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Distribution, biomass and production of the freshwater mussel, *Hyridella menziesi* (Gray), in Lake Taupo, New Zealand

M. R. JAMES Taupo Research Laboratory, Division of Marine and Freshwater Science, DSIR, Taupo, New Zealand

SUMMARY. 1. A study of the distribution, biomass and production of the freshwater mussel *Hyridella menziesi* (Gray) was carried out at six sites in Tapuaeharuru Bay, Lake Taupo, New Zealand.

2. *H. menziesi* is common in the littoral zone, with clean sand and angle of slope being the most important environmental variables measured which are positively associated with mussel density. These variables are related to the accumulation of fine material which can clog the filtering mechanism of mussels. The angle of slope may also influence the movement and supply of food.

3. Density (5.6 m^{-2}), biomass (2.8 g dry weight shell free tissue m^{-2}) and potential production (0.50 g dry weight shell free tissue m^{-2} yr^{-1}) are high compared to values found for mussels from other oligotrophic lakes.

4. The age structure of *Hyridella* suggests recruitment has declined in recent years. A periodicity in generations is proposed.

Introduction

A number of environmental factors can influence the density of freshwater mussels. Sediment type has been suggested as a dominant factor in studies by Harman (1972), Stone *et al.* (1982) and Salmon & Green (1983). Other important environmental variables suggested are adequate food supply (Pequegnot, 1961; Nobes, 1980), water velocity (Walne, 1972), bed slope (Green, 1980), presence of fish hosts for the parasitic stage (Strayer *et al.*, 1981), presence or absence of a wave ripple zone (Cvancara, 1970) and degree of sedimentation (Coon, Eckblad & Trygstad, 1977). In most studies it has been concluded that the slower growth and lower densities which occur with increased depth are a consequence of lower temperatures.

The freshwater mussel *Hyridella menziesi* (Gray) can dominate the macroinvertebrate biomass in New Zealand lakes yet there have been no truly quantitative studies made of its distribution and abundance. There was the work on its life history by Percival (1931), observations on growth by Grimmond (1968) and a study of its energetics by Nobes (1980). Macroinvertebrates of New Zealand lakes (Armstrong, 1935; Fish, 1978; Forsyth, 1978; Forsyth & McCallum, 1981; Timms, 1980, 1982, 1983) were not appropriately sampled for large invertebrates with patchy distributions like *Hyridella* and in some studies their biomass was ignored (Timms, 1982).

Lake Taupo is a large, oligotrophic lake on the central volcanic plateau of the North

Correspondence: Mr M. R. James, Taupo Research Laboratory, Division of Marine and Freshwater Science, DSIR, P.O. Box 415, Taupo, New Zealand.

TABLE 1 Physical and biological characteristics of sites sampled in Tapuaeharuru Bay, Lake Taupo. Mussel biomass and production are expressed as shell free tissue dry weight, vegetation as percentage cover; chlorophyll *a* is of the water above the mussel bed; and sediment composition is for the top 3 cm of lake bed. Production estimates are for depths of 2, 5 and 10 m. Data are mean and, in parentheses, range.

Site	Depth range (m)	Mussel Density (nos. m^{-2})	Biomass (g DW m^{-2})	Production (g DW m^{-2} yr^{-1})	P/B	Vegetation (%)	Slope (m/100 m)	Water Chl. *a* (μg l^{-1})
1	1–20	12.0 (0.1–60.8)	6.82 (0.04–34.90)	2.79 (0.32–7.07)	.4	0	9.1 (0.3–25.6)	0.70 (0.60–0.86)
2	.1–30	3.6 (0–20.0)	1.56 (0–8.49)	0.63 (0.12–1.61)	.4	2.5 (0–10)	7.2 (0–11.1)	0.63 (0.54–0.69)
3	1–30	7.3 (0–47.2)	3.22 (0–20.81)	1.72 (0.04–5.04)	.5	0	8.1 (0–25.0)	0.99 (0.52–2.51)
4	1–30	1.1 (0.1–3.0)	0.44 (0.05–1.22)	0.14 (0.05–0.25)	.3	21.4 (0–90)	3.8 (0–5.0)	0.79 (0.62–1.00)
5	1–30	0.7 (0–4.9)	0.43 (0–2.94)	0.32*		0	4.2 (0–16.7)	1.22 (0.52–1.83)
6	10–20	0.4 (0–1.8)	0.17 (0–0.88)	—		0	4.5 (0–3.6)	0.84 (0.78–0.90)

