New Zealand Journal of Marine and Freshwater Research

ISSN: 0028-8330 (Print) 1175-8805 (Online) Journal homepage: https://www.tandfonline.com/loi/tnzm20

Submerged vegetation of the Rotorua and Waikato lakes

V. J. Chapman , J. M. A. Brown , F. I. Dromgoole & B. T. Coffey

To cite this article: V. J. Chapman , J. M. A. Brown , F. I. Dromgoole & B. T. Coffey (1971) Submerged vegetation of the Rotorua and Waikato lakes, New Zealand Journal of Marine and Freshwater Research, 5:2, 259-279, DOI: 10.1080/00288330.1971.9515380

To link to this article: https://doi.org/10.1080/00288330.1971.9515380

Published online: 30 Mar 2010.

SUBMERGED VEGETATION OF THE ROTORUA AND WAIKATO LAKES

1. LAKE ROTOITI

V. J. CHAPMAN, J. M. A. BROWN, F. I. DROMGOOLE and B. T. COFFEY
Botany Department, University, of Auckland, New Zealand

(*Received for publication 9 September 1969*)

ABSTRACT

Five plant communities in Lake Rotoiti, North Island, New Zealand (38° 02′ S, 176° 24′ E) are described. In shallow water (0–2 m depth) partly protected from the prevailing westerly winds, some indigenous species form characteristic mounds. From 2 to 6 m depth the exotic macrophyte *Lagarosiphon major* (Ridley) Moss is the dominant and forms dense beds which appear to have completely replaced any native vegetation. *Elodea canadensis* Michx., a longer-established exotic, may form a minor component of this zone, but may become the dominant species in water above and below the *Lagarosiphon* zone. *Lagarosiphon* appears to be primarily restricted to silty sand, but on pure silt areas it is replaced by *Elodea* and/or *Nitella hookeri* A. Braun. These zonations are probably static rather than successional. On underwater cliff faces and boulder shores a seasonal succession of algae was the major vegetation. Only filamentous cyanophytes grew within 1–2 m of geothermal springs in the lake.

INTRODUCTION

Since 1960 concern has been expressed about the explosive growth of introduced aquatic weeds in the Rotorua and Waikato lakes (Chapman 1970; Chapman and Bell 1967; Chapman and Brown 1966). In many areas of Lakes Rotorua and Rotoiti dense beds of *Lagarosiphon major* and of *Elodea canadensis* seem to have completely replaced any previous plant communities at water depths greater than 2 m. (For authorities for most plant names not given in text *see* Table 1.)

The submerged vegetation of the lakes had not been studied before the exotics became established. Thus the pre-existing indigenous flora is largely unknown, although no doubt some of the communities Cockayne (1928) described were present. Today, even when *Lagarosiphon* is killed by Diquat (1, 1′-ethylene-2, 2′-dipyridylium dibromide) no native phanerogamic species appear able to establish themselves before a new crop of *Lagarosiphon* grows. In areas where the charophyte *Nitella hookeri* already exists as a ground cover under the *Lagarosiphon,* there is a temporary upsurge in its growth until the density of the *Lagarosiphon* again increases.

Our current work has revealed that *Lagarosiphon* is already established, though as yet to a limited extent, in Lakes Tarawera, Tikitapu and Okataina. Thus it has become desirable to study the submerged vegetation of all the Rotorua and Waikato lakes to give some indication of the type(s) of vegetation displaced by the exotics, how such displacements occur, and whether the native vegetation can return and come to an ecological equilibrium with the exotics.

The present paper describes the submerged vegetation of Lake Rotoiti as examined over the period 1967–70; the emergent vegetation was not studied. (Kirk (1871) gave a brief account of emergent communities and referred to *Typha angustifolia* (= *T. orientalis* C. B. Presl.), *Scirpus lacustris* L. and *Eleocharis sphacelata* R. Br. as dominants.) Later papers in the series will report the survey of the other Rotorua and Waikato lakes.

Geographical place names used in this paper are taken from N.Z. Lands and Survey Department maps NZMS 1 Sheet N76 (Rotorua) 2nd Ed., NZMS 152 (Rotorua Lakes) 2nd Ed., and Irwin (1969).

Full details of the morphometry of Lake Rotoiti and its catchment, the rock types and surrounding land development are given by Chapman (1970) and by Fish and Chapman (1969). The lake, at an elevation of 279.32 m above mean sea level (Irwin 1969), originated in part of a large caldera and extended westwards by erosion to its present outlet, the Kaituna River. The shoreline is irregular and varies from cliffs with steep underwater slopes (particularly on the northern edge of the lake) to the shallow sloping western basin. Water level in our experience varies a maximum of only 0.7 m. The lake is in a thermal area, and there are springs, especially on the south shore (Fig. 1), with hot water running into the lake. At Te Rei Bay the springs are on the lake edge. Water temperatures in the epilimnion, except in the immediate vicinity of these hot water discharges, range from 10.0°C in August to 21.5°C in February.

Fish (1969) regards the lake as having "retained many characteristics of oligotrophy" except in the western basin where water from the Ohau Channel, draining Lake Rotorua, mixes before draining down the Kaituna River. However, he also notes that, in 10 years, the annual minimum dissolved oxygen has decreased from 3.1 ppm (Jolly 1968) to 0.08 ppm in his own surveys.

The meteorological data of de Lisle and Kerr (1963) for the region indicate (a) a mean annual rainfall of 70–80 in. (1.8–2.0 m) with winter monthly maxima and a spring secondary maximum, (b) air temperatures at Whakarewarewa range from mean daily maxima of 74°F (23°C) and 53°F (11.7°C) and mean daily minima of 55°F (12.8°C) and 36°F (2.2°C) in February and July respectively (annual mean temperature 56–58°F or 13.3–14.4°C), (c) winds at Whakarewarewa mainly (31.5%) 4–15 mph (4.8–24 km/hr) from the south to west quadrant with north-easterlies of similar speed as the next most frequent (9.5%) (calm 48.0%). Lake Rotoiti is partly protected over a large part of its length by a ridge to the south, and would probably have a greater proportion of westerly winds than the weather station at Whakarewarewa.

