

# Potential for Re-Establishment of Aquatic Plants in Lake Ellesmere (New Zealand)

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## ABSTRACT

Past and present aquatic plant surveys show that *Ruppia megacarpa* R. Mason and *Potamogeton pectinatus* L. were major contributors to aquatic plant biomass in Lake Ellesmere, a shallow coastal lagoon located on the east coast of the South Island (New Zealand). Today, in response to natural and anthropogenic pressures (wind, lake openings to the sea), the lake environment appears too stressed and too disturbed to provide suitable conditions for growth of these two species, leaving only space to sparse growth of stress-tolerant ruderal species (*Ruppia polycarpa* R. Mason, *Lepilaena bilocularis* Kirk). However, research conducted in the field between 1985 and 1988 has shown that potential for re-establishment did exist. The role of water-level schedules and associated effects on salinity is discussed in relation to past and present aquatic plant strategies. Management that could foster re-establishment of submerged aquatic vegetation is then suggested.

**Key words:** coastal lagoon, stress, disturbance, water-level fluctuations, *Ruppia* spp., *Potamogeton pectinatus*.

## INTRODUCTION

Between 1985 and 1988, an ecological research was conducted in Lake Ellesmere, a large (16,000 to 20,000 ha) brackish coastal lagoon located on the east coast of the South Island (New Zealand), in order to identify the main factors that could have affected regeneration of aquatic plant stands after these were washed away in 1968 during what is known locally as the Wahine storm. A study of the optical properties of the lake water and a glasshouse experiment showed that light availability in the water column and salinity were two factors controlling growth of *Ruppia* spp. seedlings and potentially limiting submerged vegetation biomass in the lake (Gerbeaux 1989, Gerbeaux and Ward 1991). Penetration of photosynthetic active radiation fluctuates in response to natural and anthropogenic disturbances such as wave resuspen-

sion of sediments and wind-controlled or man-controlled water-level fluctuations (seiches, artificial opening of the bar at the mouth of the lake). Lake openings existed before Europeans settled around the lake, and the lake is known to have been opened to the ocean by the Polynesians (known locally as Maoris) in the years 1852, 1854, 1856, 1861, 1863, 1865, and 1867. After and until 1875, it was opened every year by European settlers (Bray 1875). During Maori time, digging through the bar was done by hand (with sticks) to lower the water level and prevent flooding of villages. Today, openings are achieved with the use of bulldozers and drag-lines, and take place to prevent flooding on surrounding pastoral lands. Closings occur naturally. Lake Ellesmere is a wildlife habitat of international importance (O'Donnell 1985) and critical considerations for wildlife management are the duration of lake openings, the magnitude in the drop in water, the prescribed levels at which the lake is opened and the timing of the openings. These considerations are linked to aquatic plant management needs. A fluctuating water regime is necessary to maintain saltmarsh productivity but it can also be a source of disturbance to the submerged vegetation through sudden drops in water level. If the lake remains open for a long time, the level is so low that shallow areas dry out completely and expose submerged plants. Lake openings are equally a potential source of stress through the salinity and underwater light climate fluctuations they create. This paper relates historical data (over the last 70 years) on frequency and duration of openings to qualitative and quantitative data on aquatic vegetation and investigates what is the optimum water regime for re-establishment of submerged plants in the lake.

## METHODS

**Lake openings.** A long record of data related to the openings (water-level fluctuations, dates and length of openings) was made available by the Canterbury Regional Council who also processed the data to produce lake-level duration curves. Water-level schedules may determine the actual vegetation response and Rorslett (1984) suggested that the probability distribution of water levels should preferably be used in place of the mean annual range of water-level variation in an analysis of response features. Thus, lake-level duration

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curves display the relationship between lake levels and the percentage of time they are exceeded. These curves were obtained for the period 1970-1987 in order to understand how they could have affected regeneration of aquatic plant stands after the 1968 storm. The values have been computed for each year, over the growth season only (September through March).

Data on salinity levels prior to 1985 were obtained in the literature (Hughes *et al.* 1974, Lineham 1983) and salinity was also measured fortnightly in the course of the present study with an YSI Model 33 salinometer (Yellow Springs Instrument Co., OH, USA) below the surface and near the bottom in order to estimate salinity fluctuations in relation to lake openings.