Site	Depth range (m)	Sediment composition Organics (%)	Mud (%)	Fine sand (%)	Coarse sand (%)	Gravel (%)	Pebbles (%)
1	1–20	3.2 (1.7–4.7)	10.7 (1.8–31.2)	18.5 (0.7–43.8)	40.8 (0.3–79.7)	26.6 (1.5–84.7)	4.2 (0–13.9)
2	1–30	2.9 (0.8–4.0)	13.0 (6.3–22.3)	53.8 (30.4–66.8)	17.9 (5.5–25.7)	11.6 (4.8–25.4)	4.2 (0–12.2)
3	1–30	3.5 (1.4–6.6)	43.3 (3.8–89.9)	12.2 (9.7–18.6)	24.7 (0.1–54.7)	15.0 (0–33.1)	5.4 (0–17.3)
4	1–30	8.6 (7.0–10.5)	79.2 (39.7–98.8)	12.5 (1.0–32.3)	3.6 (0.1–17.0)	0.9 (0–2.8)	0
5	1–30	4.3 (0.6–7.6)	29.5 (2.3–96.7)	16.5 (0.6–34.4)	32.5 (0–68.4)	21.8 (0–86.5)	1.8 (0–7.3)
6	10–20	9.2 (6.4–12.0)	91.2 (84.7–97.8)	8.5 (1.7–15.2)	0.1 (0.1–0.1)	0.2 (0–0.4)	0

—, not sampled. *, One value.

Island, New Zealand, with an area of 612 km^2 and average depth of 97 m. Its limnology is described by White *et al.* (1980) and Forsyth & Howard-Williams (1983). Benthic invertebrates were recorded from Lake Taupo by Armstrong (1935), and a quantitative study of the benthic fauna was made by Forsyth & McCallum (1981).

For logistic reasons the present study was limited to Tapuaeharuru Bay at the north-eastern end of Lake Taupo and its object was to estimate the population density, biomass and potential production of the *Hyridella* population and relate these to environmental variables.

Methods

Mussels were collected between February and May 1983 at six sites chosen to represent varied environmental features in Tapuaeharuru Bay (Fig. 1). These features included presence of an abrupt increase in slope at a depth of 2.5 m (dropoff), a gradual sloping shelf down to 10 m, presence of large macrophyte beds and exposure to the prevailing westerly winds. Duplicate belt transects 5–10 m long and 1 m wide were made along depth contours of 1, 2, 5, 10, 15 and 20 m by SCUBA. Mussels were located by hand sifting of the sediment and the long axis of each

Bay, Lake Taupo. Mussel
on as percentage cover;
the top 3 cm of lake bed.
es, range.

ope m 100 m)	Water Chl. *a* ($\mu g\ l^{-1}$)
 .3–25.6)	0.70 (0.60–0.86)
 11.1)	0.63 (0.54–0.69)
 25.0)	0.99 (0.52–2.51)
8 5.0)	0.79 (0.62–1.00)
2 16.7)	1.22 (0.52–1.83)
5 3.6)	0.84 (0.78–0.90)

Gravel (%)	Pebbles (%)
26.6 1.5–84.7)	4.2 (0–13.9)
11.6 4.8–25.4)	4.2 (0–12.2)
5.0 (0–33.1)	5.4 (0–17.3)
0.9 (0–2.8)	0
1.8 (0–86.5)	1.8 (0–7.3)
0.2 0–0.4)	0

tween February and chosen to represent tures in Tapuaehar- e features included crease in slope at a , a gradual sloping ence of large macro- e to the prevailing belt transects 5–10 m made along depth , 15 and 20 m by ated by hand sifting long axis of each

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individual was measured. Mussels from 30 m were collected by dredging from a boat along a 20 m transect. Density was estimated by pooling all mussels collected along each belt transect. A representative number of animals (twenty) from each station were used for shell free tissue dry weight (DW) determination (oven dried at 70°C for 72 h). Power curves for length–dry weight relationship were calculated for each station. Total and average mussel biomass for the bay was estimated from area of depth intervals and station biomasses.