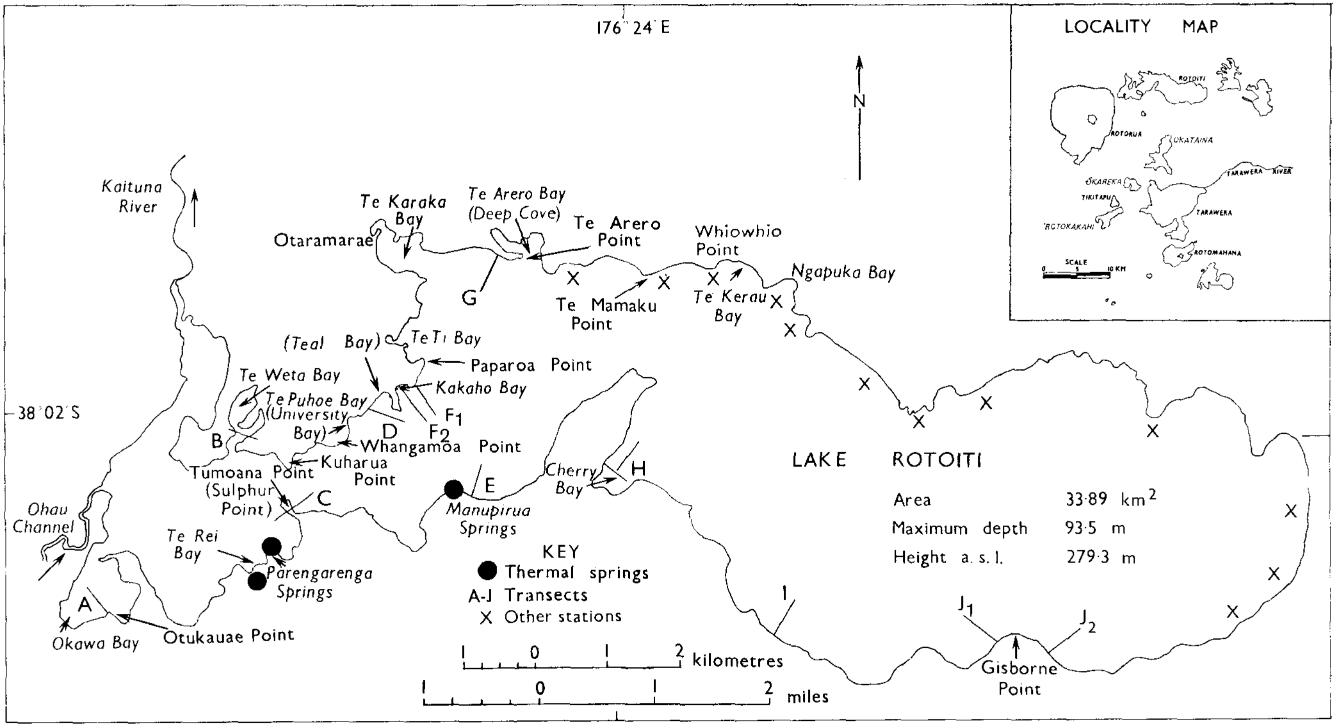

FIG. 1—Sketch map of Lake Rotoiti, North Island, New Zealand. The detailed transects are represented by the lettered bars, other stations by X and thermal springs by ●. (Names in parentheses are in local use but do not have the sanction of the N.Z. Geographic Place Names Board; *for* Te Puhoe Bay *read* Te Pohoe Bay.)

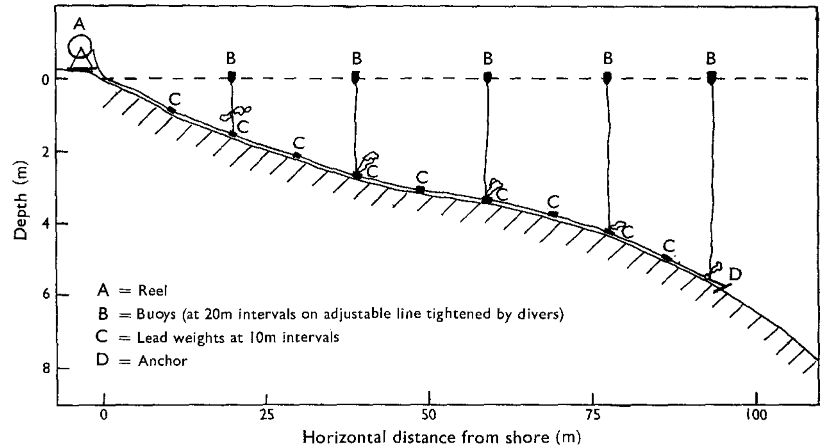

FIG. 2—Diagram of underwater line transect in position.

METHODS

During 1968 SCUBA divers obtained general information on the types of plant communities associated with varying degrees of underwater slope by making numerous spot dives around the lake. Preliminary profiles of the denser weed beds were also made with an echo sounder using a 40 fathom (73 m) scale.

With this information and an unpublished detailed bathymetric map (1 : 15,840) made available by N.Z. Oceanographic Institute, sites typical of various lake features were selected, e.g., shallow basin, sheltered bay and rocky slope. Additional areas were selected because of previous known sprayings with Diquat. At each site a transect line was laid from a boat, at 90° to an identifiable spot on the shore. The line commenced either in water 10 m deep or 100 m from shore in shallower areas. The line, of 0.25 in. (6.2 mm) diameter non-stretch white polypropylene cord, was marked at 1 m intervals and buoyed every 20 m (Fig. 2). Two divers swam along the line detailing vegetation and substrate every metre either on a tape recorder or an underwater "slate" (perspex and wax pencil). Depth records were also made of each vegetation zone with depth gauges previously calibrated to ± 0.25 ft (0.075 m) at this altitude. By numerous spot dives each side of the transect line, or along a shore showing a similar slope on the bathymetric map the divers were usually able to confirm the typical nature of the vegetation in the transect. Where anomalies were found a further transect was examined, e.g., Kakaho Bay (Transects F_1 and F_2). On steep slopes the transect line could not be used satisfactorily and divers recorded the vegetation by depth and an estimate of distance.

At some transect sites the divers obtained substrate samples with a simple core sampler from the centre of each zonation belt recognised. The samples were analysed at the field station in a set of standard sieves. Physical features of the water, such as light penetration and temperature, were measured simultaneously from the boat: both substrate and water quality analyses will be reported separately. All original records, together with details of transect locations, have been deposited in the Biological Sciences Library, University of Auckland.

DESCRIPTION OF TRANSECTS AND OTHER STATIONS

Fig. 1 shows the location of the transects and other stations; Fig. 3 shows the vegetation profiles and substrates at the transects. Except for those specifically noted otherwise, transects were surveyed in August 1968 and checked in February 1969. Unless indicated as depths, measurements in the following are distances from the shore-line.

TRANSECT A Otukauae Point, Okawa Bay

This area was first examined in late 1967 and again in 1970. In 1967 terrestrial grasses from the adjacent grassland extended 3 m into the shallow water. From 4 m to 11 m a low mat of *Glossostigma submersum* and *G. elatinoides* was present with a patch of the aquatic moss, *Drepanocladus fontinaliopsis*, and the phanerogam, *Elatine gratioloides*, at 5 m. In April 1970 the terrestrial grasses had disappeared leaving a zone of bare sand, the *Glossostigma* zone extended to 12 m and now contained *Lilaeopsis lacustris*, *Limosella lineata* and *Enteromorpha nana* f. *rivularis* as additional species. The two species of *Glossostigma* were still the most abundant species (85% ground cover), but no trace of the *Drepanocladus* remained. (*Glossostigma elatinoides* and *G. submersum* commonly graded into each other and in the absence of flowers and fruits, they have been grouped together.)

The first scattered plants of *Lagarosiphon* appeared at 7 m, and between 12 and 70 m this species became so abundant that, except for a patch of *Potamogeton ochreatus* at 13 m, it had eliminated all other phanerogamic vegetation. There was a low basal floor layer of the charophyte *Nitella hookeri* from 14 to 27 m. At 70 m *Lagarosiphon* changed to a community of *Potamogeton ochreatus* with some attached *Cladophora crispata* (Roth) Kütz.