**Plant survey and plant life-cycle observations.** Prior to 1985, visual observations on macrophyte stands that grew in the lake were made by Mason (1946, 1951); other observations are reported in Hughes *et al.* (1974). Between December 1978 and May 1982, Webb (1982) made monthly records of *Ruppia megacarpa* height in four enclosures located at four sites of the eastern part of the lake. Plant harvesting was carried out in 1986, as part of the present study, in two bays

of the western side during the peak biomass period (in early February). Harvesting was made along transect lines, as described in Gerbeaux and Ward (1991), and standing crops were obtained for all the species present. Resource allocation in *R. megacarpa* and *Potamogeton pectinatus* L. was also quantified. Harvesting was repeated in 1987 in one of the bays along the same 600-m-long transect line. Information on life cycles was obtained from the literature and from a glasshouse growth experiment with *Ruppia* spp. (Gerbeaux 1989). Strategy traits were assigned using classification of survival trait characteristics proposed by Murphy *et al.* (1990). Additional visual observations were made by the author until early 1992.

## RESULTS

**Lake openings.** The frequency and length of the openings since the 1910s are summarized in Figure 1. A change in management can be seen in the figure as lake levels became more controlled from the late 1940s, with more frequent openings. New prescriptions were indeed ordered in 1947, and since then the lake is opened when levels reach 1.05 m

