Ecological impacts of water net *(Hydrodictyon reticulatum)* in Lake Aniwhenua, New Zealand

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Abstract: The ecological impacts of *Hydrodictyon reticulatum* blooms (1989-94) were studied at Lake Aniwhenua (a constructed lake) in North Island, New Zealand by collating fish, invertebrate and macrophyte data collected towards the end of a four year bloom period and following its decline. *Hydrodictyon reticulatum* had some localised impacts on the biota of the lake. Some macrophyte beds were smothered to the extent that they collapsed and disappeared, and dense compacted accumulations of *H. reticulatum* caused localised anoxic conditions while it decayed. However, fish and some invertebrates in the lake benefited from the *H. reticulatum* blooms. High numbers of *Ceriodaphnia* sp. (maximum, 5.5 x 104 m^{-2}) were recorded amongst *H. reticulatum,* and gastropods were exceptionally abundant, the most common being *Potamopyrgus antipodarum* (maximum, 1.8 x IOS m^{-2}). *Hydrodictyon reticulatum* was consumed by three species of common gastropods in experimental trials, with *Austropeplea tomentosa* consuming up to 1.3 g dry weight *H. reticulatum* g^{-1},live weight of snail day^{-1}. Gastropods comprised the major portion of the diet of *Oncorhynchus mykiss* in Lake Aniwhenua during and after the *H. reticulatum* bloom. A marked peak in sports fishing (with exceptional sizes and numbers of fish caught) coincided with the period of *H. reticulatum* blooms and the abundant invertebrate food source associated with the blooms.

Keywords: filamentous algae; *Hydrodictyon reticulatum; Oncorhynchus mykiss* diet; *Potamopyrgus antipodarum.*

Introduction

Hydrodictyon reticulatum, or water net, is a colonial, unattached, filamentous green alga which has been seasonally troublesome in New Zealand. It was first recorded in 1987 and reached nuisance levels in 1989 in a number of locations throughout the Waikato and Bay of Plenty regions, particularly in Lake Rotorua, Lake Aniwhenua and in the marina at Kinloch, Lake Taupo (Hawes *et al.,* 1991; Wells *et aI.,* 1999). Nuisance levels were sufficient to cause public alarm and considerable political interest.

Blooms of *H. reticulatum* have been reported overseas (Fitzgerald, 1981; Dineen, 1953; Rai and Chandra, 1989; Flory and Hawley, 1994) but they have not been as problematic as in New Zealand, where many water based activities such as boating, fishing, swimming, tourism, power generation and supply of water have been affected. There were concerns thatH. *reticulatum* could be a potential ecological disaster (e.g., New Zealand Herald, front page, 12 December 1991), with dense growths causing oxygen depletion, shading, and smothering of plants and benthic fauna (Hawes *et al.,* 1991). There was considerable concern also over the potential of *H. reticulatum* to cause unfavourable impact on the trout fishery in Lake Aniwhenua when abundant growths appeared in the lake in 1990. Surprisingly, however, angling was considered to have improved, with fishermen reporting an increase in the size and number of healthy rainbow *(Oncorhynchus mykiss)* and brown *(Salmo trutta)* trout caught (Thomas, 1996). In early 1994, some preliminary sampling of invertebrates within *H. reticulatum* blooms was undertaken, with a major study of the ecological impacts of *H. reticulatum* planned for the following year. However, following its seasonal pattern of decline in July 1994, *H. reticulatum* failed to re-establish the following spring, as it had done in the previous five years.

This paper is a collation of data on impacts of *H. reticulatum* in Lake Aniwhenua. It presents evidence of: large areas of surface, mid-water and benthic *H. reticulatum;* an increase in phytophyllous invertebrates associated with *H. reticulatum;* evidence that *H. reticulatum* provided habitat and a major source of food for gastropods; data that indicate gastropods were the main dietary component of rainbow trout in the lake; and evidence that rainbow trout attained exceptionally large sizes and had exceptionally fast growth rates during the bloom period.