This transect appeared to be typical of the shallow western basin vegetation though it has more protection from both easterly and westerly winds than many areas.

TRANSECT B Te Weta Bay

This area which is well protected from the prevailing winds had been sprayed with Diquat in November 1968. On the transect line in December 1968 there were patches of *Glossostigma* near the shore with a low mat of *Nitella hookeri* covering the remainder of the floor of the bay,

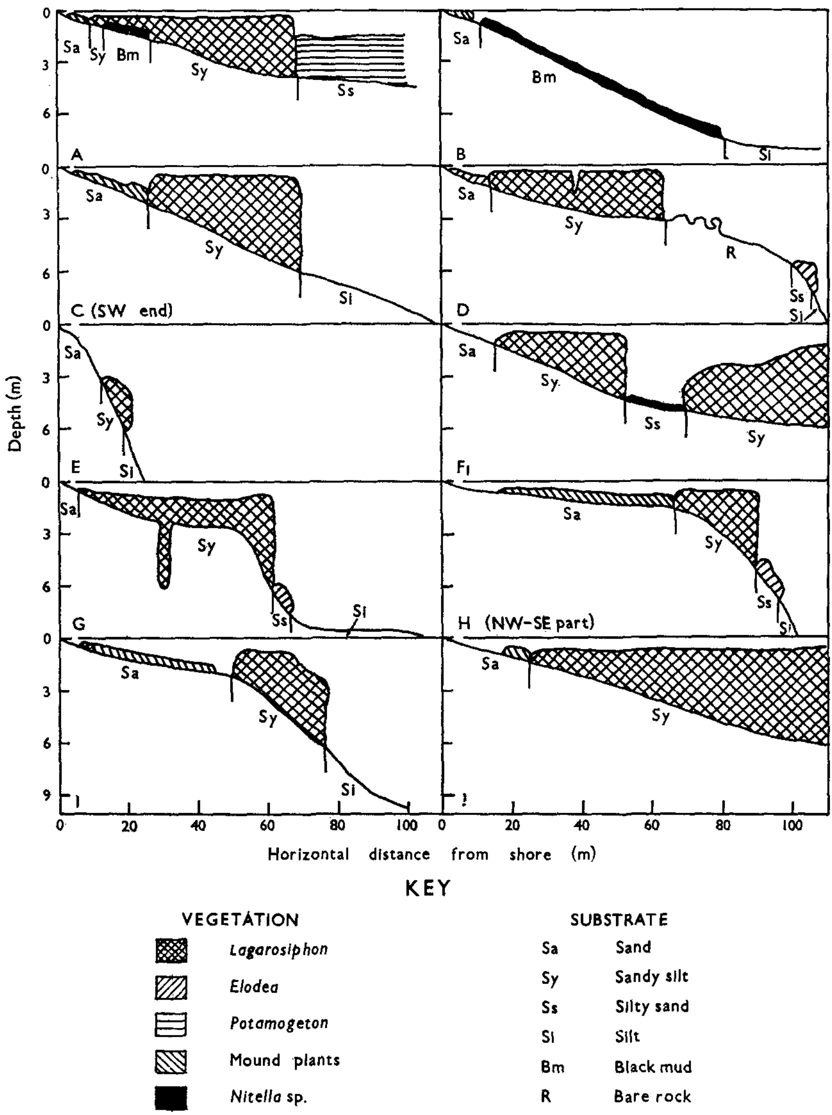

FIG. 3—The profiles, major vegetation types and substrates found in Transects A–J at Lake Rotoiti, August 1968.

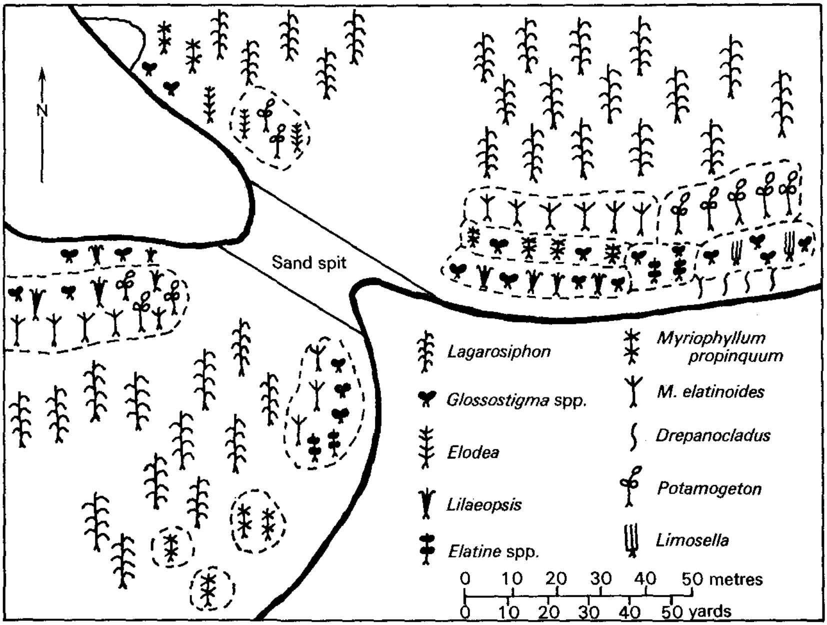

FIG. 4—Sketch map of the vegetation at Tumoana Point (Transect C), Lake Rotoiti, showing the distribution of the vegetation patches relative to the main *Lagarosiphon* beds, August 1968.

to a depth of 7.5 m. Occasional low plants of *Lagarosiphon* were found down to a depth of 6 m.

In both arms of the bay spot dives then revealed occasional plants of *Potamogeton cheesemanii*. By February 1970 these had disappeared from the eastern arm because a massive regrowth of *Lagarosiphon* had taken place despite further spraying in October or November 1969.

From just below the water line to a depth of about 2 m on the sheer eastern cliff at the bay entrance there is an encrusting mat of a sponge (*Spongilla* sp.) coloured green by the algal symbiont, *Chlorella parasitica* Brandt. The cliff is shaded for much of the day.

TRANSECT C Tumoana Point

The transect was laid from near the sand spit (Fig. 4) to both the south-west and north-east. The profile of only the south-west end is shown in Fig. 3C.

In water up to 1.8 m deep island patches or mounds of a characteristic type were found. Isolated patches of *Lagarosiphon* were scattered through the 1.5–2.0 m depth zone but from 2.0 m to 6.0 m depth the *Lagarosiphon* formed dense beds which excluded all other types of vegetation.