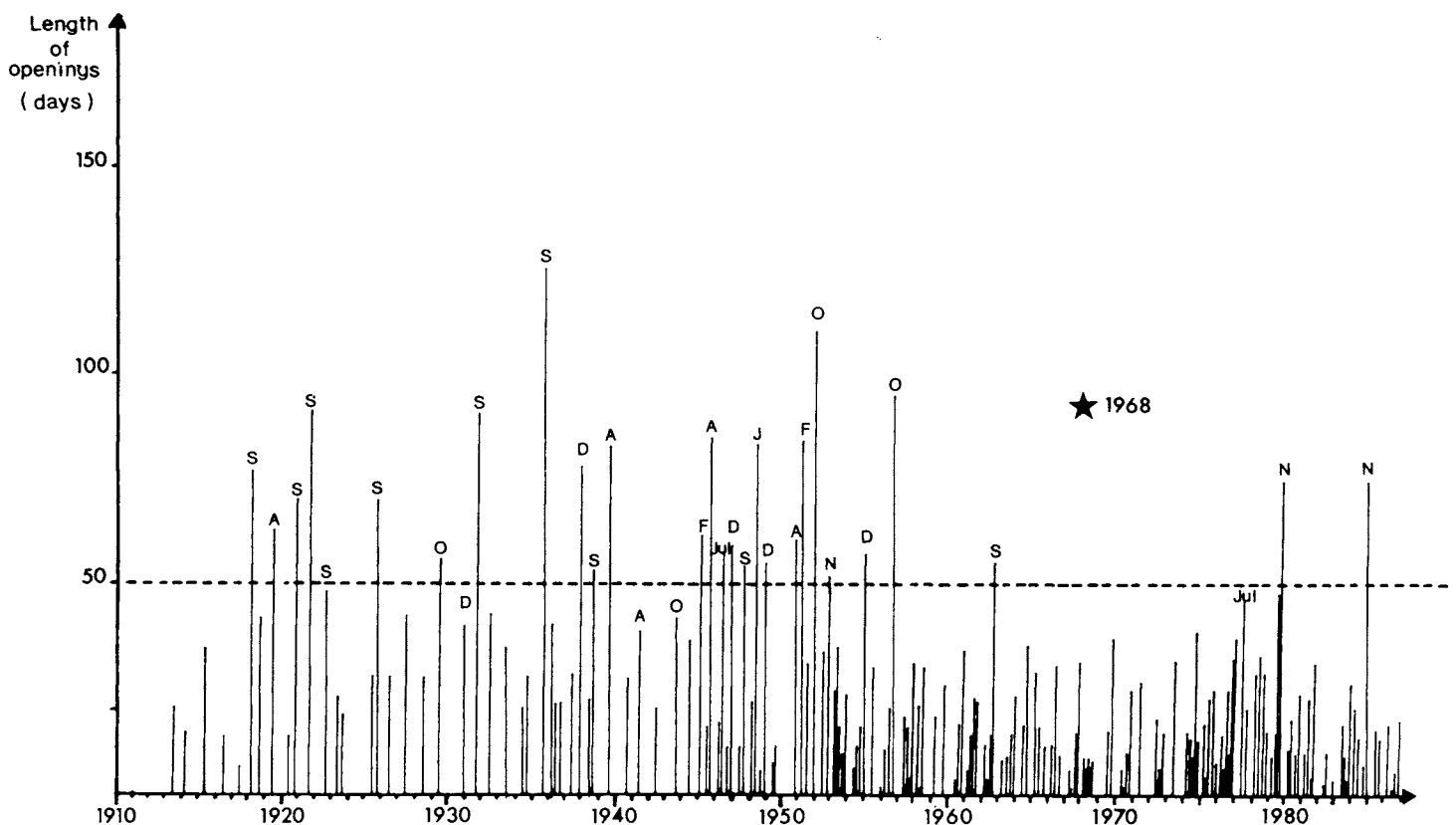


Figure 1. Frequency and length of lake openings between 1910 and 1987. (Letters relate to the starting month of openings that lasted 20 days at least and that resulted in the lake being opened during the growth season (September-March): Jul: July; A: August; S: September; O: October; N: November; D: December; J: January; F: February).

above mean sea level (msl) from September to April, and 1.13 m above msl from May to August (Hughes *et al.* 1974). The average number of openings per year increased from 1.59 between 1913 and 1947 to 3.46 between 1947 and 1986. Over the same periods, the average length of opening decreased from 42.5 days to 23 days.

While water levels continually and irregularly change with time in response to natural events (floods, seiches), the lake level drops very suddenly after an opening. The higher the lake at the time of opening, the greater the scour at the outlet. Thus, while the new policy contributed in lowering the average opening level (from 1.53 m to 1.18 m), it also resulted in increasing the average closing level (from 0.46 to 0.63 m).

The analysis of lake-level fluctuations performed over the period 1970 to 1987 for each growth season highlighted three types of water level schedules. Figure 2 illustrates one example of each type. In the first one, the lake remains at low levels for a long period with short periods at higher levels; in the second one, no particular level is prominent; and in the third type most of the time the lake is at moderate to high levels, being at lower levels for short periods. Each type depends on the timing of opening and on the rainfall pattern after the opening: type 1 corresponds to a late spring opening followed by low rainfall, type 2 to a late winter/very early spring opening followed by one or several openings over the period due to high rainfall, and type 3 to an early opening without subsequent opening (due to low to moderate rainfall). Table 1 presents some additional hydrological information over the same period. The level 0.5 m was arbitrarily chosen (from field observations) as the threshold that could expose plant to

desiccation, and the percentage of time spent below this threshold is indicated in the table. The minimum level is another important parameter since it determines, along with turbidity, the maximum amount of light penetrating the water column to the bottom.

Lake openings also affect salinity. From the data obtained in the literature and from the fortnightly measurements the following conclusions could be made: (a) salinity lies most of the time within the 5 to 10 parts per thousand (ppt) range; (b) minimum values recorded were just below 3 ppt; (c) openings lasting between 20 and 30 days raise the level by 1 to 4 ppt; (d) salinity will be higher than 10 ppt if openings last more than 30 days, and more than 15 ppt if they exceed 50 days; (e) in such an event, it will take from 3 to 9 months for the level to return to normal range (5 to 10 ppt) depending on freshwater inflows; (f) long periods without opening may bring the level below that range; (g) salinity could vary from 7 ppt near the surface to 22 ppt near the bottom during opening and calm periods; (h) increase in salinities were observed following storms as a result of wave overtopping.