Study Site

Lake Aniwhenua is a long narrow lake (4.5 km by c. 0.5 km), 255 ha in area, situated on the Rangitaiki River, 11 km downstream from Murupara, North Island, New Zealand (Fig. 1). The lake was formed in 1980 on previously grazed pasture, when a dam was built and a 25 megawatt hydro-electric power scheme commissioned. The maximum depth of the lake is 10 m (against the barrage) but it is mostly less than 3 m deep. The lake and its margins are a valued recreational area, used for water skiing, fishing, swimming, game shooting and camping. In 1991 and 1993, it was used as avenue for international trout fishing competitions. *Hydrodictyon reticulatum* was first noted in the lake in November 1990 when it was already widespread and forming extensive surface mats. Subsequently, prominent blooms occurred each summer until 1994. The lake has a residence time of *c.* 3 days (depending on power generation and inflows). Water temperature is generally cool, ranging from 9 to 18°C at the head of the lake, but in localised areas of still surface

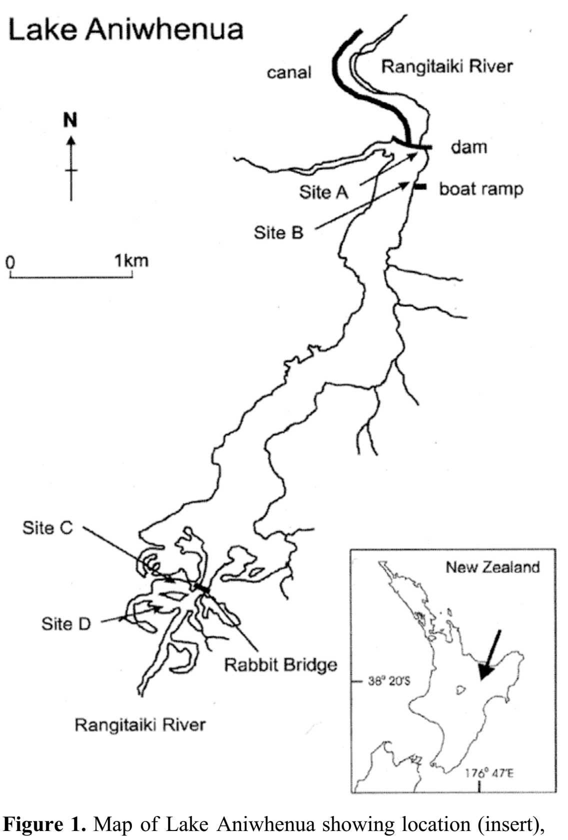

Figure 1. Map of Lake Aniwhenua showing location (insert), invertebrate sampling Sites A, B, C, and the macrophyte transect Site D.

water temperatures up to 34°C were recorded among floating *H. reticulatum* on hot summer days. Nutrient levels were low (measured 29 February 1996) in the in- flowing water of the Rangitaiki River below Rabbit Bridge (Fig. 1) with NO_3 and NH_4 below 1 $\mu g l^{-1}$ and PO_4 less than 3 $\mu g l^{-1.}$ However, they rose markedly in the lake and in backwaters such as that near Site C (Fig. 1), where mean monthly readings for 1996 (excluding months of June, July, August and November) were 152± SD 55$\mu g l^{-1}$ NO_3 and 14.6± SD 2.8 $\mu g l^{-1}$ PO_4 and were favourable for rapid growth of *H. reticulatum* (Hall and Cox,1995; Hall and Payne, 1997).

Methods

Plant measurements

Surface growths of *H. reticulatum* were sketch-mapped from a boat each year from 1990 to 1994, during late summer maxima. Standing crop was measured by determining the dry weight (80°C for 48 h) of *H. reticulatum* present in vertical cores used for invertebrate sampling (see below).

A 20-m long transect in the headwaters of Lake Aniwhenua (Site D, Fig. 1) was established in an area with dense *H. reticulatum* growing on macrophytes. The transect was monitored in January, February, March and July 1994, using SCUBA. Macrophytes (including *H. reticulatum)* were identified and each species' height and % substrate cover within a 0.1 m^2 quadrat, placed at 1 m intervals along the transect, were recorded. Full details of the method are described by Clayton (1983).

Invertebrates

Invertebrates were sampled in February/March, 1994 (during a *H. reticulatum* bloom) and March 1997 (without *H. reticulatum)* at three sites representing distinct *H. reticulatum* habitats (Fig. 1, Sites A – C.)

In 1994 Site A, which was 3 m deep, had a mobile surface-floating mat of *H. reticulatum* 0.4 m thick which moved around the lake depending on wind direction. In 1997 it was an open water site without *H. reticulatum* present.