Grimmond (1968) and McCuaig & Green (1983) have shown the validity of using winter growth interruption lines in the periostracum and prismatic layer as indications of annual growth. Twenty specimens from 2, 5 and 10 m at each site were aged using this technique. Calculations of production follow Magnin & Stanczykowska (1971). Age–dry weight relationships established the rate of growth, which combined with density–age data, provided the potential gross annual production of the mussel population.

G

β

Sediment samples were taken at most stations with an Ekman grab 19×19 cm (0.036 m^2). Samples were dried, weighed and combusted at 500°C for percentage loss on ignition and sieved to obtain size fractions (mud <63 μm, fine sand 63–699 μm, coarse sand 699–2000 μm, gravel 2–12 mm, pebbles <12 mm). Abundance of vegetation was estimated as percentage cover, slope was calculated using a depth sounder and bathymetric charts, and chlorophyll *a* concentrations of water above the mussel bed were measured fluorometrically (Golterman, 1969). Site variables are given in Table 1.

Arc-sine transformations were performed on sediment type data and a log$_{10}$ transformation on depth data.

Pearson's product moment correlations were

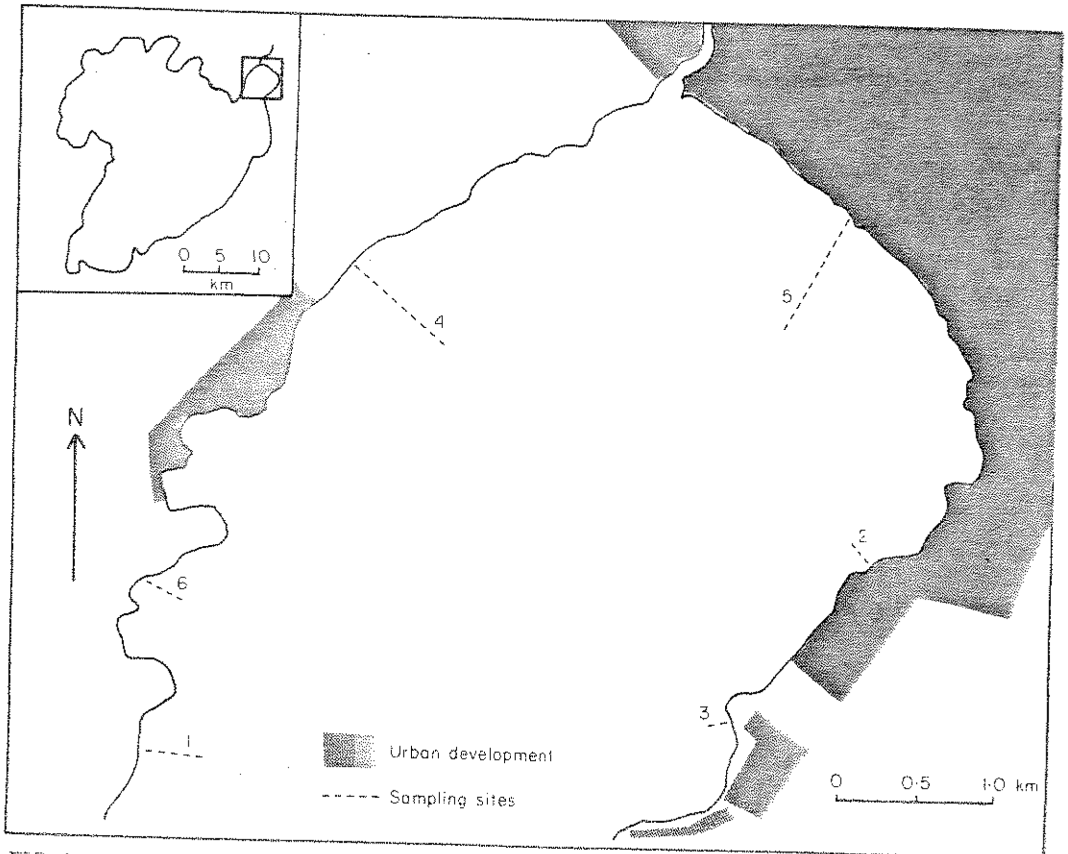

FIG. 1. Tapuaeharuru Bay, Lake Taupo, showing sampling sites. Inset shows position of Tapuaeharuru Bay in Lake Taupo.

TABLE 2. Distribution of mussels with depth expressed as the mean no. m^{-2} (range). Sites 1 and 3 have an abrupt increase in slope from 2.5 to below 5 m and no macrophytes; Sites 2 and 6 have a large macrophyte bed from 2 to 5 m and Sites 4 and 5 have a gradual slope down to 30 m.

Depth (m)	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
1	0.1 (0–0.2)	1.2 (1.1–1.35)	0	1.1 (0.8–1.3)	0	0
2.5	6.8 (6.5–7.1)	0	0.7 (0.6–0.7)	3.0 (2.6–3.4)	0.2 (0.1–0.2)	0
5	60.8 (54.2–67.4)	20 (18.9–21.1)	47.2 (43.3–51.1)	2.7 (2.5–2.9)	4.9 (4.8–5.0)	0
10	4.0 (3.7–4.4)	1.4 (1.3–1.5)	0.9 (0.7–1.0)	0.4 (0.2–0.6)	0	0.3 (0.2–0.3)
