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The Structure of the Littoral Invertebrate Communities of the Kosciuszko Region Lakes

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The littoral macroinvertebrate assemblages of Lakes Albina, Blue, Club and Cootapatamba in the Mt. Kosciuszko region were sampled by two methods: sweeps and cobble picks. Thirty-six species were collected with total abundance and species richness greatest in Lake Albina. Common species included the molluscs *Pisidium kosciusko* and *Glacidorbis hedleyi*, the crustaceans *Metaphreatoicus australis* and *Neoniphragus* n. sp., and an unidentified limnephid trichoperan. Community structure was influenced by the nature of the substrate, with cobble sites having greater richness and abundance than boulder sites. The importance of the major taxonomic groups (crustaceans, insects and molluscs) varied with sampling method and among lakes. Crustaceans (isopods and amphipods) usually dominated in sweeps, with molluscs and insects varying in importance among lakes, while insects mostly dominated in cobble pick samples. Oligotrophic lakes are typically thought to be dominated by insects, however this study shows such lakes may appear to be dominated by insects or crustaceans depending on the sampling method used and the presence of fish.

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KEYWORDS: alpine, Kosciuszko, littoral, macroinvertebrates, oligotrophic.

INTRODUCTION

The four lakes in the Mt. Kosciuszko region, Albina, Blue, Club and Cootapatamba, are unique among Australian mainland lakes, being the only ones formed by glacial processes and the highest in altitude. They contain a distinct fauna, elements of which are endemic either to these lakes or to alpine areas. Their geomorphology (Dulhunty 1945), physicochemical features (Williams et al. 1970; Raine 1982), plankton (Bayly 1970; Powling 1970; Benzie 1984) and eubenthos (Timms 1980) are known, but except for collections by some taxonomists (e.g. Ball 1977; Campbell 1988), their littoral fauna has not been studied. The littoral zone of these lakes is stony making them unusual in Australia. Most Australian lakes have sandy/muddy shores that are well vegetated. Also, in contrast to most other lakes on mainland Australia, waters of the four lakes have very low levels of nutrients (Williams et al. 1970).

The fauna of the stony littoral zone of Australian lakes have not been well studied, but data are available on four lakes in Tasmania (Leonard and Timms 1974; Knott et al. 1978), and Lake Purrumbete in Victoria (Timms 1981; Quinn et al. 1996). Macroinvertebrate diversity is lower in most of these lakes than in northern hemisphere lakes, but the same major groups are important – planarians, annelids, molluscs, crustaceans and insects (Leonard and Timms 1974). In general, insects dominate in unproductive waters, but with increasing trophic status non-insect groups predominate (Macan and Maudesley 1969; Leonard and Timms 1974). However fish may be influential, for Knott et al. (1978) have suggested that crustaceans may dominate in upland Tasmanian lakes where fish are absent, but Quinn et al. (1996) reported that crustaceans and molluscs may dominate in lowland lakes where fish supposedly eat the insects (or molluscs out-graze them).

The aim of the present work is to investigate the community structure and standing crop of the littoral fauna of the four lakes in the Mt Kosciuszko region with particular reference to the physical nature of the substrate and the presence/absence of fish.

MATERIALS AND METHODS

Study area

Lakes Albina, Blue, Club and Cootapatamba are located in the highest part of the Australian Alps at altitudes from 1890m (Blue Lake) to 2070m (Lake Cootapatamba). Blue Lake is the largest (14.4 ha) and deepest (28m), followed by Lake Albina (6.6 ha, 8.5m), Lake Cootapatamba (3.4 ha, 3.1m) and Club Lake (1.6 ha, 2m) (Timms 1992). Each was formed by cirque glaciation and still freeze over for 5-6 months during winter and summer temperatures reach 12°C in Blue Lake (Raine 1982) and 19°C in Lake Cootapatamba (Benzie 1984). Water in each is slightly acid (pH ca 6), of very low total dissolved solids (2-3 mgL^{-1}) and very low nutrients ($NO_3 < 0.01$ mgL^{-1}, $PO_4 < 0.017$ mgL^{-1}, $Ca < 0.15$ mgL^{-1}) (Williams et al. 1970). The mountain minnow *Galaxias findlayi* is common in Blue and Club Lakes but is not present in Albina and Cootapatamba (Timms 1980).