Fig. 4 is a sketch map of the area showing the boundaries of the areas occupied by the mounds of vegetation. The variations in size of individual mounds were similar to those at Cherry Bay (*see* later). In the shallower water (0.6–1.0 m depth) the dominants were *Glossostigma submersum* and *Lilaeopsis*. One, or more, of the following was present in some of the mounds: *Limosella, Elodea, Elatine* spp., *Drepanocladus, Triglochin*. The milfoils, *Myriophyllum elatinoides* and *M. propinquum*, formed the lower edges of the mounds in the zone from 1.0–1.8 m depth. Beneath these plants there was clear evidence of erosion associated with a pattern and process phenomenon to be described more fully later (Chapman, Coffey and Brown, in press). After 1968 most of these mounds disintegrated, probably because Diquat had been sprayed in the area. Isolated patches of *Potamogeton cheesemanii* were observed but consisted mainly of plants with only the submerged leaf type.

PARENGARENGA SPRINGS

These springs are underwater very near the lake shore. Elevated temperatures (up to 60°C) through the whole column of water are found within 1–2 m of the springs, but only in the top 0.1 m of water at greater distances. The exact distribution of these higher temperatures is dependent on wind direction and wave action. Sulphur is deposited on the mud and rocks near the springs.

In the area of hot water there was always an assembly of filamentous cyanophytes attached to the substrate. Elsewhere the plant zonation was similar to that of Transect C. All the plants, however, had a thick layer of epiphytic blue-green algae over their surfaces. None of the molluscs with the macrophytes were observed here.

TRANSECT D Te Pohoe Bay

Apart from one or two patches of *Glossostigma submersum* and *Limosella* and the *Elodea* beds, the entire vegetation in the transect consisted of what appeared to be pure, dense *Lagarosiphon* down to a depth of 3.5 m. A rock ridge at this depth carried only the encrusting sponge *Spongilla* with its symbiont *Chlorella*. Elsewhere in the bay the *Lagarosiphon* extended down to 6.0 m depth.

Detailed analysis of this bay (Coffey, unpublished, 1970) has shown that up to 13% *Elodea*, on a dry weight basis, may be present. A similar situation may occur in other *Lagarosiphon* zones.

Fig. 5 shows the results of sieve analyses from areas taken in the centre of each zone, and is typical of analyses from other transects. The proportion of silt-like material increased progressively with depth of water whilst that of sand decreased. The *Lagarosiphon* bed contained a substantial amount of sand and its substrate is thus defined as a sandy-silt.

The bay is exposed only to north-easterly winds.

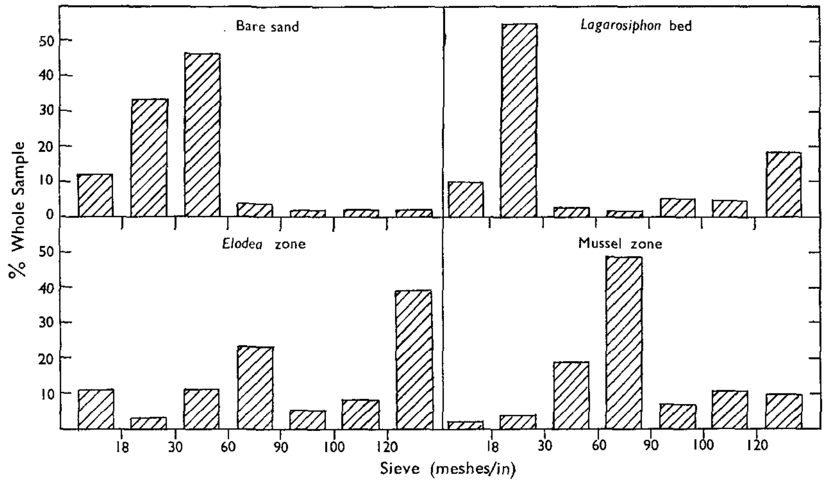

FIG. 5—Particle sizes of substrate samples taken from the different zones in Te Pohoe Bay (Transect D), Lake Rotoiti, August 1968.

TRANSECT E Manupirua Springs

Since about 1963, the area around the wharves has been regularly sprayed. In August 1968, there was a low growth of *Lagarosiphon* between 3.5–6.0 m depth (i.e., 10–22 m off the end of the wharf). Beyond the *Lagarosiphon* belt was a rock outcrop at 7.5 m depth with the sponge *Spongilla* (and its symbiont *Chlorella*) present on it. At greater depth, where the bottom becomes silty, only freshwater mussels (*Hydridella menziesi hochstetteri*) were found.

About 85 m west of the wharves patches and mounds of *Myriophyllum elatinoides* and *Lilaeopsis* were found in shallow water. About 200 m from the wharf bright green mounds of *Glossostigma submersum* were conspicuous. Closer to the wharf there are extensive islands of *Glossostigma elatinoides* with a little *Limosella,* some *Myriophyllum elatinoides* and *Elatine* sp. ined. On the extensive areas of boulders in this area are small patches of a low growing *Nitella* (probably *N. gracilis,* but not adequately identified without sex organs). Although this area appears exposed to the west it is partly protected close inshore by a small promontory.

On the east side of the wharves there were in 1970 similar mounds and swards of vegetation in which *Lilaeopsis lacustris* was fairly common.

TRANSECT F Kakaho Bay

Two transects were laid here. The first, F_1 (Fig. 3F), laid from a wharf at the eastern point, showed a dense bed of *Lagarosiphon* extending out for 52 m and to a depth of 4 m. This bed was growing in silty sand and the plants reached almost to the water surface. On a silt area beyond this was a low growing community of *Elodea* mixed with *Nitella hookeri*. At 68 m from the wharf and 4.5 m depth this was replaced, again in silty-sand, by another *Lagarosiphon* bed which extended to well beyond the end of the transect line. These plants were shorter than in the belt near the wharf.

The second transect, F_2, was in the bay itself and ran through an area which had been sprayed with Diquat some 3 months previously (i.e., May 1968). *Lagarosiphon* was present up to 35 m from the shore, where it was replaced by freshwater mussel beds in silt.

Kakaho Bay is exposed to north-easterlies but wave damping by dense beds of *Lagarosiphon* up to 200 m from the shore lessens the effects of rough weather.

Te Karaka Bay

No transects were laid in this bay. Isolated patches of *Lagarosiphon* formed a zone along both northerly and southerly shores and were somewhat thicker in the northern side. At the western end, off the jetties to the houses at Otaramarae, there was a continuous zone of *Lagarosiphon* containing very little *Nitella hookeri* down to 6.0 m depth where it was replaced by a pure *Nitella* belt to 7.5 m depth.

Transect G Te Arero Point

A transect laid from just to the west of the entrance to Te Arero Bay revealed a thick bed of *Lagarosiphon* from 5–50 m offshore on sandy silt. Within this bed there was a deep hole, possibly a freshwater spring outlet, also containing *Lagarosiphon*. A narrow 2-m belt of *Elodea* occurred in the steep slope at the edge of the *Lagarosiphon* belt. Beyond this was a silt substrate occupied by freshwater mussels with the sponge and its symbiont alga on rock outcrops. Te Arero Bay itself contains a thick bed of *Lagarosiphon* ranging down to depths from 4.5–6.0 m.

Northern Shore

The shore east of Te Arero Bay is exposed to the west and south-west winds sweeping down the lake from the western basin. Except in sheltered bays, there are boulder substrates, mainly swept clear of sand, or sheer underwater rock faces.