15	0.1 (0–0.2)	1.5 (1.2–1.8)	1.1 (1.0–1.2)	0.2 (0.2–0.2)	0	0.5 (0.5–0.5)
20	0.2 (0.2–0.2)	1.2 (1.2–1.2)	1.0 (0.8–1.2)	0.1 (0–0.2)	0	1.7 (1.1–2.2)
30	—	0	0	0.1 (0–0.1)	0.02 (0–0.04)	—

—, not sampled.

calculated for all combinations of measurements of standing crop, percentage loss on ignition of sediment, sediment type, chlorophyll *a* of water, slope and depth. A multiple regression of mussel density with environmental variables was also performed.

Results

H. menziesi is common in the littoral zone of Tapuaeharuru Bay and occurs to a depth of 30 m (Sites 4 and 5, Table 2). Except at Site 6, maximum density occurred at about 5 m and reached 67.4 m^{-2} at Site 1. Mussels were most common where there was an abrupt increase in slope from 2.5 to below 5 m (Sites 1 and 3) and were least common on gentle slopes (Sites 4 and 5). At Site 2 maximum density occurred at 6 m below a large *Lagarosiphon* bed. The 100% weed cover at 2–5 m at Site 6 (a sheltered bay) excluded mussels, but low densities occurred in flocculent mud at depths of 10, 15 and 20 m.

Correlation coefficients between environmental parameters measured are given in Table 3. As expected, high correlations ($P < 0.001$) were found between some sediment characteristics; for instance, mud and percentage loss on ignition ($r = +0.802$), coarse sand and percentage loss on ignition ($r = -0.761$), coarse sand and $\log_{10}$ depth ($r = -0.783$), mud and $\log_{10}$ depth ($r = +0.649$) and mud and coarse sand ($r = -0.769$). Significant correlations ($P < 0.05$) were found between density of mussels and coarse sand ($r = +0.514$) and between density and slope ($r = +0.481$). Although not significant at 95% C.L., density decreased

TABLE 3. Pearson's product moment correlations (r) between standing crop of mussels and environmental variables measured. $n = 24$. A $\log_{10}$ transformation was performed on depth and arc sine on the percentage composition of the sediment.