Sample Collection

The lakes were visited on 8-10 December 1997 and 20-22 March 1998. The littoral zone (to a depth of 1m) is highly variable in each lake, with sections dominated variously by bedrock, boulders (particle size diameter > 265mm), cobbles (64-256mm), pebbles (4-64mm), gravel (2-4mm), and sand (<2mm) (Cummins, 1962). The proportion of each substrate size class in each lake was estimated by walking the perimeter with a tape measure. Sites dominated by boulders and/or cobbles were chosen. The number of sites chosen for each lake varied to represent the size of the lake (Albina – A1 to A4, Blue – B1 to B5, Club – C1 to C3, Cootapatamba – D1 to D3) (Fig. 1). All sites were sampled in December, but in March only one site per lake was worked (A2, B1, C1, D1).

At each site the relative proportions of different particle sizes were estimated by dropping randomly a 1 m^2 quadrat three times and averaging the perceived proportions of the Wentworth size classes mentioned above by three investigators. The fauna was then sampled by two methods, sweeping and cobble picking. Sweeping involved investigators disturbing a strip of habitat 1m x 10m with their feet and sweeping the disturbed water with a pond net of aperture 700 cm^2 and mesh size of 0.5 mm for one minute. For the cobble picking method, 10 cobbles per site were selected. These were approximately 10-20 cm diameter and were removed one by one with the net underneath to catch escaping organisms. The cobbles and the net contents were then placed on a tray and the organisms removed. The bottom area of each rock was estimated by measuring two perpendicular diameters and the average diameter used to calculate area. In both methods, the organisms caught were preserved in 70% ethanol for later identification, enumeration and weighing. Oligochaetes and platyhelminthes were counted in the field due to individuals in these groups breaking up on preservation, although they were still included in collections for biomass measurements. Biomasses were estimated by blotted wet weights using a Sartorius top-loading electronic balance (±0.001 g). The shells of molluscs and cases of caddis fly larvae were removed prior to weighing.

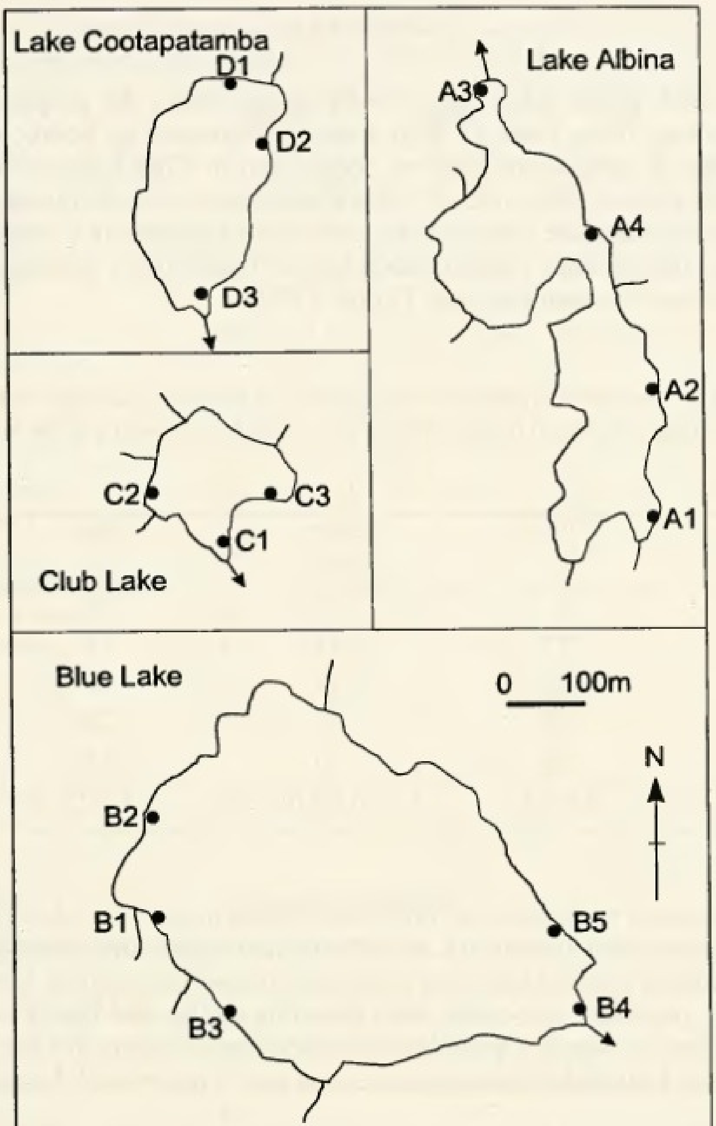

Figure 1. Sampling sites in the Alpine lakes of the Kosciuszko region (Modified from Dulhunty, 1945). Scale bar applies to all lakes. Major creeks indicated – outflows are distinguished with an arrow.