Site B in 1994 had a shoreline accumulation of *H. reticulatum* and was sampled in 0.6 m depth of water where wave-compressed algal mats were present through the water column. In 1997 *H. reticulatilm* was not recordedat Site B, although *Elodea canadensis* was present with 30% cover.

Site C in 1994 was characterised by a benthic mat of *H. reticulatum,* 0.3 m thick, covering lake sediments in 1. 7 m depth of water. In 1997 there was 100% cover of macrophytes up to 0.4 m tall at Site C, with *E. Canadensis* > 90% substrate cover and *Potamogeton*

Six cores were collected from each site using 0.6 m lengths of 86 mm internal diameter PVC piping. Cores were inserted into the *H. reticulatum* (or other species present in 1997) and the biota were enclosed by inserting rubber stoppers into the top and bottom of the pipe. Benthic invertebrates were not sampled, but species on the sediment surface (such as gastropods) were included at Sites B and C. At Site A the top 0.6 m of the water column was sampled (as there was a surface mat of *H. reticulatum* there in 1994).

Samples were returned to the laboratory and emptied into sorting trays. Plant material was separated from the invertebrates and plant dry weight was determined (80°C for 48 h). Invertebrates were identified and counted under a binocular microscope (up to 40 times magnification). Species that usually live within lake sediments (such as oligochaetes) were not counted.

Gastropod consumption of *H. reticulatum*

Three species of gastropod, *Potamopyrgus antipodarum, Austropeplea tomentosa* and *Lymnaea stagnalis,* which were commonly observed on *H. reticulatum,* were collected and placed in tanks with *H. reticulatum.* Changes in *H. reticulatum* dry weight were measured in response to different levels of gastropod biomass. The rationale for these experiments was to determine the density of snails that would reduce *H. reticulatum* biomass, since they were considered a potential biocontrol agent.

The experiments were conducted using 18 (20 litre) plastic aquaria. To each tank was added 109 fresh weight of *H. reticulatum* (healthy green colonies with daughter nets present) and 15 litres of Hamilton tap water. Tap water was used as its dissolved inorganic nitrogen levels were too low to permit growth of *H. reticulatum* during the trials. Three replicates were established for each of five live weights of gastropods (5, 10, 15,20 and 25 g of live gastropods per tank). These biomasses corresponded to 2, 4, 6, 8 and 10 *L. stagnalis,* about nine times as many *A. tomentosa* and 100 times as many *P. antipodarum.* Three controls were established with no gastropods.

Tanks were maintained at 20°C with 24 h artificial illumination in a climate-controlled room. After 48 h, *H. reticulatum* from each tank was harvested, gastropods removed and *H. reticulatum* dried to constant dry weight at 80°C in a forced air drying oven for 48 h. Visual observations were made of the feeding behaviour and location of gastropods in the tanks during the experiments.

The average dry weight of *H. reticulatum* from the three control tanks at the end of the trial was 0.34 g ± SD 0.03 and this value was used as an estimate of *H. reticulatum* biomass available for gastropod grazing during each experiment.

Fish

Size and stomach content data were obtained for 13 large (525-710 mm) *O. mykiss* caught by anglers in Lake Aniwhenua between 12 November 1994 and 26 January 1996. Stomachs were assessed for fullness, and for the 11 fish with stomachs ≥40% full, the relative importance of different items was expressed as percentage volume of all stomach contents. The data available did not include fish caught during a *H. reticulatum* bloom in the lake but it was assumed that these fish (caught shortly after the bloom period) had spent much of their time in the lake during the period of the bloom.

Length and weight data were collected in the field, whereas age estimates for fish were made using otoliths. Whole otoliths were read using reflected light after being soaked in a 50% glycerol / 50% ethyl alcohol mixture for two weeks. Thin unburnt sections were also read (Graynoth, 1996). Fish were aged from 1 October (assumed birthday) and checked against estimates using otolith weight/age relationships derived from trout in Lake Tarawera and various other Rotorua and South Island lakes.