	Standing crop nos.	Depth	% Loss on ignition	Mud	Fine sand	Coarse sand	Gravel	Pebbles	Slope
Depth	−0.253								
% Loss	−0.365	0.431*							
Mud	−0.370	0.649***	0.802***						
Fine sand	0.097	−0.143	−0.441*	−0.412					
Coarse sand	0.514*	−0.783***	−0.761***	−0.769***	0.282				
Gravel	−0.061	−0.158	−0.241	−0.517	−0.254	0.042			
Pebbles	0.166	−0.164	−0.314	−0.396	0.115	0.075	0.425*		
Slope	0.481*	−0.239	−0.063	0.030	−0.084	0.010	0.082	−0.275	
Chl. *a*	−0.283	0.500*	0.288	0.359	−0.378	−0.484	0.105	−0.072	−0.007

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

with increase in mud content and percentage loss on ignition.

A multiple regression equation of mussel density with the two most important predictor variables coarse sand and slope was

$$y = -8.86 + 0.358X_1 + 1.04X_2$$

where y is mussel density, X_1 is the arc sine of the percentage of coarse sand and X_2 is slope (coefficient of determination, $R^2=0.49$). A stepwise multiple regression analysis showed that all parameters measured accounted for 74% of the variation in mussel density with coarse sand contributing 26.4% and slope 22.7%.

The shell length/tissue dry weight relationship for all stations was best described by the power curve $DW=1.13\ L^{2.73}\times10^{-5}$, $r=0.73$, $n=360$. The power curves used in biomass estimates for each station were all significant at 95% C.L. Biomass showed a similar trend to density with maximum biomass of 34.9 g DW m^{-2} (Site 1, 5 m) and an average of 2.8 g DW m^{-2} for the bay (0–20 m). Changes in shell length with age (annulus number) are shown in Fig. 2. Rapid shell growth occurred in the first few years and then gradually declined. The ages of mussels ranged from 1 to 13 years (Fig. 3) with 7-year-olds forming the major year class. Few juveniles (less than 5 years) were collected. Age structure did not differ significantly between stations but juveniles were restricted to areas of clean sand. There was a trend towards decreasing shell length with increasing depth ($r=0.99$, $P<0.001$).

Production and P/B ratio for stations where age was measured averaged 0.50 g DW $m^{-2} yr^{-1}$ and 0.18 respectively. Estimates of total biomass and production for Tapuaeharuru Bay are 14,000 kg DW and 3000 kg DW yr^{-1} respectively.

Discussion

The density of mussels in Tapuaeharuru Bay appears to be influenced by a number of physical and biological factors, with coarse sand and slope being the most important. Although steep slopes are inhabited by few mussels, results of this study suggest that slopes in the range measured may allow a continuous movement of food from shallower depth while remaining free of fine sediment and accumulation of organic matter. Other studies have found positive correlations of mussel density with coarse sand content (Sal-

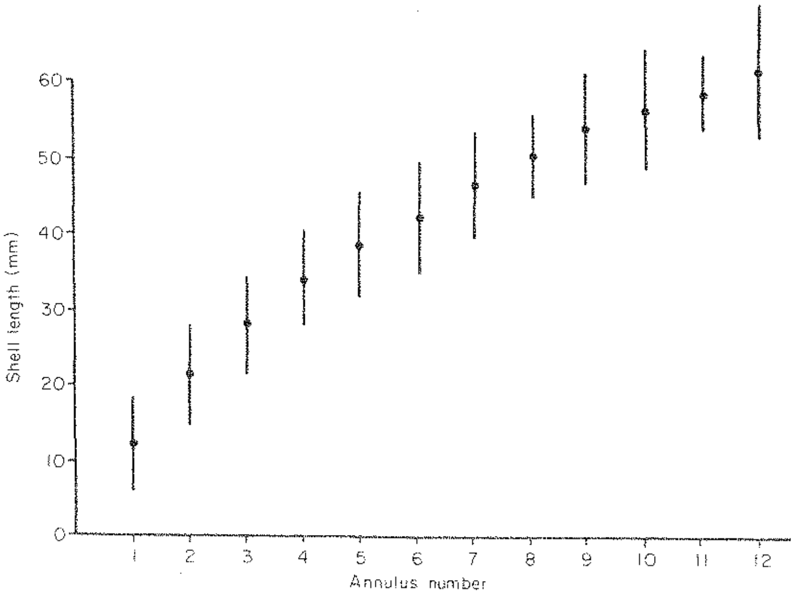

FIG. 2. Increase of shell length versus annulus number for mussels from all sites sampled in Tapuaeharuru Bay, Lake Taupo. Vertical lines are 95% confidence intervals.