Statistical Methods

Similarities in macroinvertebrate assemblage composition among lakes and seasons were examined using a non-metric multidimensional scaling (NMDS) ordination. Bray-Curtis dissimilarities were calculated for each pair of samples on abundances of all species. To ordinate the data, the subroutine MDS in PRIMER was used, employing 99 random starts to minimise the risk of erroneously accepting solutions trapped in local minima (Clarke and Warwick 1994). The ANOSIM (Clarke and Warwick 1994) procedure was used to test for differences between lakes. Environmental variables were correlated with ordination scores using Primary Axis Correlation (PCC) in PATN.

The relationship between sweep sample biomasses and substrate type was examined using a Pearson correlation. Substrate type was expressed as a substrate index, calculated by ranking each rock size class (boulders=1, cobbles=2, pebbles=3, gravel=4, sand=5) and then calculating a weighted average based on the percentages of each size class in the quadrats.

RESULTS

Although each of the lakes has a rocky littoral zone, the proportion of rock size classes varies among sites (Table 1). Blue Lake is dominated by bedrock and boulders in a littoral zone that is narrow and shelves deeply and in Club Lake cobbles and pebbles dominate a broad littoral. One side of Lake Cootapatamba is dominated by boulders in deeply shelving water and the other side by cobbles and pebbles in a broad littoral. Habitat complexity is greatest in Lake Albina, aided further by its much greater relative shoreline length, i.e. shoreline development (see Timms 1992).

Table 1 Proportion of dominant littoral substrate types around each lake. Substrate index range for each lake. Substrate index explained in text. Particle sizes classified according to the Wentworth Scale (Cummins 1962).

Substrate Type	Albina	Blue	Club	Cootapatamba
	%	%	%	%
Bedrock	4	24	2	4
Boulders	27	61	15	42
Cobbles	38	14	44	22
Pebbles	19	0	26	15
Gravel	12	0	13	17
Substrate Index	1.6-2.8	0.9-2.6	2.6-2.9	1.9-3.1

Thirty six taxa of macroinvertebrates were found in the four lakes (Table 2). Species richness was considerably greater in Lake Albina than in the other lakes and was higher in sweeps than in cobble picks. There was a decrease in species richness between early summer and autumn, probably associated with breeding cycles and insect emergence. Many insects were in late instars in December and apparently absent in March, while crustaceans bred early as judged by the many juveniles and females with larvae but not eggs in December.

Flatworms and tubificids were widespread but not common and probably not speciose. Molluscs and crustaceans were also of limited diversity but were common, often dominant and widespread (Table 2). A bivalve, a snail (the endemic *Glacidorbis hedleyi*), a phreatoicid isopod and an amphipod (probably endemic) occurred in almost all lakes, while Blue Lake had a further snail of widespread distribution in Australia, *Austropeplea tomentosa*. By contrast insects were diverse, but distribution was patchy and typically they were not abundant (Table 2). Mayflies were common in only Lakes Albina and Cootapatamba, stoneflies (particularly *Eusthenia venosa*) in Blue Lake, chironomids in Albina and Blue Lakes, and beetles in Lake Albina. Only trichopterans were relatively common and shared between the lakes, with an unidentified limnephid caddis widespread and often abundant.

Biomass of sweep samples suggested Albina and Club Lakes had the highest standing crops and Blue Lake by far the lowest (Fig. 2). However, the cobble picking method gave a different order: Club and Blue Lakes the highest, with Albina and Cootapatamba Lakes with about half as much (Fig. 2).

Contributions by major taxa to these totals also varied with method and within and between lakes (Fig. 2). Crustaceans (mainly *Metaphreatoicus australis*) usually dominated in sweeps, with molluscs (mainly *Psidium kosciusko*) important in Club Lake, and insects (mainly mayflies) of some importance in Lake Albina. The cobble picking method gave a different result – Molluscs hardly featured at all (except in Blue Lake), crustaceans

Table 2 Littoral species in the Kosciuszko lakes. S = mean number of individuals per m^2 of sweep in each lake (bold) ; C = mean number of individuals per m^2 of cobble in each lake.

