in New Zealand in the 1970s and early 1980s (e.g., Paerl 1977; Paerl & MacKenzie 1977; White & Payne 1977, 1978; Burnet & Davis 1980; Mitchell & Burns 1981; Vincent 1983) provided the necessary information to allow relationships between phytoplankton biomass, productivity, and various indices of eutrophication to be examined, including effects of land development on phytoplankton production (see earlier, under eutrophication). These studies have also revealed spectacular differences in the timing of peaks in phytoplankton biomass and productivity that can be related to patterns of mixing, nutrient availability, and light which, in turn, reflect New Zealand's maritime climate and weather patterns. Whereas most temperate lakes of the Northern Hemisphere typically experience their lowest algal production in winter, Lake Taupo and nearby lakes exhibit highest algal biomass and phytoplankton productivity in winter (Vincent 1983). Mixing extends to the bottom of the lake at this time, thereby increasing the availability of potentially limiting nutrients so that, despite low temperatures and reduced light, algal biomass can develop. The progressive depletion of nutrients over time in response to algal uptake means that the spring increase in biomass, that is typical of most northern temperate lakes, is either very small or absent (Viner & White 1987). An additional source of variability to plant growth cycles in New Zealand lakes is imposed by storm-induced spasmodic influxes of nutrients (McColl et al. 1977).

Species composition The importance of microbially-sized plankton (< 5µm) to aquatic food webs is currently the subject of intense research inter-

nationally. Paerl (1977), however, drew attention to their importance when he used techniques of size fractionation and autoradiography to reveal that organisms 0.2–3 μm in diameter (picoplankton) contributed 11–35% of the biomass, and 33–76% of the phytoplankton productivity, of oligotrophic and mesotrophic lakes in the South Island and central North Island. Paerl & MacKenzie (1977) showed also that the proportional contribution of “net” phytoplankton (20–90 μm) to total phytoplankton fixation changed during the day and pointed out that this lack of uniformity could affect assessments of long-term trends in eutrophication that were based on short-term daylight measurements of ^{14}C fixation. Studies of phytoplankton associations of New Zealand lakes over the past 25 years suggest that they are similar to those elsewhere although there are some differences in distribution patterns of diatom genera (Viner & White 1987), and large-sized taxa may be relatively more abundant in New Zealand (Malthus & Mitchell 1989). Dense populations of *Chlorella* spp. and *Euglena anabaena* colour the water emerald green in acidic, geothermal Lakes Rotowhero (pH 3.1) and Rotokawa (pH 2.1), respectively (Forsyth & McColl 1974; Forsyth 1977).

Microbial studies

Trophic indices and biomass In the mid 1970s, the advent of new techniques for counting and measuring the activity of heterotrophic bacteria stimulated studies of microbial ecology in lakes throughout the world. In New Zealand, microbial activity was shown to be closely related to trophic condition (Bowie & Gillespie 1976; Gillespie 1976; Ramsay 1976; Spencer 1978). In a study of humus-stained Westland beech forest lakes, Paerl et al. (1979) recorded the exceedingly unusual situation in which bacterial biomasses far exceeded those of the phytoplankton, and concluded that organic production in these lakes must be largely allochthonous.

More recent microbial studies in New Zealand lakes have been concerned with the role of bacteria in recycling nutrients, particularly N, or as food for higher organisms (e.g., Vincent & Downes 1981; Forsyth & James 1984; James 1987b; Downes 1988). The low N : P ratios in some New Zealand lakes, and N limitation of algal growth have prompted ecological and physiological studies of N_2 fixation as a potential source of N, and factors affecting it (e.g., MacKenzie 1984; Viner 1985), as well as N transformations in the water column and sediments (see below).

New Zealand's geothermal lakes and hot springs have attracted considerable physiological, bio-

chemical, and taxonomic research on micro-organisms that can grow at high temperatures and often high acidity (pH < 2). For example, new micro-organisms capable of chemical transformations of molecular N and sulphur have been discovered; thermophilic bacteria have provided thermostable enzymes of potential industrial use (Vincent & Forsyth 1987). The contribution of micro-organisms to rate processes and production in geothermal lakes has received little study, however.