Results

***Hydrodictyon reticulatum* biomass and distribution**

Hydrodictyon reticulatum was seasonally abundant throughout the lake between November and June each year from 1990 to 1994, with low biomass in winter and early spring < 1 g dry weight m^{-2} from July to October). Peak abundance of *H. reticulatum* was noted during late summer and autumn. Prolific growths formed extensive surface-floating mats, submerged benthic mats on sediments and, commonly, mats that covered beds of macrophytes. In the shallows, drifting *H. reticulatum* was common, with dense accumulations resulting from water flowing through the lake, and from wind effects. In most years during the study there was about 12 ha of mobile, surface-floating *H. reticulatum* with 100% cover, 180 ha of macrophytes with an average *H. reticulatum* cover of 40%, and 75 ha of deeper channels (without macrophytes) with < 5% cover of *H. reticulatum.* Overall, the average cover of *H. reticulatum* for the lake was estimated to be 25%.

Biomass of *H. reticulatum* varied considerably within the lake. In floating mats (Site A) the average (±SD) biomass of 6 cores was 35 + 14 g dry weight m^{-2}, against the shore (Site B) in 0.6 m depth of water it was 68 ± 55 g dry weight m^{-2}, whereas in the benthic mat (Site C) average biomass was 51 ± 14 g dry weight m^{-2}.

Macrophytes

In mid-January 1994 the transect at Site D (Fig. 1) had a near surface-reaching macrophyte bed of *P. ochreatus* (average substrate cover 65%) and *E. canadensis* (average cover 21 %) with 72% average cover of *H. reticulatum* (Fig. 2). By early February the macrophytes were prostrate and only half the height recorded in January but still heavily covered with *H. reticulatum.* By mid-

March there were no macrophytes present on the transect, but a 0.22 m thick benthic mat of *H. reticulatum* remained covering the otherwise bare sediment (Fig. 2). By early July, the *H. reticulatum* mat was only 1 mm thick and substrate cover was reduced to an average of 48% on the transect. At that time, macrophytes such as *E. canadensis* were starting to re-establish and formed a low cover of < 5%.

Invertebrates

Site A

In surface-floating *H. reticulatum* (March 1994) the dominant macro-invertebrates were gastropods, with *P. antipodarum* (3.9 x 10^3 m^{-2}) having by far the highest biomass although *Ceriodaphnia* sp. was more numerous (5.5 x 10^4 m^{-2}, Table 1). *Sigara* sp., although not caught by the sampling method, was observed in large numbers amongst *H. reticulatum,* as were *Anisops assimilis.* In March 1997, when *H. reticulatum* was absent, no macro-invertebrates were present in the surface 0.6 m of water.

Site B

In the compacted shoreline accumulations of *H. reticulatum* sampled at Site B in 1994, *Potamopyrgus antipodarum* was much less common (733m^{-2}) than at Site A (3.9 x 10^3 m^{-2}). *Ceriodaphnia* sp. was abundant (2x 10^3 m^{-2}). Mosquito larvae, caddis flies, and the aquatic moth *Hygraula nitens* were also recorded. In 1997, when a 30% *E. canadensis* cover was present without *H. reticulatum, P. antipodarum* was the dominant species (6.5 x 10^3 m^{-2}) and *Ceriodaphnia* sp. numbers had decreased markedly to 67 m^{-2}

Site C

Potamopyrgus antipodarum was exceptionally abundant (1.8 x 10^5 m'2) amongst benthic *H. reticulatum* in 1994, dominating all other species (Table 1). The abundance of *Ceriodaphnia* (5.3 x 10^4 m^{-2}) was similar to that found at Site A and high densities of daphniids were concentrated in the upper layer of benthic *H. reticulatum* mats giving them a marked white appearance.