*Macrophyte surveys before 1985.* Dense weed beds of *R. megacarpa* and *P. pectinatus* with plants 6 to 8 ft long are reported to have fluctuated during the first half of the century, with a decline starting from the 1920s and being more rapid in the early 1940s, moving north from the outlet (Mason 1946, 1951). The recovery of the weed beds during the 1950s was spectacular and luxuriant growth persisted until the devastating effect of the Wahine storm in 1968 (Hughes *et al.* 1974). Webb (1982) reported that *R. megacarpa* and *P. pectinatus* were still present here and there between 1978 and 1982. He further added that there was better growth after 1980 (plants

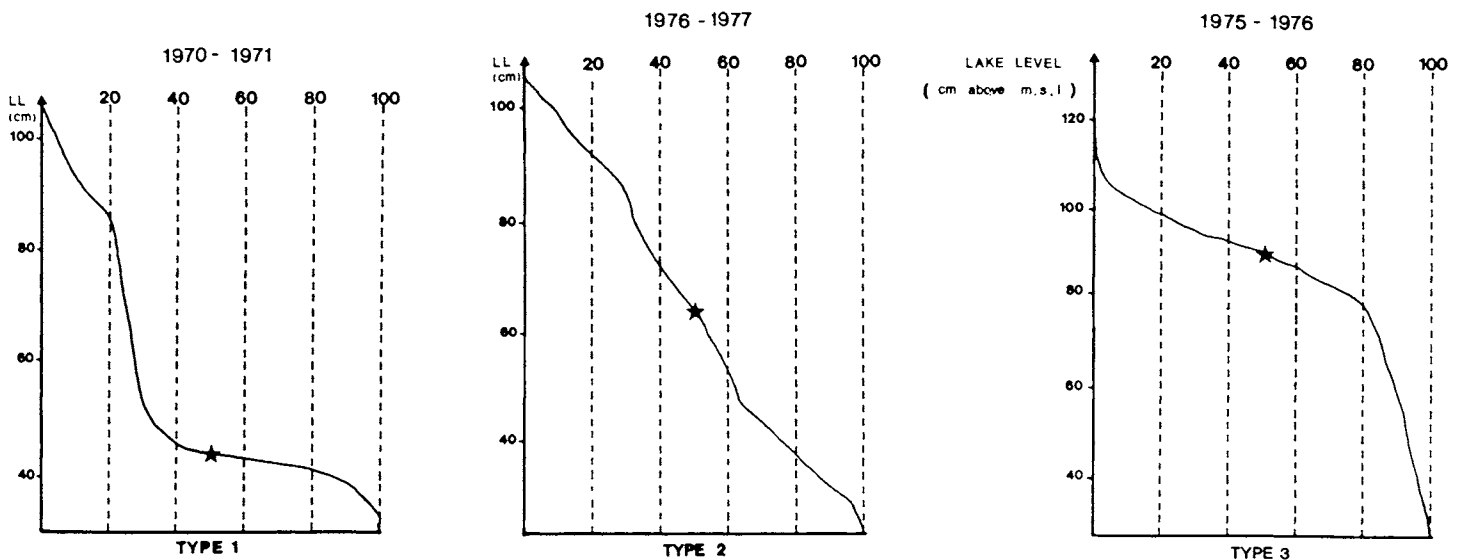


Figure 2. The different types of lake-level duration curves. The star indicates the median value.

TABLE 1. LAKE-LEVEL PARAMETERS IN LAKE ELLESMERE OVER THE AQUATIC PLANT GROWING SEASON FROM 1970-1991 (CANTERBURY REGIONAL COUNCIL DATA)

Parameter	Lake status in 19__																					
	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91
Type of duration curve	1	3	1	3	2	3	2	3	2	2	3	3	3	3	1	3	3	1	3	1	1	3
Lake level < 0.5 (% time)	70	0	3	0	15	5	38	7	12	30	10	15	0	2	50	0	4	20	0	8	0	0
Minimum level (cm ab msl)	32	62	49	58	35	30	25	19	38	16	36	25	63	31	28	51	41	40	78	42	50	76
Median level (cm ab msl)	45	82	55	78	70	91	64	83	67	63	77	67	79	90	50	91	90	58	85	61	62	91

NOTE: ab msl—above mean sea level.

observed were taller). When our first observations took place over summer 1984-1985, only sparse seedlings of *R. polycarpa*, *Lepilaena bilocularis*, and *Lamprothamnium papulosum* (Wallr.) J.Groves could be found in exposed areas due to low lake levels.