Nitrogen fixation and Cyanobacteria Physiological and biochemical aspects of N_2 -fixation dominated studies in the late 1970s (e.g., Paerl 1978; Paerl & Kellar 1978; Vincent & Silvester 1979). Later work was more concerned with the relative importance of nutrients, toxins, temperature, and light on the rates of N fixation and growth of Cyanobacteria (reviewed by Viner 1987b). Until 1987, however, there had been only a few ecological studies of Cyanobacteria in lakes (Viner 1985); no studies of faunal grazing on Cyanobacteria or attempts to model the dynamic interactions of factors that control cyanobacterial populations had been completed. At an international forum held at Taupo, February–March 1987, to which the *New Zealand Journal of Marine and Freshwater Research* devoted a special issue (Vincent 1987b), concurrent experimental research programmes tested the relative importance of competing hypotheses relating to thermal stability and mixing, light, buoyancy regulation and biochemical composition, N : P ratios, and grazing in determining the formation and maintenance of cyanobacterial blooms. Many of the conclusions of these studies conducted in Lakes Rotongaio and Okaro (reported by Vincent et al. 1987; Vincent 1989) apply generally to lakes throughout the world which are experiencing cyanobacterial blooms. For example, the results raise doubts about the importance of N : P ratios in controlling cyanobacterial dominance; suggest that Cyanobacteria may influence the vertical distribution and migration of zooplankton (see also Forsyth et al. 1990); and demonstrate strong interactive coupling between horizontal and vertical mixing regimes in lakes and properties of Cyanobacteria at the cellular and community levels.

Nitrogen transformations Studies in New Zealand lakes have furthered understanding internationally of the mechanisms involved in, and the scope and scale of, transformations among the various inorganic forms of N, viz. nitrate, nitrite, ammonia, and gaseous oxides of N. In a study in Lake Taupo, Vincent & Downes

(1981) first identified the primary sites of nitrifier activity in a lake. Studies of N in the water column and sediments of eutrophic and oligotrophic lakes were continued by Priscu et al. (1986) and Priscu & Downes (1987). The first evidence for a dual role of nitrifying bacteria in the metabolism of nitrous oxide in lakes was provided by Downes (1988) who suggested that the concentration of dissolved oxygen determined which of three processes (one nitrifying, two denitrifying) prevailed, and hence which products accumulate.

Zooplankton

Populations and biomass The applied orientation of much of the limnological research in New Zealand has been less apparent in studies of zooplankton. These have focused primarily on population dynamics and productivity of dominant crustaceans (e.g., Chapman 1973; Green 1976; Burns 1979; Forsyth & James 1991). Compared with Australian and northern temperate lakes, the crustacean zooplankton of New Zealand lakes show low species diversity with few invertebrate predators. In particular, predatory cladocerans and midge larvae (*Chaoborus* spp.) are absent. Most species in New Zealand occur widely and in a variety of lakes, which implies that these species can tolerate a wide range of combinations of biotic and abiotic factors (Chapman et al. 1975; Chapman & Lewis 1976; Chapman & Green 1987). Studies of zooplankton communities in both North and South Islands during the last two decades have revealed little obvious seasonality in total zooplankton abundance, or in the relative importance of major groups. Furthermore, peaks in abundance may occur in winter. In contrast to their counterparts in northern temperate lakes, the crustacean zooplankton in New Zealand lakes at low altitude breed year-round (Chapman & Green 1987). These features of the zooplankton community reflect the major role played by New Zealand's mild, but windy and unpredictable, oceanic climate in determining patterns and processes in lakes. Pulses of algal productivity sustained by wind-induced replenishment of nutrients provide a continuous, but temporally fluctuating, food resource for the largely herbivorous zooplankton; relatively mild temperatures allow breeding to continue in winter.