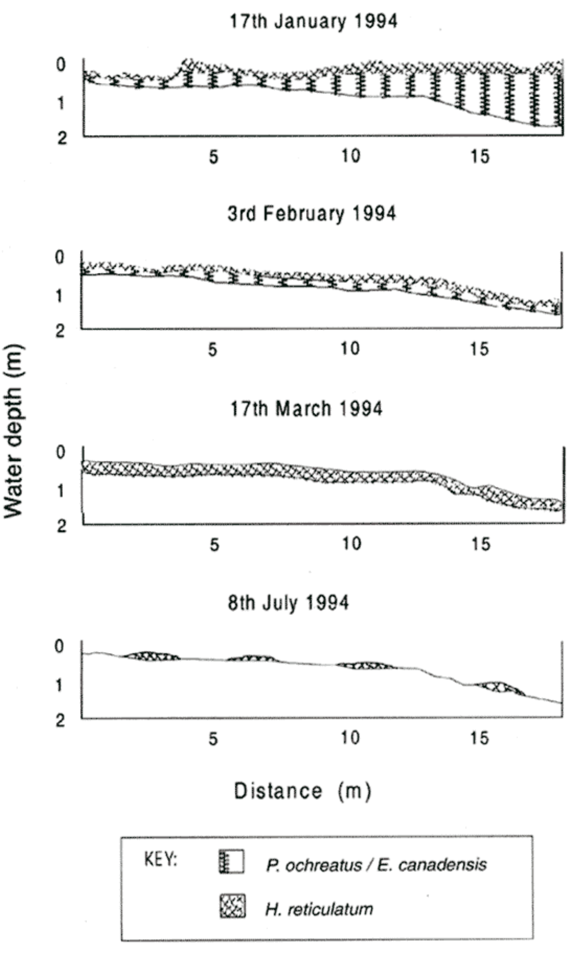

Figure 2. The macrophyte transect, Site D (located as shown in Fig. 1), showing the disappearance of *P. ochreatus* and *E. canadensis* under dense *H. reticulatum* during 1994. The *H. reticulatum* persisted as a benthic mat until winter 1994 then all but disappeared from the lake.

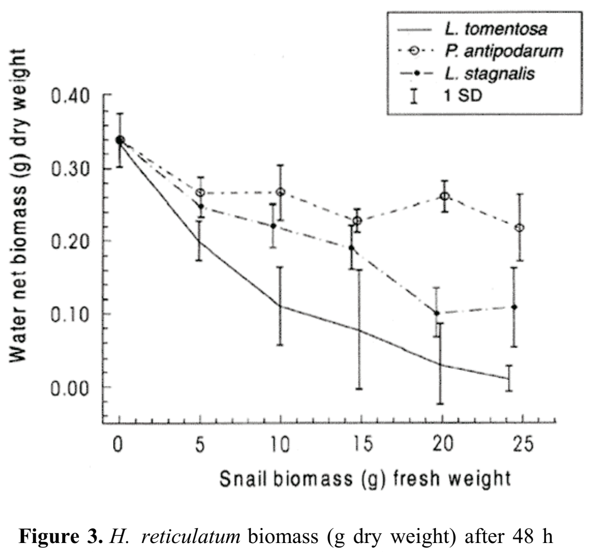

Figure 3. *H. reticulatum* biomass (g dry weight) after 48 h grazing by 3 species of aquatic gastropod *(P. antipodarum* = circles; *A. tomentosa* = triangles; *L stagnalis* = squares) at different densities (g fresh weight). Initial biomass of water net = 10g. The graph has been drawn using Flexi 2.2 and a Bayesian smoother {Wheeler and Upsdell, 1994), 85% confidence intervals are shown.

Table 1. Invertebrates in core samples at Sites A, B and C during and after the *H. reticulatum* bloom in Lake Aniwhenua (March 1994 and 1997 respectively). Biomass of water net at each site in 1994 is given in the text. In 1997 no water net was present but macrophytes occurred at Sites B and C.

SITE	Invertebrates	March 1994 No.m^2	SD	March 1997 No.m^2	SD
SITE A	Gastropoda:				
	Potamopoyrgus antipodarum	3967	8448	0	
	Physa acuta	267	242	0	
	Gyraulus corinna	100	109	0	
	Austropeplea tomentosa	67	163	0	
	Crustacea:				
	Ceriodaphnia sp.	54767	6009	0	
	Copepoda	7433	7539	0	
SITE B	Gastropoda:				
	Potamopoyrgus antipodarum	733	702	6500	6208
	Physa acuta			133	221
	Crustacea:				
	Ceriodaphnia sp.	c. 2000	n.a.	67	103
	Odonata:				
	Zygoptera	67	1I5	33	75
	Diptera:				
	Culicidae	333	577		
	Trichoptera:	67	115		
	Olinga feredaya	67	115	200	219
	Hydropsychidae	33	75		
	Lepidoptera:				
	Hygraula nitens	33	75		
SITE C	Gastropoda:				
	Potamopoyrgus antipodarum	183167	86219	27133	13389
	Physa acuta	1200	1152	100	244
	Planorbis sp.	1200	789		
	Gyraulus corinna			3600	4265
	Crustacea:				
	Ceriodaphnia sp.	53000	20548	1167	907
	Odonata:				
	Procordulia grayi			133	326
	Trichoptera:				
	Triplectides sp.			33	81
	Hydrophychidae			333	301
	Ephemeroptera:			233	320

In 1997, although the macrophytes *P. ochreatus* and *E. canadensis* had replaced *H. reticulatum, P, antipodarum* remained the dominant invertebrate, although it was less numerous (2.7 x 10^4 m^{-2}). Similarly, there were fewer *Ceriodaphnia* (1.2 x 10^3 m^{-2}). Trichoptera and Ephemeroptera larvae, and nymphs of the dragonfly *Procordulia grayi* were recorded (Table 1).