*Life-cycles and reproductive patterns of macrophytes observed after 1985.* The luxuriant and unusual growth (as reported by fishermen) which occurred during the study enabled observations in the glasshouse to be compared with

observations in the field. Information on the main contributors to standing crop obtained from these observations and from the literature (reviewed by Madsen 1991) is summarized in Table 2. Surveys around the lake often led to the observation of young seedlings of *R. megacarpa* floating near the shore after lake openings. No such observations were made for *P. pectinatus*. Some *R. megacarpa* fruit were collected from Lake Ellesmere for a test of viability. Only 4% were found viable. The remaining ones did not contain a developed

TABLE 2. REPRODUCTIVE/LIFE CYCLE TRAITS, BIOMASS ALLOCATION AND STRATEGY TRAITS FOR SUBMERGED MACROPHYTES IN LAKE ELLESMERE.

Species	Propagule	% germination	Period of propagule formation	Propagation	Maximum standing crop in 1986/87 g DW m <sup>2</sup>	Resource allocation in % of mean standing crop		Strategy traits <sup>1</sup>		
						Seeds	Vegetative underground parts	C	S	D
<i>R. megacarpa</i> R. Mason	Seed	27.8 <sup>2</sup>	Jan/Feb	Horizontal then vertical (canopy)	496	14	6.1	3	3	0
<i>R. polycarpa</i> R. Mason	Seed	35 <sup>3</sup>	Nov-Dec/ Jan-Feb	Horizontal	107	21	—	1	2	3
<i>P. pectinatus</i> L.	Tuber/seed	100/8 <sup>4</sup>	Dec-Apr/ Jan-Feb	Horizontal and vertical (canopy)	176	7.2	11.1	6	0	2
<i>L. binocularis</i> Kirk	Seed	85 <sup>3</sup>	Nov-Dec/ Mar-Apr	Horizontal	89	29	—	1	2	3
<i>L. papulosum</i> (Wallr.) J. Groves	Bulbil seed	Not known	Dec-Apr/ Dec-Feb	Horizontal	77	Not known	Not known	1	2	4

<sup>1</sup>Using classification of survival trait characteristics (Murphy et al. 1990) (C = competitive, S = stress, D = Disturbance).

<sup>2</sup>Brock (1982).

<sup>3</sup>Vollebergh and Congdon (1986).

<sup>4</sup>van Wijk (1983).

seed. The fruit cavity had a full-size testa but no embryo or food reserve had developed within.

## DISCUSSION

Prior to the 1968 storm, high standing crops of aquatic vegetation that existed in Lake Ellesmere could have been the result, as suggested by Johnstone (1986) in other New Zealand lakes, of minimal biomass loss rather than maximal growth in a unit time. Our 1986 and 1987 records (see Table 3 in Gerbeaux and Ward 1991) support this suggestion. Assuming that the large perennial *Ruppia* beds which existed in the past had a slow biomass turnover (a stress-tolerant trait), they were able to dampen short-term and rapid oscillations in the environment such as the periods of low lake levels and high salinities recorded until the early 1950s. It should be acknowledged here, however, that Delroy (1976) and Congdon and McComb (1979) suggested from field observations in Australia that flowering of *R. megacarpa* was stimulated by increasing salinities. Light at that time was not considered to be a stress factor as the dense beds acted as baffles against wave action, reducing inorganic turbidity. There is thus evidence that decline of *R. megacarpa* occurred through a shift in resource allocation from vegetative growth into flowering under high salinities. Meanwhile, populations of *P. pectinatus* are known to produce higher number of shoots and tubers at low salinities, *i.e.*, *ca.* 3 ppt (van Wijk *et al.* 1988). Periods of long openings of the late 1930s and 1940s (see Figure 1) would have thus played a significant role in the decline that was reported then. Conversely, the low salinities that resulted from the absence of long openings in the late 1950s and in the 1960s could have both stimulated germination of seeds and tubers present in the seed bank and subsequently encouraged vegetative growth. In comparison with the effects induced by lake openings, the 1968 storm was a type of environmental oscillation which had a frequency slower than the characteristic frequency of the dominant macrophytes, resulting in the disruption of the organization in the system and the decline of macrophytes.