	Albina		Blue		Club		Cootapatamba	
Species	**S**	**C**	**S**	**C**	**S**	**C**	**S**	**C**
Platyhelminthes								
Unidentified planarians	**1.5**	21.1		1.1	**0.1**	14.3		55.1
Annelida: Oligochaeta								
Unidentified tubificids	**0.2**	3.5	**0.2**	1.4	**0.3**	2.9	**0.3**	1.5
Mollusca: Bilvalva								
Pisidium kosciusko	**10.7**	1.3	**1.4**	194.6	**141.1**	13.0	**0.2**	
Mollusca: Gastropoda								
Glacidorbis hedleyi	**5.4**	10.6		1.4	**8.4**			32.9
Austropeplea tomentosa			**2.6**	6.4				
Crustacea: Isopoda								
Metaphreatoicus australis	**32.1**	61.6	**0.4**	35.3	**82.2**	43.1	**16.8**	19.6
Crustacea: Amphipoda								
Neoniphragus n.sp.	**0.3**	0.9			**0.4**	2.9	**11.0**	128.0
Insecta: Ephemeroptera								
Tasmanophlebia lacascoerulei	**0.9**	3.6	**0.1**					
Ameletoides lacusalbinae	**1.7**	26.6					**0.2**	1.5
Nousia sp. and *Tillyardophlebia alpina*	**0.2**	7.8			**0.1**		**0.5**	31.5
Insecta: Plecoptera								
Eusthenia venosa			**0.6**	21.7				
Notonemouridae nymph	**0.1**		**0.1**		**0.2**	5.8	**<0.05**	
Insecta: Hemiptera								
Sigara sp.							**<0.05**	
Insecta: Mecoptera	**Insecta: Coleoptera**							
Nannochorista sp.					**0.1**			
Insecta: Trichoptera								
Ecnomus sp.	**0.2**	7.5						
Plectrocnemia sp.	**0.3**	4.3					**0.1**	5.4
Austrorheithrus sp.	**0.1**		**<0.05**	3.1	**<0.05**		**<0.05**	
Limnephidae larvae		0.9	**<0.05**	21.2	**0.6**	62.3		38.3
Leptoceridae larvae	**0.1**						**0.1**	
Insecta: Diptera								
Procladius villosimanus	**0.5**	4.0						
Tanytarsus sp.	**0.3**							
Paramerina levidensis?	**0.0**	2.6						
Botryocladius grapeth	**0.1**							
Polypedilum sp.	**0.2**	1.7	**0.1**	7.8	**0.1**		**0.1**	
Unidentified ceratopogonid					**<0.05**			
Tipulidae sp 1	**<0.05**							
Tipulidae sp 2					**<0.05**			
Antiporus femoralis adults							**<0.05**	
Sternopriscus wehnekei adults	**0.2**	1.3						
Sternopriscus larvae	**2.6**	5.3						
Elmidae sp 1 adults	**0.2**	5.3						
Elmidae sp 2 adults	**0.2**	1.8		1.0				
Elmidae larvae	**0.2**							
Curculionidae adults			**0.1**		**0.1**			
Sclerocyphon basicollis larvae			**0.0**	2.0				
Scirtidae larvae							**<0.05**	
Species Richness	**25.0**	19.0	**12.0**	12.0	**15.0**	7.0	**14.0**	9.0
Total Species Richness	26.0		15.0		15.0		17.0	

were sometimes important (in Lakes Albina and Cootapatamba) but insects usually dominated (mayflies, caddis and beetles in Lake Albina, large stoneflies and caddis in Blue Lake, caddis in Club Lake and Lake Cootapatamba).

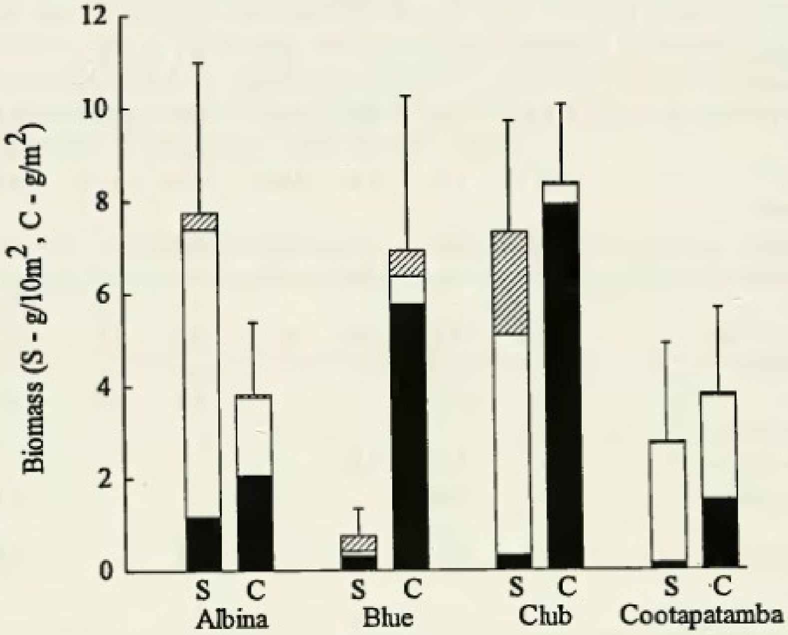

Figure 2. Mean total biomass for Lakes. S indicates sweep samples and C cobble samples. Standard error bars shown. Proportion of biomass consisting of insects (black), crustaceans (open) and molluscs (hatched). All other invertebrates <0.09 and not shown.