Calanoid copepods often dominate zooplankton communities numerically, especially in the South Island, and have received the most attention. Detailed studies of populations of *Calamoecia* and *Boeckella* in a variety of lakes have revealed that birth and death rates are often 10 times lower than those recorded for calanoid populations elsewhere. Although breeding

is continuous, fecundities are low and changes in population size result principally from changes in mortality. Low birth rates have been attributed to deficiencies in quantity and/or quality of food available, and low mortality to weak, or no, predation on copepods in New Zealand lakes. A possible consequence of low predation pressure is that parasitism may assume a more important regulatory role than it does on zooplankton populations elsewhere. For example, in two *Boeckella* populations in South Island, an egg parasite reduced the birth rate by as much as 49% (Burns 1985a, 1989). Production (P), biomass (B), and P/B of copepods are also extremely low by international standards (Chapman & Green 1987). Although there have been fewer studies of cladocerans in New Zealand lakes, similar generalisations seem to apply, although predator-induced mortality may be important at times (e.g., Chapman & Green 1987; Forsyth & James 1991). These studies thus suggest a major contrast to most northern temperate lakes in which invertebrate and vertebrate predators exert strong selective pressure on populations of cladocerans and small calanoids: the major factor regulating macrozooplankton populations in New Zealand lakes is the quantity and quality of food available, and in some instances, perhaps, parasitism.

Physiological and ecological studies Studies of the survival, growth, and reproduction of New Zealand zooplankton in the laboratory under a range of conditions have augmented population studies and allowed production to be measured (see above); they have also provided plausible reasons for the distribution and success of some *Boeckella* species (Jamieson 1986; Jamieson & Burns 1988). Laboratory studies of feeding, excretion, and respiration in New Zealand species of *Daphnia*, *Ceriodaphnia*, *Calamoecia*, and a few species of *Boeckella* indicate that although rates of these processes fall within those recorded for their northern hemisphere counterparts, there are some interesting adaptations. For example, based on its respiration, growth, and exceptional resistance to starvation, the endemic South Island calanoid *Boeckella dilatata* appears adapted to cool, oligotrophic waters (Green & Chapman 1977; Burns 1985b, 1988; Jamieson & Burns 1986). Anoxic hypolimnia of lakes are generally considered toxic and unavailable to metazoan zooplankton; however, James (1987a) showed that *Ceriodaphnia* migrated daily into the anoxic, hydrogen sulphide-containing, hypolimnion of Lake Rotongaio where their respiration dropped to 3% of that in the epilimnion,

and he suggested a possible metabolic advantage of these daily excursions.

It is well known that some strains of Cyanobacteria can release toxins that are harmful to mammals, for example cattle, but little is known about effects of extra cellular cyanobacterial toxins on zooplankton (Lampert 1987). In some of the first studies to examine potential effects of biological toxins on zooplankton, Burns et al. (1989) and Forsyth et al. (1990) showed that extra cellular toxins released by *Anabaena minutissima* var. *attenuata* in Lake Rotongaio severely inhibited feeding rates of cladocerans and weakly depressed those of *Boeckella propinqua*, although the latter ingested sufficient *Anabaena* to sustain growth and reproduction. Subsequent studies have shown that a variety of non-toxic filamentous Cyanobacteria can be utilised by several *Boeckella* spp. although they are poor-quality food (Burns & Xu 1990; Xu & Burns 1991).

Recycling of nutrients by zooplankton has received less attention in New Zealand than elsewhere. James (1987b), however, showed that excretion by calanoid copepods provides a major source of N for the phytoplankton in Lake Taupo, although not in eutrophic Lake Rotongaio where phytoplankton are not nutrient-limited. In Lake Rotongaio, some small mixotrophic phytoflagellates (< 5 µm) are not grazed by *Boeckella* and so benefit from regenerated nutrients and increased bacterial numbers in the presence of calanoids (James & Forsyth 1990). By comparing phytoplankton loss rates with calculated grazing rates of the major crustacean zooplankton in Lake Hayes and Lake Johnson, Mitchell & Burns (1981) estimated that specific grazing rates could have accounted for at least 50% of the phytoplankton specific loss rates for most of the year.