With no established populations of macrophytes left in the lake, the assessment and understanding of regenerative strategies is essential in the planning of future lake management. As stated by Harper (1977) "the presence or absence and the density of a seedling population depends not only on the availability of seeds but on the frequency of safe sites that provide the precise conditions required by a particular seed." First, is the number of propagules present in Lake Ellesmere sufficient to enable the regeneration of macrophytic vegetation in Lake Ellesmere? The high number of seeds produced by stress-tolerant ruderals such as *R. polycarpa*, *L.*

*bilocularis*, or *L. papulosum* added to their life-cycle characteristics confers on these species an obvious advantage for survival under high disturbance and stress pressure (see also Brock and Canasova 1991) and explains why they were the only species found in 1984-1985. The seeds and seedlings of *R. megacarpa* found along the shoreline in some areas suggest they also are an important component of the seed bank. Their morphology with long and solid stalks may however prevent dispersal, as seeds have often been seen entangled into large balls buried in the sediment or rolled up on the shore. Wave action on the lake bottom at low lake levels encourages such phenomenon. Their low germination rate is a handicap as it prevents large-scale re-establishment; but it is also a means of maintaining a stock and increasing the chance of survival. The development of *P. pectinatus* populations in one area leads to the conclusion that it also has propagules present in the lake sediment.

Second, what conditions are required for the germination processes and seedling establishment to proceed in Lake Ellesmere? One first condition is related to salinity. Brackish aquatic macrophytes all have low salinity germination requirements (see Dubois (1968) for *L. papulosum*, Brock (1982) for *R. megacarpa*, van Wijk (1986) for *P. pectinatus* and Vollebergh and Congdon (1986) for *Lepilaena cylindrocarpa*, a species close to *L. bilocularis*). Low salinities also favored the development of *Ruppia* seedlings from Lake Ellesmere, and good illumination improved rhizome elongation, contributing to a more developed anchoring capacity, a condition necessary for successful survival of *Ruppia* seedlings as shown by Gerbeaux (1989). With regard to temperature, optimum conditions of growth are found for *P. pectinatus* and for most macrophyte species from above 17°C (Spencer 1986, Barko and Smart 1981). Traits like shoot elongation and rapid canopy formation, besides the possibility to rely on its tuber reserves, appear sufficient to guarantee survival of *P. pectinatus* in turbid freshwater habitats (Hootsmans and Vermaat 1991). In fact, van Dijk and van Vierssen (1991) showed that *P. pectinatus* responded to shading by increasing the allocation of available carbohydrate to the tubers, but such response largely depended on how long the above biomass could sustain tuber production. Tubers and a well-developed rooting system also confer *P. pectinatus* a firm anchoring system likely to be an advantage in wind-exposed lakes. Other barriers for plant regeneration such as exposure to desiccation and grazing are less species selective.

It appears that regeneration windows were opened during spring 1985 in Lake Ellesmere on several potential safe sites around the lake. At this time, a low lake level provided increased light intensity and favored higher temperatures on the lake bottom on sunny days. Furthermore, salinities were