Gastropod consumption of *H. reticulatum*

The tank containing *P. antipodarum* had 25% less *H. reticulatum* than the control after 48 h and there was no further reduction in *H. reticulatum* biomass with increasing biomass of *P. antipodarum* (Fig. 3). This appeared to be due to *P. antipodarum* consuming all the small cells of *H. reticulatum,* since only large cells of mature colonies remained.

Austropeplea tomentosa had the highest feeding rate of all three species tested, with 1.29 g dry weight of *H. reticulatum* consumed per 100 g live gastropod day^{-1}. and plentiful food available at the lowest stocking rate. *Austropeplea tomentosa* grazed all of the *H. reticulatum* in the 20 and 25 g gastropod treatments (Table 2). A reduction in consumption rate was noted as increasing biomass of gastropods increased competition for food (Table 2). Increased gastropod biomass markedly reduced *H. reticulatum* biomass remaining after 48 hours (Fig. 3).

Lymnaea stagnalis markedly reduced *H. reticulatum* biomass within 48 h in the 20 and 25 g gastropod treatments (Fig. 3). Snails were usually found clustered on the remaining *H. reticulatum* and were large enough to be observed consuming it. *Lymnaea stagnalis* consumed up to 0.93 g dry weight of *H. reticulatum* per 100 g live weight gastropod day^{-1}.

Table 2. Mean *H. reticulatum* consumption rates by *P. antipodarum, A. tomentosa* and *L stagnalis* at five densities. Rates are expressed as *H. reticulatum* consumed (g dry weight) per 100 g fresh weight of gastropod day^{-1}. SD are shown in parentheses and * = all *H. reticulatum* was consumed within 48 h.

	Gastropod biomass (g fresh weight tank^{-1})				
	5	10	15	20	25
P. antipodarum	0.74 (0.1)	0.37 (0.08)	0.38 (0.08)	0.21 (0.04)	0.25 (0.03)
A. tomentosa	1.29 (0.18)	1.09 (0.23)	0.85 (0.23)	*	*
L stagnalis	0.93 (0.34)	0.64 (0.16)	0.52 (0.18)	0.62 (0.14)	0.48 (0.16)

Fish

The average estimated age of the 13 trout sampled (Table 3) was 2.8 y, their mean length was 642 mm, and mean weight 3 kg. The main prey species found in stomachs was *P. antipodarum* (65% by volume), with most fish feeding exclusively on small gastropods. No *L stagnalis* were found in *O. mykiss* stomachs. Algae and occasional fragments of macrophytes, pumice and terrestrial plant material were also found in the stomachs and two fish had been feeding mainly or wholly on dragonfly larvae and chironomid larvae, respectively (Table 3).

Discussion

Hydrodictyon reticulatum was seasonally abundant throughout Lake Aniwhenua, peaking in late summer. Maximum standing crop was estimated to be 18 tonnes dry weight, calculated from the average cover of 25% (over the 255 ha lake) with an average dry weight of 28 g m^{-2}, giving it an estimated free drained wet weight of > 540 tonnes (4% dry weight). The large biomass of *H. reticulatum* had considerable nuisance potential with growth rates of 30% day^{-1}) recorded in the lake (Wells *et al.,* 1994). The large turnover of algal biomass, as evidenced by the high standing crop and fast growth rate, also affected management operations at the Lake Aniwhenua hydro-electric power station. The large amounts of *H. reticulatum* present did not cause any obvious signs of oxygen stress for biota (as indicated by the large numbers of fish and invertebrates present amongst it), except where it was packed against the shore and decaying. In Lake Rotorua, diel oxygen concentrations monitored in a dense lake edge accumulation of *H. reticulatum* (March 1992) showed water was super-saturated by day and had > 60% saturation at night. Anoxic conditions were recorded only where *H. reticulatum* was compacted and decaying, a condition that was most pronounced in water less than 0.3 m deep (R. Wells and J. Clayton, *unpubl.).*