Since Brooks & Dodson (1965) first postulated effects of planktivorous fish on zooplankton communities, there have been numerous studies throughout the world of these effects. In New Zealand, however, studies of the impact of fish on zooplankton are relatively recent (reviewed by Chapman & Green 1987), probably because there are no obligate planktivores and only three relatively widely distributed, facultative planktivores: smelt (*Retropinna retropinna*), bullies (*Gobiomorphus cotidianus*), and koaro (*Galaxioides brevipinnis*). Studies of the gut contents and feeding behaviour of these fish show that, as predicted by Brooks & Dodson (1965), it is the cladocerans, particularly the large cladocerans, that sustain the greatest impact from fish predation (Chapman & Green 1987; Cryer 1988; Forsyth et al. 1990). The species composition of zooplankton

communities in New Zealand lakes, however, are probably less influenced by fish predation than those in lakes elsewhere that contain fish (Forsyth & James 1988; Forsyth et al. 1990) because the latter frequently contain obligate planktivores.

Limnetic invertebrate predators are relatively sparse in New Zealand lakes. Although widely distributed, the water mite *Piona exigua* and copepod *Mesocyclops leuckarti* are rarely abundant and are carnivorous only in later instars. In a series of studies, Jamieson (1980) and Butler & Burns (1991a, 1991b) quantified predation rates and food preferences of these species in a variety of conditions. Although cladocerans, particularly *Ceriodaphnia*, are very susceptible to attacks from both predators, their impacts on zooplankton communities in New Zealand lakes are small compared to the effects of voracious Chaoboridae larvae and predatory species of calanoids in lakes elsewhere. Occasionally, medusae of *Craspedacusta sowerbyi* ("jellyfish") appear in large numbers in lakes of both islands (Fish 1971, 1975b; Burns pers. obs.) but the long-term impact of their predation on other zooplankton is probably negligible owing to their rare appearance and brief planktonic existence.

Studies of microzooplankton have largely been confined to descriptions of the seasonality of rotifers, particularly predatory *Asplanchna* spp. (Chapman et al. 1975; Green 1976; Burns & Mitchell 1980; Forsyth & McCallum 1980; Chapman et al. 1981; Forsyth et al. 1983; Stout 1984). In eutrophic Lake Okaro, rotifers and ciliates show patterns of diel vertical migration that change seasonally, probably in response to development and breakdown of an oxycline (Forsyth & James 1991).

Benthic and littoral fauna

Studies of benthic macrofauna of lakes in the central North and South Islands have shown that benthic communities have fewer species than in most lakes outside New Zealand, there is no correlation between species composition and trophic state, and standing crop relates only poorly to trophic state (Timms 1982, 1983). Therefore, whereas associations of larval chironomids may be used in the Northern Hemisphere to classify lakes according to trophic level, benthic chironomids of New Zealand are of little value as indicators of water quality (Forsyth 1978). The poor association between standing crop and trophic state may reflect differences between lakes in the amount of organic matter that enters (Timms 1980). In oligotrophic Lake Rotokawau, a spectacularly dense mussel (*Hyridella*) population (up to 814 m⁻²) relies

extensively on allochthonous input (James 1987c); in eutrophic Lake Okaro an equally impressive concentration of larval chironomids ($309\ 000\ m^{-2}$) is sustained largely by organic material from dense cyanobacterial blooms in the lake (Forsyth & James 1988). The pervasive effect of New Zealand's mild, but variable, climate is evident also in the larval chironomids which dominate the benthos of eutrophic Lakes Hayes, Rotongaio, and Okaro. In these lakes, there are several generations per year but large interannual variations in abundance (Forsyth & McCallum 1983; Graham & Burns 1983; Forsyth 1986; Forsyth & James 1988).