low, daily wind velocities were below average (and therefore turbidities were lower) and an extremely low number of waterfowl were grazing in the area. These regeneration windows were again opened the following year. The type 3 water-level schedule (see Figure 2) which prevailed over the growth season of both years as well as in the early 1980s (Table 1) made habitats more favorable and more predictable. It is likely (see Kautsky 1988) that the resulting low disturbance and stress pressure led to re-establishment of stress-tolerant competitors like *R. megacarpa* and competitive ruderals like *P. pectinatus* (CS and CD strategists, respectively). Such a lake schedule can only be favorable: it optimizes temperature and light conditions during early growth, and thus rapid horizontal propagation. Short low lake levels decrease the risk of desiccation and grazing by birds before completion of the life cycle. The later stabilization of the lake level at a medium to high median values also provides favorable conditions for canopy development. The impact of the long opening in 1984-1985 remains uncertain. The resulting exposure to desiccation in the areas where the luxuriant growth was recorded, followed by favorable environmental conditions, may have triggered a large-scale germination through disruption of the exocarp of achenes (see also Congdon and McComb 1981). It may also have improved the quality of the sediment. Follow-up visual observations at the same sites revealed that no luxuriant growth has taken place again after 1987. Overgrazing has undoubtedly put pressure on the macrophytes in 1987 (25 swans per hectare in the area surveyed, which is a lot higher than the 4 swans per hectare obtained by Mitchell *et al.* (1988) on the basis of a relationship between macrophyte biomass and swan number for another South Island coastal lake). However, the various water-level schedules which took place between 1987 and 1991 also provided some unfavorable conditions (20% of the growth season in 1987 below 0.5 m, low median level in 1989 and 1990, high minimum level in 1988 and 1991). Moreover, they may have represented a lack of predictability which the plants could not cope with.

In future management all causes of stress and disturbance should be addressed. It is suggested that the third type of water-level schedule reported above would reduce most of these causes and provide the best potential for aquatic vegetation re-establishment. With respect to lake management goals such as maintenance or improvement of water quality, wildlife habitat, fishing, boating and sailing conditions, it is also attractive. For instance, high summer water levels can reduce nutrient resuspension from the sediment and reduce phytoplankton growth; the proposed timing for opening the lake in spring enables inward fish migration and prevents outward migration, thereby increasing fishery value of the lake; recreational uses (boating and sailing) benefit from

relatively high summer levels although excessive growth may impede some areas; and the strategy alleviates Maori grievances, especially through retaining the lake at its optimum level for eel fishing. It thus shows that management of aquatic plants may contribute to enhanced ecological, economic and recreational values and balance conflicts between user-groups.

## ACKNOWLEDGMENTS

The study was supported by the National Water and Soil Conservation Authority, the Department of Internal Affairs and the New Zealand Acclimatization Society. Graham Horrell (Canterbury Regional Council) kindly provided lake level data.

## LITERATURE CITED

- Barko, J. W. and R. M. Smart. 1981. Sediment-based nutrition of submerged macrophytes. *Aquat. Bot.* 10:339-352.
- Bray, W. B. 1875. The drainage of Lake Ellesmere. Report to the Public Works Department. By order of the Superintendent, Provincial Government of Canterbury. 32 pp.
- Brock, M. A. 1982. Biology of the salinity tolerant genus *Ruppia* L. in saline lakes in South Australia. II. Population ecology and reproductive biology. *Aquat. Bot.* 13:249-268.
- Brock, M. A. and M. T. Canasova. 1991. Plant survival in temporary waters: a comparison of charophytes and angiosperms. *Verh. int. Ver. Limnol.* 24(4):2668-2672.
- Congdon, R. A. and A. J. McComb. 1979. Productivity of *Ruppia*: seasonal changes and dependence on light in an Australian estuary. *Aquat. Bot.* 6:121-132.
- Congdon, R. A. and A. J. McComb. 1981. The vegetation of the Blackwood river estuary, South-West Australia. *J. of Ecol.* 69:1-16.
- Delroy, D. B. 1976. The food of waterfowl (Anatidae) in the southern Coorong salt water habitat of South Australia. *S. Aust. Ornithol.* 26:157-163.
- Dubois, A. 1968. Observations sur la morphologie et la biologie des formes naines de *Lamprothamnium papulosum* J.Groves (characées) *Naturalia monpelliensia (série Botanie)* 19:37-41.
- Gerbeaux, P. 1989. Aquatic plant decline in Lake Ellesmere: a case for macrophyte management in a shallow New Zealand lake. Ph.D Thesis, Univ. of Canterbury, New Zealand. 281 pp.
- Gerbeaux, P. and J. C. Ward. 1991. Factors affecting water clarity in Lake Ellesmere, New Zealand. *N. Z. J. of Mar. & Freshw. Res.* 25:289-296.
- Harper, L. 1977. *Population Biology of Plants*. Academic Press, London, New York, San Francisco. 892 pp.
- Hootsmans, M. J. M. and J. E. Vermaat. 1991. Macrophytes, a key to understanding changes caused by eutrophication in shallow freshwater ecosystems. International Institute for Hydraulic and Environmental Engineering, Report Series 21.
- Hughes, H. R., R. H. S. McColl, and D. J. Rawlence. 1974. Lake Ellesmere, Canterbury, New Zealand. A review of the lake and its catchment. DSIR Information Series No. 99, Wellington.
- Johnstone, I. M. 1986. Macrophyte management: an integrated perspective. *N. Z. J. of Mar. & Freshw. Res.* 21: 47-53.
- Kautsky, L. 1988. Life strategies of aquatic soft bottom macrophytes. *Oikos* 53:126-135.