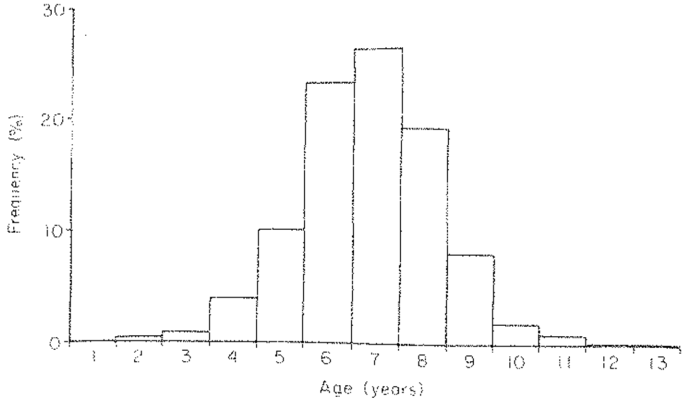

FIG. 3. Age structure for the mussel population from all sites sampled in Tapuaeharuru Bay, Lake Taupo.

mon & Green, 1983; Stone *et al.*, 1982) but negative correlations with increased slope (Green, 1980). In shallow regions of the bay wave action, as indicated by sand ripples on the bottom, inhibits settlement by young mussels. The wave affected region extends down to a greater depth in Lake Taupo (2 m) than in most lakes because some areas have a wind fetch greater than 10 km (Howard-Williams & Vincent, 1983). Such conditions were claimed to be unsuitable for mussels by Cvancara (1970), and Forsyth & McCallum (1978) commented on the lack of mussels in this zone. In Lake Taupo this region also tends to have larger, more robust individuals. This wave ripple zone forms the upper depth limit for high mussel density with the lower depth limit being influenced by an increase in flocculent mud and accumulation of organic material. No mussels were found below 30 m where flocculent mud up to 30 cm deep may clog their filtering mechanisms (Johnson, 1971; Walne, 1972). The top of the metalimnion in Lake Taupo is at 30 m and below this the temperature does not exceed 12.5°C until March (unpublished data), when the parasitic larval stage has probably left the host fish and is most vulnerable to low temperatures. The decrease in shell length with increased depth may be the result of flocculent mud and lower temperatures slowing metabolic rates. The influence of wave action and survival of the larval stage in relation to temperature may account for some of the variation in mussel density not explained by the parameters quantified and used in the multiple regression.

Nobes (1980) found highest densities of *H. menziesi* in areas of *Elodea canadensis* Michx. at a depth of 2 m in the Waikato River, New Zealand. This is probably the most stable region in rivers, but in lakes the accumulation of silt and organic matter in macrophyte beds causes substrate conditions to occur there similar to those at depths greater than 30 m.

The density, biomass and production of *Hyridella* in Lake Taupo are compared with mussels in other freshwaters in Table 4. The values in this study are high compared to other oligotrophic systems in the northern hemisphere such as Mirror Lake, but low compared to more productive lakes in New Zealand such as Lake Rotorua. Comparisons with other New Zealand lakes (Forsyth, 1978; Timms, 1980, 1982, 1983) cannot be made because so few mussels were collected where Ekman grabs were used. Invertebrates with patchy distribution like *H. menziesi* require more intensive sampling methods. The high population density in eutrophic Lake Rotorua (Fish, 1978) compared with Lake Taupo is consistent with the idea that there is an increase in filter feeders as lakes become increasingly eutrophic (Forsyth, 1978; Strayer *et al.*, 1981). Highly eutrophic small lakes, however, tend to have no mussels due to microstratification of oxygen at the bottom (Forsyth, 1978). This study highlights the importance of physical and biological interactions in determining mussel density. Although oligotrophic lakes may be unproductive in terms of phytoplankton, presence of macrophyte beds and abrupt changes in slope may enhance the supply of food to mussel populations.