The fauna of acidic, geothermal lakes is dominated by insects (beetles, flies), crustaceans, and mites which, lacking competitors and predators, may become very abundant. In Lake Rotowhero, larval *Chironomus zealandicus* thrive at 30–34°C and attain densities exceeding $30\ 000\ m^{-2}$ (Forsyth & McColl 1974).

Although there have been only a few studies, it appears that few invertebrate species colonise the littoral vegetation of New Zealand lakes compared with those elsewhere (Talbot & Ward 1987). This is probably a consequence of New Zealand's small invertebrate species pool (see also Winterbourn 1991: this issue).

Submerged macrophytes

Invasions by adventives Much of the impetus for research on submerged macrophytes in New Zealand lakes over the past 25 years has stemmed from concerns about the explosive growth and spread of adventive water weeds. Problems created by adventives such as *Egeria densa*, *Lagarosiphon major*, and *Ceratophyllum demersum* in the Rotorua lakes and Waikato River hydroreservoirs in the 1960s (Chapman 1970) prompted a series of aquatic plant community and autecological studies, surveys, and research into methods for controlling the spread and growth of adventives (reviewed by Coffey 1987). Cyclic changes of colonisation, maturation, and erosion were documented (e.g., Chapman et al. 1971b), and the initial spread of some adventives from inocula and their subsequent formation of colonies were described (e.g., Brown & Dromgoole 1977). The principal direct effect of these invasions was found to be the replacement of native assemblages, especially the displacement of native characeans (Howard-Williams et al. 1987; Howard-Williams & Davies 1988).

Studies of macrophyte invasions and their consequences in New Zealand lakes have made an

important contribution to our understanding of biological invasions. Autecological studies, including physiological studies, have shown that no single attribute, or suite of attributes, distinguishes successful invaders from others. Although major problems related to excessive macrophyte growth in some lakes in the early 1970s coincided with a period of heightened awareness of eutrophication, there was no obvious causal link between eutrophication and potential for invasion (Hughes 1976). These studies and others have helped revise hypotheses concerning the invasion potential of macrophytes in New Zealand; the ability to succeed is now considered to be influenced more by an absence of abiotic or biotic constraints to growth (e.g., turbidity or wave action) than by the possession of special attributes (Howard-Williams et al. 1987; Howard-Williams & Davies 1988), although current invasion of North Island lakes by *Hydrodictyon* challenges the validity of this proposition (Hawes et al. 1991).

Species associations, production, and biomass

During the decade 1970–81, three depth-related plant communities were recognised and described for several Rotorua lakes. These were the shallow-water community, mid-depth community, and deep charophyte community (Chapman et al. 1971a; Clayton et al. 1981). Since then, the species composition and depth distribution of submerged macrophytes in lakes throughout the country have been described and classified into their major communities (e.g., Ward & Talbot 1984; Howard-Williams et al. 1987; de Winton et al. 1991). In the course of these studies, some spectacularly high biomasses, by world standards, of both native and adventive macrophytes have been recorded. For example, at one site in Lake Rotoma, the dry weight of *Lagarosiphon major* exceeded $3500\ g\ m^{-2}$ (Clayton 1982). High biomasses have been attributed to New Zealand's long growing season and to a lack of control, or weak control, by aquatic herbivores in this country although shelter from wave action may also be important (reviewed by Howard-Williams et al. 1987). The dramatic effects that herbivores can impose on macrophyte communities are illustrated in experiments with introduced grass carp on a small *Egeria*-infested lake (Mitchell et al. 1984; Tanner et al. 1990).

Some constraints to macrophyte growth in New Zealand have been quantified. Vant et al. (1986) examined limits to macrophyte growth imposed by high turbidity in nine New Zealand lakes; they developed an empirical relationship for predicting

the effect of changes in water clarity on the depth to which macrophytes will grow. In Lake Taupo, a constraint to growth of bryophytes is probably imposed by freshwater crayfish (Coffey & Clayton 1988).