In areas of the greatest exposure the boulder substrates were, in November 1969, clear of vegetation except for transient patches of *Nitella* (unidentified in the absence of sex organs) in the occasional pockets of sand.

Where exposure was somewhat reduced, boulder substrates from 0.15–0.75 m depth were completely covered with *Spirogyra* and *Ulothrix* during calm weather, but were rapidly removed by wave action. From 0.75–5.0 m depth there were frequent patches of *Spirogyra-Ulothrix*.

In winter *Enteromorpha nana* f. *rivularis* replaced these filamentous algae.

On sheer underwater faces the 0.15–0.75 m zone was again occupied by *Spirogyra* and *Ulothrix* but rarely to the extent of 100% cover. *Drepanocladus fluitans* and *D. fontinaliopsis* formed patches up to 3 cm thick down to depths of 3 m in places where some roughness was present on the cliff face to provide anchorage. The *Spongilla* (sponge)/ *Chlorella,* association was frequent to a depth of 5.5 m. A matted complex of blue-green algae, in which the principal genera were *Oscillatoria, Anabaena* and *Schizothrix,* was variably present from the surface to 10 m depth. The filaments projected up to 3 cm from the rock face.

In the sheltered bays where a sandy substrate was present in the beach, e.g., Ngapuka and Te Kerau Bays, the vegetation pattern was closely similar to that at Te Arero Point.

TRANSECT H Cherry Bay

This area was comparable in many ways with Tumoana Point (Transect C). The transect contained patches or mounds of vegetation containing the species listed in Table 1. These plants occupied the zone off shore from 30–45 m to 1 m depth. The mounds varied in size in much the same way as at Tumoana Point (*see* Fig. 4). At slightly greater depths (1.0–1.8 m) the same community could be found except that *Myriophyllum propinquum* replaced *M. elatinoides*. Here, as in the Tumoana Point transect, the phenomenon of pattern and process was in evidence. Below 1.8 m depth, 65–90 m off-shore, an extensive bed of *Lagarosiphon* up to 2 m high was found. Beyond, shoots of *Lagarosiphon* were lying on the lake bed mixed with *Nitella hookeri.* Beyond 90 m sandy silt was replaced by deep organic silt, and the only plant species persisting was *Elodea*.

North of the first transect, a further transect parallel to the shore at depths of 0.15–1.00 m was laid to pass through the patches of vegetation. The distribution of the various species is shown in Fig. 6.

TRANSECT I

From the beach to 50 m out, the lake bed was pumice sand with patches of *Elodea-Nitella hookeri-Limosella*; these patches varied greatly in size and some were up to 35 m across. The substrate then changed to a silty sand, and from 50 m (2 m depth) to 75 m (6 m depth) there was a belt of *Lagarosiphon,* the tallest plants of which did not exceed 3.5 m in length. Below the vegetation limit at 6 m depth, only freshwater mussels were found.

TABLE 1—Plant species found in the mounds of the Low Mixed Community (Ai) in Transect H at Cherry Bay, Lake Rotoiti, August 1968. * = exotic; † = species considered distinct by Miss R. Mason (pers. comm.)

GROUP	SPECIES	SUBJECTIVE FREQUENCY
ALGAE	*Nitella hookeri* A. Br.	Frequent
	N. gracilis (Sm.) Ag.	Locally abundant
	Enteromorpha nana (Somerf.) Bliding var. *rivularis* (Collins) comb. nov.	Abundant (summer)
	Ulothrix subtilis (Kütz.) Kirchn.	Present
	Spirogyra sp.	Present
	Anacystis cyanea Dr. & Daily	Present
BRYOPHYTE	*Drepanocladus fontinaliopsis* (C.M.) Dix.	Occasional
CRYPTOGAM	*Isoetes kirkii* A. Br.	Locally abundant
PHANEROGAMS	*Glossostigma elatinoides* Benth.	Frequent to locally dominant (older mounds)
	Glossostigma submersum Petrie	Locally dominant
	**Elodea canadensis* Michx.	Locally frequent
	**Lagarosiphon major* (Ridley) Moss	Present
	Limosella lineata Gluck	Local
	Lilaeopsis lacustris Hill	Codominant
	**Ludwigia palustris* (Linn.) Ell.	Frequent (older mounds)
	Myriophyllum elatiniodes Gaud.	Codominant
	M. propinquum A. Cunn.	Codominant
	Potamogeton cheesemanii A. Benn.	Locally frequent
	**P. crispus* Linn.	Present
	P. ochreatus Raoul	Present
	Elatine gratioliodes A. Cunn.	Occasional
	†*Elatine* sp. ined.	Rare
	Utricularia protrusa Hook. f.	Present

TRANSECT J Gisborne Point

This area had been sprayed with Diquat before August 1968, but dead plants of *Lagarosiphon* remained to indicate the former extensive belt. On the western side of the point (J_1; *see* Fig. 3) there was a completely bare belt up to 18 m off shore. Beyond this there was a narrow zone occupied by isolated plants of *Isoetes kirkii* and *Elatine gratioloides*, but there was no evidence of compact vegetation patches or mounds like those at Sulphur Point and Cherry Bay; clearly, an extensive *Lagarosiphon* belt had existed out to 120 m, beyond which the *Lagarosiphon* plants became more scattered and were associated with *Nitella hookeri*. The pattern on the east side of the point (J_2) was similar: 0–20 m bare or patches of *Elatine*, rather more *Isoetes* and a little *Lilaeopsis*; 20–50 m patchy *Lagarosiphon* with a dense *Lagarosiphon* bed from 50–175 m where the depth was 6 m.