Hydrodictyon reticulatum was considered to have the potential to displace macrophytes through shading and smothering (Hawes *et. al.,* 1991; Coffey, 1991). This was confirmed in the present study. Macrophytes on the monitored transect were smothered and replaced by a dense 0.22 m thick mat of *H. reticulatum,* which persisted as a benthic algal mat until mid-winter. However, macrophytes persisted at adjacent sites where there was less *H. reticulatum.* Macrophyte collapse from *H. reticulatum* was not a common outcome within the lake, since *H. reticulatum* usually co-existed with macrophytes. In the latter case, macrophyte production was likely to have been reduced by *H. reticulatum* shading.

Concerns over the potential for widespread undesirable biotic impacts from dense growths of *H. reticulatum* were not supported by the results of this study. Negative impacts recorded where *H. reticulatum* was compacted and decaying accounted for less than 1 ha of the lake compared with 12 ha of surface-floating mats and 180 ha of *H. reticulatum* covering macrophytes (average 40% cover). In fact, many macro-invertebrates were exceptionally abundant in the extensive *H. reticulatum* habitats in comparison with other lakes without *H. reticulatum.* For example, *P. antipodarum,* the dominant gastropod in Lake Aniwhenua was recorded at densities up to 1.8 X 10^{5} m^{-2} amongst *H. reticulatum.* In Lake Alexandrina, South Island, Talbot and Ward (1987) reported *P. antipodarum* to be the dominant macro-invertebrate within six macrophyte communities, and found that it contributed between 66 and 90% of total invertebrate abundance. Maximum numbers of *P. antipodarum* in Lake Alexandrina (5 x 10^{3}m^{-2}) were associated with macrophyte detritus in late summer. In lakes of the upper Clutha Valley, South Island, Biggs and Malthus (1982) also reported *P. antipodarum* to be the dominant invertebrate. There, characeae supported the highest numbers, with 4.9 x 10^{3} m^{-2} compared with 1.3 x 10 m^{-2} for *E. canadensis.* A similar pattern was reported in Lake Waikaremoana, North Island (Mylechreest,1978). In Lake Aniwhenua the large gastropod *L. stagnalis* could also be very abundant on *H. reticulatum* with up to 200 m^{-2} (R. Wells and J. Clayton *unpubl.),* but this species had a clumped distribution and did not feature in the samples collected during this study.

The presence of extremely large populations of gastropods in Lake Aniwhenua was thought to be primarily due to *H. reticulatum* serving two purposes. Not only did it provide an extensive habitat, it also contributed by being a direct food source. The results of the laboratory studies suggested a direct trophic relationship, with all three gastropods tested grazing

Table 3. Age, length, weight, stomach fullness (% full) and stomach contents (% composition of algal and animal food by volume) of 13 *O. mykiss* caught in Lake Aniwhenua following the *H. reticulatum* blooms. Algae, water plants, pumice and terrestrial plants were not considered to be food items.

Date	Sex	Age (yrs)	Length (mm)	Weight (kg)	Stomach fullness	snails	*Sphaerium*	Chironomidae	Odonata	Terrestrial invenebrates	Algae	Water plant	Pumice	Terrestrial plant
12.11.94	m	3.1	700	4.1	50	35	0	0	0	0	55	5	5	0
12.11.94	f	2.1	645	3.2	10	50	0	0	0	0	50	0	0	0
12.11.94	f	2.1	695	3.8	40	25	I	0	0	0	60	10	0	4
12.11.94	f	2.1	575	2.3	50	0	0	0	50	5	30	10	0	5
12.11.94	f	4.1	710	4.6	75	38	4	0	0	0	55	I	2	0
12.11.95	f	2.1	660	4.1	60	30	2	0	0	0	60	5	3	0
09.01.96	m	2.3	565	2.0	50	34	0	0	0	0	60	5	1	0
10.01.96	f	4.3	620	2.5	60	35	5	0	0	0	60	0	0	0
20.03.96	f	2.4	525	2.0	60	30	15	0	0	0	50	0	0	5
20.03.96	m	2.4	535	2.3	40	35	10	0	0	0	40	5	10	0
20.03.96	m	2.4	575	3.0	50	35	30	0	0	0	35	0	0	0
26.01.96	f	4.3	660	2.8	10	80	0	0	0	0	20	0	0	0
26.01.96	m	2.3	595	1.7	60	0	0	95	0	5	0	0	0	0
Mean		2.8	643	3.0	47	33	1	10	5	I	45	3	I	I
Mean % volume food items						66	2	20	10	2				

heavily on *H. reticulatum.* Even the smallest gastropod tested, *P. antipodarum,* fed on significant quantities of *H. reticulatum.*