Over the past 25 years, there have been few studies of contributions made by macrophytes to total primary production in New Zealand lakes, or of their role in nutrient cycling and as links between benthic and pelagic communities. The first estimate of the proportional contribution of macrophytes to total primary production (phytoplankton plus macrophytes) of a New Zealand lake was made in Lake Waikaremoana where littoral macrophytes were found to contribute significantly to total primary production (Howard-Williams et al. 1986), although in a shallow coastal lagoon their contribution was relatively small and changed from year to year (Mitchell et al. 1988; Mitchell 1989).

Vertebrates

Fish and birds are important components of lake ecosystems, but there have been few studies in New Zealand of nutrient cycling, trophic interactions, and production that include vertebrates. This omission is due partly to institutional separation of governmental scientists engaged in research on plankton, fish, and wildlife. Research on freshwater fish (see McDowall 1991, this issue) and wetland birds has largely been management-oriented. In a nation-wide survey completed in 1985, 1600 freshwater sites (lakes, ponds, swamps, bogs) were evaluated as wildlife habitat; other studies have assessed habitat requirements of wetland birds, and effects of changes in water level, turbidity, and vegetation on wildlife (Williams & Ogle 1987).

Conservation

A valuable source of theory and guidelines for conserving and managing wetlands, based on studies of New Zealand lakes, is the *Lake Managers Handbook* (Vant 1987b). Case studies include control of water levels and nutrients, removal of exotic macrophytes, restoration of marginal vegetation, and catchment protection. The wetland survey (see above) and other studies have highlighted the international importance of several New Zealand wetlands, some of which have been designated under the Convention on Wetlands of International Importance especially as Waterfowl Habitat (at Ramsar, Iran in 1971), e.g., Lake Ellesmere, Whangamarino Swamp.

CONCLUDING REMARKS

Studies over the past 25 years have highlighted the diversity of lakes in New Zealand, their sensitivities to perturbation, whether human-induced or natural, and the profound influence that the vagaries of New Zealand's oceanic climate have on physical and biological processes that occur in them. Research has also shown that paradigms and models based on northern hemisphere lakes do not necessarily fit New Zealand lakes which mix to relatively greater depths in summer, generally have fewer species of organisms, and are frequently N-limited. Despite an exponential increase in our knowledge of New Zealand lakes since the mid 1960s, we still lack baseline information for some recreationally important lakes against which changes can be measured (e.g., Lake Wanaka, Lake Wakatipu); contributions of microzooplankton (heterotrophic flagellates, protozoans, rotifers), fish, and birds to nutrient recycling in New Zealand lakes need to be investigated; population dynamics and rate processes in lakes of karst landscapes, sand-dunes, peaty soils, and alpine regions have received little study; geothermal lakes, in particular, provide exciting opportunities to study fundamental ecosystem processes (respiration, photosynthesis, nutrient recycling, energy transfer) under extreme conditions of temperature, pH, and unusual water chemistry; there has been no integrated study of a whole-lake ecosystem. Advantage should be taken of New Zealand's windy climate to gain better understanding of direct and indirect effects of turbulence and temperature on lake processes; general ecological theories relating to food webs and production in aquatic ecosystems may be tested in lakes which have few predators and low species diversity; New Zealand wetlands also provide natural laboratories for studying theory, causes, and management of invasions by plants and animals; the biogeographic origins and evolution of some native aquatic organisms still need to be clarified. These and other aspects of New Zealand's remarkably diverse lakes should continue to provide exciting challenges to scientists and managers in the next 25 years.

ACKNOWLEDGMENTS

This paper was written while the author was on refresher leave at Dartmouth College, Hanover NH, USA. I thank J. I. Hubbard for encouragement and word processing, E. White for references, Dartmouth College for providing facilities, and Marianne V. Moore and two referees for comments on the paper.

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