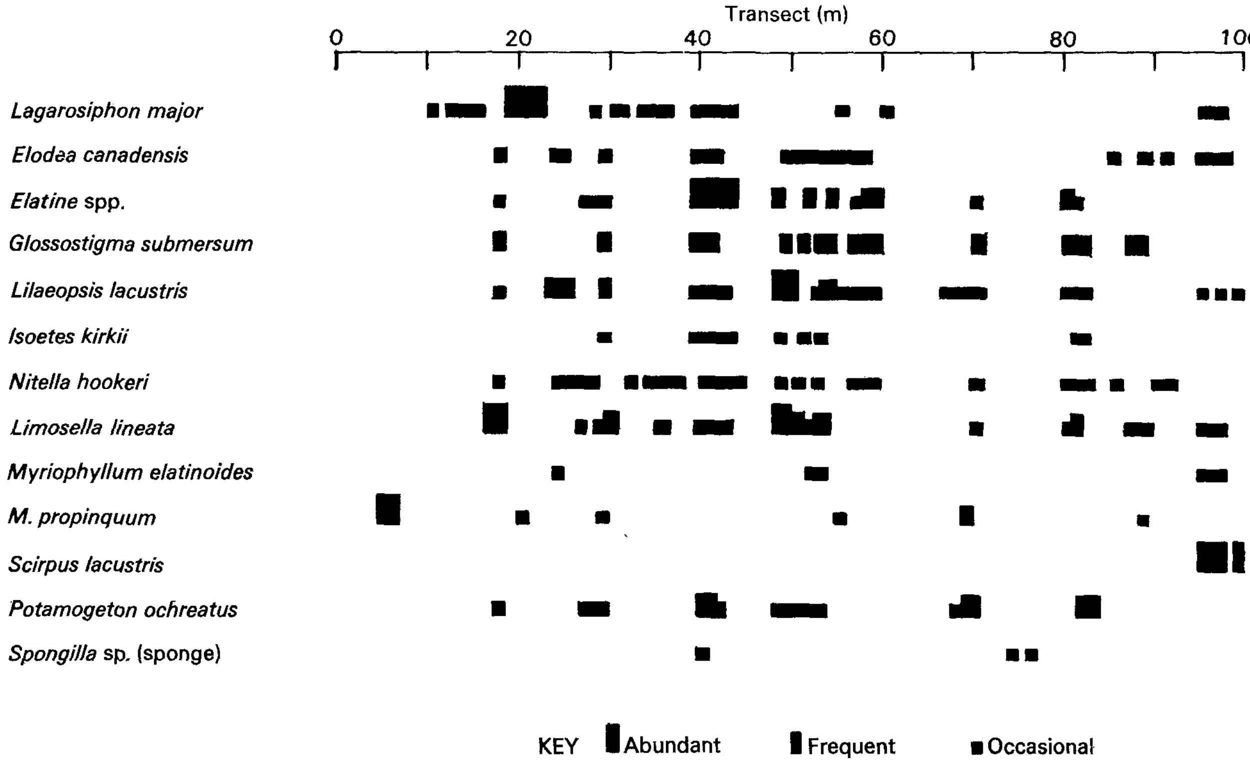

FIG. 6—Plant species and their relative density assessed subjectively by B.T.C. on a part of Transect H through the vegetation mounds parallel to the shore at Cherry Bay, Lake Rotoiti, August 1968.

EASTERN SHORE

Numerous spot dives along the eastern shore revealed extensive belts of *Lagarosiphon* similar to those already described. Aerial photographs (D. Spiller, pers. comm.) confirm this and show "clear" areas at intervals. These appeared to us to correspond to stream inflows which, when in flood, cause the *Lagarosiphon* to lie flat or wash the plants away altogether from a narrow strip.

No patches or mounds of the mat forming plants were found along this exposed shore.

CLASSIFICATION OF VEGETATION

From this survey the submerged aquatic communities in Lake Rotoiti can be classified as:

A. Sandy Communities
  i. Low Mixed Community
  ii. *Lagarosiphon* Community
B. Silty Communities
  i. *Elodea* Community
  ii *Nitella hookeri* Community
C. Rock and Cliff Community
D. Shingle Beach and Coarse Stone Community
E. Thermal Spring Community

LOW MIXED COMMUNITY (Ai)

Table 1 lists all 23 species recorded in this community on the sandy substrate of Cherry Bay (Transect H) in water up to 1.8 m deep. Elsewhere in the lake the community has similar forms but may be less rich floristically, e.g., Transects A and B.

It exists in three forms:

(a) Small "islands" of vegetation which may be level with the substrate (patches) or slightly elevated above the substrate (mounds). These mounds vary considerably in size and species composition (Fig. 6) but frequently have one of the *Myriophyllum* spp. bordering their deepest edge, e.g., Transects C and H.
(b) Extensive mats covering most of the substrate in an area, and which also have *Myriophyllum* at their deepest edge, e.g., Transect I.
(c) Isolated individual plants not fused into mounds or patches, e.g., Transect J_1.

The dominants can be one or more of *Glossostigma elatinoides*, *G. submersum*, *Limosella lineata*, or one of two species of *Myriophyllum*. It is probably a matter of chance which become dominant, because apparently there are no obvious correlations of dominance with specific factors such as substrate or exposure.

When sufficient plants accumulate to form a distinct patch they may trap and bind sand and silt to form the mounds which can become elevated 0.10–0.15 m above the adjacent bare substrate.

Many mounds showed clear evidence of erosion on the side most subjected to wave action, i.e., from the direction of maximum exposure. Thus at Tumoana Point it was the south-west or north-east lower lakeward edges which exhibited this erosion. East of Manupirua Springs, the western eroded edges were approximately at right angles to the shore. However, at Cherry Bay, the edges nearest the shore were eroded, despite exposure only to the east in this area. This erosion was later found (Chapman, Coffey and Brown, in press) to be caused by backwash from the breaking of easterly waves.

We have applied the term Low Mixed Community to this group of species because many have a low habit, e.g., *Glossostigma, Limosella, Lilaeopsis* and *Isoetes*. However, the two species of *Myriophyllum* and those of *Potamogeton* are taller; *Myriophyllum* in this community ranged from 0.10 to 0.40 m high. Plants of both genera break the water surface in some areas of New Zealand, but in this community have not been observed closer than 0.15 m to the surface. To some extent this will be dependent upon the water level of the lake, which tends to be at its minimum in summer. All the taller species die down in the late summer–early autumn period and perhaps the growing season is normally insufficient to enable them to reach the water surface. The fact that very much taller plants of *P. ochreatus* were observed in Transect A (*see* Fig. 3A), does tend, however, to suggest that some special feature of the Low Mixed Community restricted the growth of these taller species.

Lagarosiphon COMMUNITY (Aii)

This community was most frequently monospecific but it could contain plants of *Elodea* (Fig. 7) and a ground flora of *Nitella hookeri* (*see* Fig. 3A). The community occurred in water from approximately 1.5 m deep to a very sharp disappearance at 6.0 m depth. The dominant appeared to colonise a sandy-silt lake base.

In the various profiles shown in Fig. 3 the height of the *Lagarosiphon* beds appear to show variation between different lake areas. Subsequent work (Coffey, unpublished, 1970) has shown that *Lagarosiphon* beds in unsprayed areas of Lake Rotoiti exhibit cyclic change. After initial colonisation of bare sand areas the plants grow right to the water surface and accumulate silt in the sheltered base of the bed. Eventually an overmaturing of the dense bed occurs, possibly due to shading of the lower parts of the plants. Wave action then removes much of the bed and the accumulated silt, and this is followed by active growth of the basal portions remaining, so restarting the cycle. The time for this sequence is approximately 18 months at Te Pohoe Bay but only 9 months on the south shore near Manupirua Springs. Thus the variations noted in the height of the plants during the course of our work probably represent different phases of this natural cycle or possible variations induced by spraying with Diquat.

Elodea COMMUNITY (Bi)

This was more restricted in its distribution than Community Ai and was found only in Transects D, F, G, and H, and between Whangamoa and Kuhurua Points. The *Elodea* is capable of occupying the lake bed between 0.7 and 7.5 m depth (*see* Fig. 7) but was eliminated from 2 to 6 m depths by *Lagarosiphon*. Only in Transect D was it found both above and below the *Lagarosiphon* belt. Elsewhere it was restricted to the zone from 6.0 to 7.5 m depth and showed its maximum height development of 2–3 m between Whangamoa and Kuhurua Points. The community when occurring in its lower zone, was on a more silty substrate than *Lagarosiphon* (*see* Fig. 5, Te Pohoe Bay).