Mean standing crop of mussels in the 0–20 m

TABLE 4. Density, biomass and production of freshwater mussels in a variety of aquatic habitats

Habitat	Density (nos. m^{-2}) Max.	Density (nos. m^{-2}) Av.	Biomass (g DW m^{-2})	Production (g DW m^{-2} yr^{-1})	P/B	Source
River Thames	—	—	12.1	2.1	0.17	Negus, 1966
Budworth Mere	89	—	—	—	—	Stone *et al.*, 1982
Mirror Lake	0.17	0.032	0.05	0.006	0.12	Strayer *et al.*, 1981
Lac St Louis	—	—	0.7*	0.07*	0.09	Magnin & Stanczykowska, 1971
Lac des Deux Montagnes	—	12.8	8.6*	1.7*	0.19	Magnin & Stanczykowska, 1971
Long Lake	54	—	—	—	—	Cvancara, 1972
Waikato River	9	4.5	—	—	12.0	Nobes, 1980
Lake Rotorua	—	—	27	—	—	Fish, 1978
Shell Lake	35	10.5	—	—	—	Green, 1980
Lake Taupo	60.8	5.6	2.8	0.50	0.18	This study

* Wet weight converted to dry weight using factor of 0.1.

zone (2.8 g DW m^{-2}) was high compared to that of other macroinvertebrates in Tapuaeharuru Bay (0.35 g DW m^{-2}; Forsyth & McCallum, 1981). The P/B ratio is comparable to that found in other studies (Table 4) but much lower than that estimated for *H. menziesi* by Nobes (1980). He used laboratory net assimilation rates as an indication of possible production but these rates may have overestimated production due to assumptions made when applied to natural conditions.

The age structure is also comparable to that reported for other mussel species (Negus, 1966; Strayer *et al.*, 1981; Bauer *et al.*, 1980). The population of *H. menziesi* in Lake Taupo is shorter lived than in Lake Waipori, where Grimmond (1968) recorded ages of up to 54 years. Lake Taupo specimens are less heavily calcified than those from Lake Waipori (N. Grimmond, pers. comm.) perhaps due to continuous movement through coarse sand so that shell erosion may cause earlier mortality and possible predation by the freshwater crayfish *Paranephrops planifrons* White.

A lack of juveniles is a feature reported in nearly all mussel population studies. Although juveniles are often under-represented due to sampling inadequacies, the lack of recruitment has been attributed in most cases to increased sedimentation (Coon *et al.*, 1977), pollution (Green, 1980) or eutrophication (Bauer *et al.*, 1980). These conclusions have been arrived at by comparison of population densities with those obtained in earlier studies at the same localities. There has been an increase in urban development near Sites 2 and 3 in Lake Taupo, but Site 1 is far removed from human settlement (Fig. 1). Nevertheless the mussel population has a similar age structure to that at the other sites. It is unlikely that increased sedimentation, pollution or eutrophication will have caused the decline in recruitment of the mussel population of Tapuaeharuru Bay over the last 8 years.

Grimmond (1968) found juveniles of *H. menziesi* near the mouths of inflowing rivers but no such areas exist for recruitment in Tapuaeharuru Bay. Although juveniles are difficult to locate, I believe those more than 2 years old (>2 cm) were recovered. It would appear that the population is not maintaining itself and may decline, as have some mussel populations in the northern hemisphere (Bauer *et al.*, 1980). As this cannot be attributed to deteriorating water quality in Lake Taupo, it is possible there is some periodicity in age structure as a result of breeding characteristics or climatic conditions. Consequently, a population will decline until conditions for recruitment improve. Unfortunately, there are no long-term records for the age structure of mussel populations. The reason for lack of juvenile freshwater mussels, in Lake Taupo and elsewhere, requires further investigation, particularly in unmodified habitats, using sampling methods suitable for smaller individuals.

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