- Lineham, I. W. 1983. Eutrophication of Lake Ellesmere: a study of phytoplankton. Ph.D Dissertation, Univ. of Canterbury, New Zealand. 335 pp.
- Madsen, J. D. 1991. Resource allocation at the individual plant level. *Aquat. Bot.* 41: 67-86
- Mason, R. 1946. Report on weed banks in Lake Ellesmere. Botany Division DSIR report, Wellington. 11 pp.
- Mason, R. 1951. Report on waterweeds found in Lake Ellesmere. Botany Division DSIR report, Wellington. 11 pp.
- Mitchell, S. F., D. P. Hamilton, W. S. MacGibbon, P. K. Bhashkaran and R. N. Reynolds. 1988. Interrelations between phytoplankton, submerged macrophytes, black swans and zooplankton in a shallow New Zealand lake. *Int. Rev. der ges. Hydrobiol.* 73: 145-170.
- Murphy, K. J., B. Rorslett and I. Springuel. 1990. Strategy analysis of submerged lake macrophyte communities: an international example. *Aquat. Bot.* 36:303-323.
- O'Donnell, C. F. 1985. Lake Ellesmere: a wildlife habitat of international importance. Fauna Survey Unit Report No. 40. N.Z. Wildlife Service, Dept. of Internal Affairs, Wellington. 219 pp.
- Rorslett, B. 1984. Environmental factors and aquatic macrophyte response in regulated lakes—a statistical approach. *Aquat. Bot.* 19:199-220.
- Spencer, D. F. 1986. Early growth of *Potamogeton pectinatus* L. in response to temperature and irradiance: morphology and pigment composition. *Aquat. Bot.* 26:1-8.
- van Dijk, G. M. and W. van Vierssen. 1991. Survival of a *Potamogeton pectinatus* L. under various light conditions in a shallow eutrophic lake (Lake Veluwe) in the Netherlands. *Aquat. Bot.* 39:121-129.
- van Wijk, R. J. 1983. Life-cycles and reproductive strategies of *Potamogeton pectinatus* L. in the Netherlands and the Camargue (France). International Symposium on Aquatic Macrophytes, Nijmegen, 18-23 Sept 1983:317-321.
- van Wijk, R. J. 1986. Life-cycle characteristics of *Potamogeton pectinatus* L. in relation to control. Proceedings EWRS International Symposium on Aquatic Weeds 7:375-380.
- van Wijk, R. J., E. M. J. van Goor, and J. A. C. Verkley. 1988. Ecological studies on *Potamogeton pectinatus* L. II. Autecological characteristics, with emphasis on salt tolerance, intraspecific variation and isoenzyme patterns. *Aquat. Bot.* 32:239-260.
- Verhoeven, J. T. A., P. W. M. Jacobs, and W. van Vierssen. 1982. Life strategies of aquatic plants and some critical notes and recommendations for further research. In: Studies on Aquatic Vascular Plants, Symoens *et al.* (eds.) pp 158-164.
- Vollebergh, P. J. and R. A. Congdon. 1986. Germination and growth of *Ruppia polycarpa* and *Lepilaena cylindrocarpa* in ephemeral saltmarsh pools, Westernport Bay, Victoria. *Aquat. Bot.* 26:165-179.
- Webb, B. F. 1982. Report on the growth of *Ruppia megacarpa* in Lake Ellesmere. Annual Report of the North Canterbury Acclimatization Society:93-112.