Nitella hookeri COMMUNITY (Bii)

Nitella only develops monospecifically in protected bays after *Lagarosiphon* has been killed by Diquat (Transect B). Normally it exists in what appears to be a semisuppressed state at the base of *Lagarosiphon* or *Elodea* plants (Transects A_1 and F_1, and in Teal Bay just to the east of Transect D). At Otaramarae the *Nitella* formed a luxuriant zone from 6.0 to 7.5 m depth. Since the area here has been sprayed regularly this zone may represent a belt formerly occupied by *Elodea*.

When *Nitella* forms a lush growth it is regarded by us as a transient in areas where *Lagarosiphon* or *Elodea* are the normal dominants. In Lake Rotoiti, *Nitella* has not been found below the compensation point (7.5 m) for *Elodea*. No extensive data is available for the upper limit of *Nitella* but it comes to within 1.5 m of the surface in parts of Te Weta Bay.

ROCK AND CLIFF COMMUNITY (C)

This community was characterised by the presence of *Drepanocladus* and the freshwater sponge, *Spongilla*, with its *Chlorella parasitica* symbiont. Seasonal algae, e.g., *Spirogyra* spp., *Ulothrix subtilis*, *Cladophora* sp. and various cyanophytes were associated with the two permanent members.

SHINGLE BEACH AND COARSE STONE COMMUNITY (D)

Seasonal successions of various algae, e.g., *Spirogyra*, *Ulothrix* and *Enteromorpha* spp. as well as attached patches of *Nitella gracilis* make up this community. Macrophytes cannot establish because the substrate is too mobile. This community was well developed along the northern shores exposed to the prevailing winds.

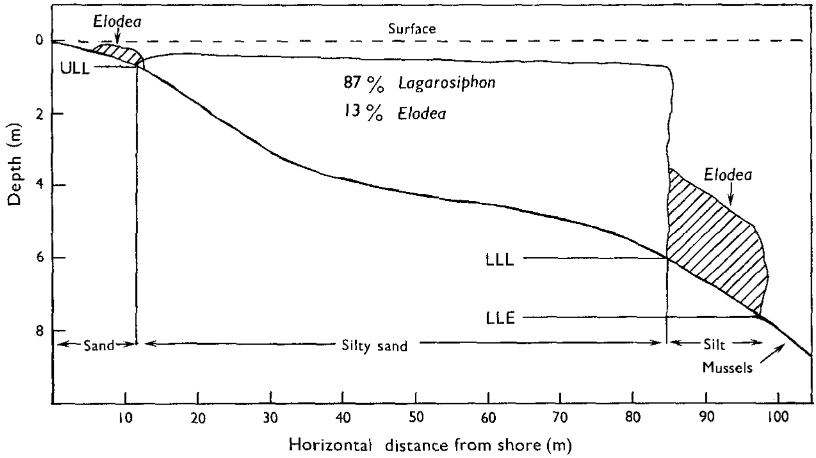

FIG. 7—Generalised profile illustrating the pattern of distribution and relative abundance of *Lagarosiphon* and *Elodea* in Lake Rotoiti. (ULL = upper limit of *Lagarosiphon*; LLL = lower limit of *Lagarosiphon*; LLE = lower limit of *Elodea*.)

THERMAL SPRING COMMUNITY (E)

Found fully developed only at Parengarenga Springs and Te Rei Bay where the hot springs discharge in or near the lake edge, this community is associated with bare rock, water temperatures up to 60°C, and sulphur deposition; it is characterised by an assembly of filamentous cyanophytes. The community developed only in the immediate vicinty of fumaroles (1–2 m away). At greater distances, or elsewhere in the lake where thermal streams discharge, the normal macrophytic vegetation was characterised by a well developed epiphytic layer of cyanophytes and/or bacteria which was perhaps due to the lack of the normal molluscs.

In our experience plants brought back to the laboratory from all parts of Lake Rotoiti frequently develop this epiphytic layer under culture conditions. Possibly, grazing by gasteropods prevents this development within the lake except near thermal areas.

DISCUSSION

From these surveys the distribution of the submerged plant communities can apparently be related to the following factors:

Shore physiography, e.g., cliff face or gentle slope,
Substrate, e.g., sand, sandy-silt or silt (*see* Fig. 3),
Exposure to wave action, e.g., on shores exposed to or sheltered from prevailing winds,
Water temperature, e.g., in thermal spring areas, and
Water depth, i.e., light.

Of these factors shore physiography is predominant. Physiography and exposure determine whether a rocky or soft substrate develops on the lake bed and thus ultimately determine the type of community which establishes itself (Table 2). In Lake Rotoiti the slope of the lake bed seems to be sufficiently gentle, except on the northern shore, to permit the accumulation of soft substrates (sand to silt) on which macrophytes can grow (*see* Fig. 3). Exposure becomes the dominant factor when wave action clears the soft substrates completely, e.g., Community D of the northern shores. Exposure probably also determines the distribution of the Low Mixed Community (Ai) which can only develop when erosion is less rapid than plant growth in sandy shallows from 0–1.8 m deep (Chapman, Coffey and Brown, in press).

The type of community appears to be related to substrate in the soft areas: the Low Mixed Community and the upper *Elodea* zone in sand; *Lagarosiphon* in sandy silt; the lower *Elodea* zone in silty sand (Fig. 5); and *Nitella* on silt in sheltered areas. The degree of exposure to wave action probably determines to some extent the relative proportions of sand and silt in the substrate. However, although Fig. 5 shows a definite relationship of particle size to plant community which could be causal, it is also possible that the community produces its own characteristic substrate. Thick weed beds may provide calm water areas in which wave removal of the finer particles is prevented. Distribution of a community could then be related, at least in part, to the amount of deposition the plants present can tolerate. On this basis the persistent *Elodea* zone in 6.0–7.5 m might be due to the inability of *Lagarosiphon* to compete in the greater proportion of silt of these deeper, calmer waters. *Nitella,* with its characteristic method of growth in sheltered bays, undoubtedly contributes to its own substrate as the lower parts of the plant decay and form an organic mud.

With increasing depth of water, light becomes an important factor which may supersede the soil substrate factor. From this survey the compensation point for *Lagarosiphon* is 6.0 m and that for *Elodea* 7.5 m (*see* Fig. 7). Because both plants can grow tall and thus receive additional light, the depth of the compensation point may be related to initial colonisation. This aspect is receiving further attention as the surveys of other lakes continue.

At present we have not been able to discover what factor, or set of factors, determines whether *Elodea* or the Low Mixed Community occurs above the main *Lagarosiphon* belt on semi-exposed shores.

Where thermal springs occur water temperatures clearly control the community near the fumarole (*see* Table 2). Except for the effects of thermal springs, the other four factors discerned in Lake Rotoiti are all regarded by limnologists as those most important in determining the distribution of macrophytes in other lakes (e.g., Rickett 1921; Denniston 1922; Wilson 1939, 1941; Wohlschlag 1950; Sculthorpe 1967).