High numbers of *Ceriodaphnia* sp: were also associated with *H. reticulatum* which provided extensive spatial refugia from predation. *Ceriodaphnia* is small enough to swim through the mesh of most *H. reticulatum* nets (colonies) and was observed in high densities out of reach of abundant predatory ,juvenile goldfish *(Carassius auratus)* and *Anisops assimilis.* These findings are consistent with those of Stansfield *et al.* (1997) who reported that *Ceriodaphnia* abundance was positively associated with refugia provided by macrophytes, except that in our case available habitat was extended by the presence of *H. reticulatum.*

Hydrodictyon reticulatum blooms may have had undesirable effects on the benthic invertebrates in Lake Aniwhenua but no data are available to test this. However, in Lake Rotorua, the mussel *Hyridella menziesi* was present under benthic *H. reticulatum* except where it was compacted and decomposing (R. Wells and J. Clayton *unpubl.).*

During the *H. reticulatum* blooms, small gastropods were the major prey species recorded in rainbow trout stomachs (Mr G. Ryder, trout fishing guide, Rotorua, N .Z., *pers. comm.).* Although rainbow trout data presented in this study were collected shortly after *H. reticulatum* had disappeared from the lake, captured trout were likely to have spent much of their time in the lake during the *H. reticulatum* blooms (1989-94) so their large sizes and rapid growth were assumed to have been influenced by its presence.

Relatively fast growth rates of *O. mykiss* have been reported by Rowe (1984) in the nearby Rotorua Lakes where forage fish were their main food. The fastest growth rates from the Rotorua Lakes were reported from Lakes Okataina and Rotoehu where smelt *(Retropinna retropinna)* was the main food (Smith, 1959). In Lake Aniwhenua, our limited trout data indicate that the mean growth rate of *O. mykiss* exceeded that reported for Lake Rotoehu and Lake Okataina (Fish, 1968; Hayes, in McCarter, 1986) with fish 2+ years of age being on average 80 mm longer and > 1.2 kg heavier. This suggests that all growth factors for trout in Lake Aniwhenua were particularly favourable. However, it is interesting to note that the value of *P. antipodarum* in particular as a food for trout has been questioned because the snails are small, have a thick shell, an operculum, and a low energy content of only 30-40 J per individual (McCarter, 1986). By comparison, many arthropods and most vertebrates are of higher calorific value, with 14500-24000 J g^{-1} dry weight for arthropods and invertebrates versus 5-6 000 J g^{-1} dry weight for *P. antipodarum* (McCarter, 1986). The abundance of *P. antipodarum* on *H. reticulatum* mats, its predominance in the diet of *O. mykiss,* and fast trout growth rates, suggest that fish compensate for the low energy content of individual snails by eating them in large numbers.

No data were available on the diet of juvenile trout, but the abundance of a wide range of invertebrates and refugia associated with *H. reticulatum* suggests that juvenile trout (observed in large numbers) would also have benefited from the *H. reticulatum* blooms.

A significant brown trout *(Salmo trutta)* fishery also existed in the lake during the period of *H. reticulatum* abundance and S. *trutta* attained sizes of up to 8.4 kg (Thomas, 1996). Goldfish and gastropods were found in the stomachs of many large S. *trutta.* In contrast with our findings for *O. mykiss,* the gastropods eaten by *S. trulla* were mostly the larger *L. stagnalis* rather than *P. antipodarum* (Thomas, 1996).

Hydrodictyon reticulatum was not the 'ecological disaster' in Lake Aniwhenua that was feared. On the contrary, it enhanced the habitat for trout in Lake Aniwhl;nua by providing refugia and a food source for the lake's invertebrate fauna, which in turn supported fast trout growth rates. However, caution is needed in extrapolating our findings to other water bodies. Lake Aniwhenua is a recently formed, artifically-dammed lake and it lacks the food web complexity found in many natural lakes.

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