TABLE 2—Schematic relationship of submerged vegetation in Lake Rotoiti to depth, substrate type and exposure

	ROCKY SITES	SOFT SITES			
DEPTH (m)	EXPOSED OR SEMI-EXPOSED	SEMI-EXPOSED	SHELTERED TO SEMI-EXPOSED	SHELTERED (after spraying)	THERMAL AREAS
0–1	Bare or patches of *Drepanocladus* and sponge. Seasonal algae.	Bare sand	Low Mixed Community (sand)	Bare	Cyanophytes
1–2		*Elodea* Community (sand)			Low Mixed Community (sand)
2–6		*Lagarosiphon* Community (sandy silt)	*Lagarosiphon* Community (sandy silt)	*Nitella hookeri* Community (silt)	*Lagarosiphon* Community (sandy silt)
6–8		*Elodea* Community (silty sand)	*Elodea* Community (silty sand)		*Elodea* Community silty sand)
8		Freshwater Mussel Community (silt)			

In a lake the size of Rotoiti the submerged vegetation can be regarded as either successionally or statically zoned. A depth succession comparable to those postulated by Pearsall (1920) for the English lakes and by Wilson (1941) for Trout Lake in Wisconsin could result thus:

Community Ai/Bi → *Lagarosiphon* → *Elodea*

However, the occurrence of *Elodea* both above and below the *Lagarosiphon* zone (Fig. 3D) is more suggestive of static zonation.

Historically, *Elodea* was distributed throughout New Zealand before *Lagarosiphon* appeared (Chapman 1970) and presumably existed in the Rotorua lakes prior to the entry of *Lagarosiphon*. It does indeed occur in Lake Rotokakahi in the absence of *Lagarosiphon* and also in Lake

Okataina where *Lagarosiphon* is only just becoming established. Thus we suggest that *Elodea,* and possibly the Low Mixed Community, occupied wider zones in Lake Rotoiti than they do now. When *Lagarosiphon* entered the lake it was able to compete successfully down to its compensation point of 6.0 m with both types of vegetation. *Elodea* still remains below this depth because of its lower depth compensation point and, possibly, its greater tolerance of accumulated silt. On this view *Lagarosiphon* successfully invaded an already existing static zonation.

Studies of the other lakes should help to show what the earlier zonation was like. The original native vegetation probably consisted of the Low Mixed Community in shallower waters with *Nitella hookeri* and *Potamogeton* spp. in the deeper waters. The first invader was *Elodea,* though we have no date for the first entry of this species into the Rotorua lakes, and this seemingly replaced much of the *Potamogeton.* Some support for this opinion comes from Transect A (*see* Fig. 3) where a belt of tall growing *Potamogeton ochreatus* still exists; *Lagarosiphon* later arrived. What has occurred represents invasion and successful competition. The present zonation is represented by Table 2. This is only likely to be further altered by changes in water level, introduction of new aquatic species, or eutrophication processes. In Lake Rotoiti enrichment at present is related to run-off from any top-dressing of adjacent pastures, from nutrients present in the streams coming from the springs, and possibly from septic tanks of the cottage owners around its shores; this last is likely to be minimal. The eutrophication process is probably a slow one in Lake Rotoiti, although oxygen data (Fish 1969) suggest an acceleration in the last 14 years.

ACKNOWLEDGMENTS

We are grateful to the New Zealand Oceanographic Institute for a survey map of Lake Rotoiti prior to its publication and to the divers of the Auckland University Underwater Club who assisted in this work. Finance from the University Grants Committee and the Marine Department (Fisheries Research Division) supported this work.

LITERATURE CITED

CHAPMAN, V. J. 1970: A history of the lake weed infestation in the Rotorua lakes and the lakes of the Waikato hydro-electric system. *N.Z. Dept. Scient. Ind. Res. Inf. Ser. 78*: 52 pp.

CHAPMAN, V. J. and BELL, C. A. (Eds) 1967: "Rotorua and Waikato Water Weeds". Auckland U.P., Auckland. 76 pp.

CHAPMAN, V. J. and BROWN, J. M. A. 1966: The lake weed problem in the North Island of New Zealand. *Phykos 5*: 72–82.

CHAPMAN, V. J., COFFEY, B. T. and BROWN, J. M. A. (in press): Submerged vegetation of the Rotorua and Waikato Lakes. 2. "Cyclic change" in Lake Rotoiti. *N.Z. Jl mar. Freshwat. Res.*

COCKAYNE, L. 1928: "The Vegetation of New Zealand". Vol. 15 *in Die Vegetation der Erde.* 3rd Ed. 1958. Engelmann, London. 456 pp.

COFFEY, B. T. unpublished 1970: A contribution to the autecology and control of *Lagarosiphon major.* Unpublished M.Sc. thesis lodged in University of Auckland Library. 210 pp.

DE LISLE, J. F. and KERR, I. S. 1963: The climate and weather of the Bay of Plenty Region. *N.Z. Met. Serv. Misc. Pub. 115 (1).* 12 pp.

DENNISTON, R. H. 1922: A survey of the larger aquatic plants of Lake Mendota. *Trans. Wis. Acad. Sci. Arts. Letters 20*: 495–500.

FISH, G. R. 1969: The oxygen content of some New Zealand lakes. *Verh. int. Verein. theor. angew Limnol. 17*: 392–403.

FISH, G. R. and CHAPMAN, M. A. 1969: Synoptic surveys of lakes Rotorua and Rotoiti. *N.Z. Jl mar. Freshwat. Res. 3*: 571–84.

IRWIN, J. 1969: Lake Rotoiti, Provisional bathymetry 1:25,000. *N.Z. Marine Dept., Fish Res. Div., Lake Series.*

JOLLY, V. H. 1968: The comparative limnology of some New Zealand lakes. 1 Physical and chemical. *N.Z. Jl mar. Freshwat. Res. 2*: 214–59.

KIRK, T. 1871: Notes on the botany of certain places in the Waikato District, April and May 1870. *Trans. N.Z. Inst. 3*: 147–8.

PEARSALL, W. H. 1920: The aquatic vegetation of the British Lakes. *J. Ecol. 8*: 163–201.

RICKETT, H. W. 1921: A quantitative study of the larger aquatic plants of Lake Mendota, Wisconsin. *Trans. Wis. Acad. Sci. Arts. Letters 20*: 501–27.

SCULTHORPE, C. D. 1967: "The Biology of Aquatic Vascular Plants". Arnold, London. 610 pp.

WILSON, L. R. 1939: Rooted aquatic plants and their relation to the limnology of freshwater lakes. Pp. 107–22 *in* "Problems of Lake Biology". *Publs. Am. Ass. Advn. Sci. 10.* (Not seen by authors; reference from Sculthorpe 1967, *q.v.*)

——— 1941: The larger aquatic vegetation of Trout Lake, Vilas County, Wisconsin. *Trans. Wis. Acad. Sci. Arts. Letters 33*: 135–49.

WOHLSCHLAG, D. E. 1950: Vegetation and invertebrate life in a marl lake. *Invest. Indiana Lakes Streams. 3*: 321–72.