Biomass figures also changed with season. Sweep biomasses declined by a factor of 1.3 to 20 between December and March, but figures for cobble picks were equivocal, declining by a factor of 2.7 and 5 in Club and Blue Lakes respectively, but increasing by a factor of 1.2 and 5 in Cootapatamba and Albina respectively. Decreases in the figures from sweeps was due mainly to insects, but the increase in the cobble pick figures was due mainly to crustaceans.

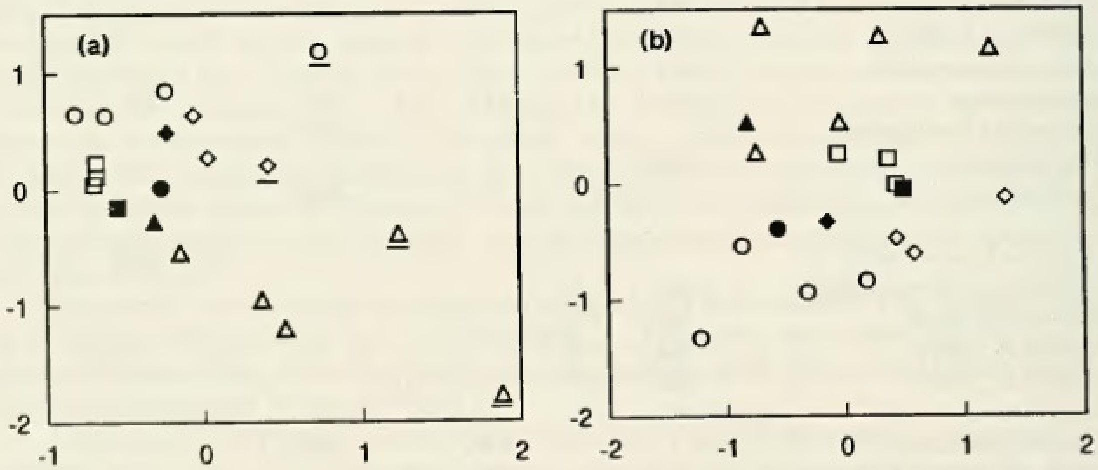

Figure 3. Ordination of littoral assemblages in lakes Albina (circles), Blue (triangles), Club (squares) and Cootapatamba (diamonds). December samples (open symbols) and March samples (closed symbols). (a) Sweep samples, stress = 0.11. (b) Cobble pick samples, stress = 0.14. Sites within each lake most dominated by boulders (high substrate index) are underlined.

Ordination of both sweep and cobble pick samples demonstrate that sites group by lake (Fig. 3). Pairwise ANOSIM tests show that the four lakes are significantly different (all pairwise tests significant $P \leq 0.05$, Global $R=0.440$, $0.006<P<0.029$). These tests also included March samples and indicate that these were similar in species assemblage to December samples. The nature of the substrate was found to be important in determining the differences among macroinvertebrate assemblages. Substrate index was significantly correlated with the ordination scores ($r=0.75$, $P<0.001$) and within each lake, sites with substrates dominated by boulders were separated from sites dominated by cobbles (Fig. 3). In addition, sites with the highest proportion of boulders (A3, B2,4,5 and D3) had fewer species and lower biomasses. However, sweep sample biomasses were only weakly correlated with substrate type when all sites were considered ($r = 0.472$, DF=14, $P=0.046$).

The presence of fish also seemed to influence species composition. The two lakes without fish (Albina, Cootapatamba) were dominated by crustaceans as measured either by their numbers (Table 2) or biomass contribution (Fig. 2). Insects or molluscs dominated in the lakes with fish (Blue and Club), though crustaceans were still important by some measures. This is especially so in Club Lake where the substrate underlying the rocks is gravel and so suitable for phreatoicids and bivalves. In addition, mayflies were far more common in the lakes without fish (Table 2).

DISCUSSION

The common invertebrates in the four Kosciuszko lakes are biogeographically distinct. Many littoral species, including the common *Glacidorbis hedleyi*, *Metaphreatoicus australis*, *Tasmanophlebia lacasoerulei*, *Tillyardophlebia alpina*, and *Eusthenia venosa* are endemic to upland areas in southeastern Australia, while *Pisidium kosciusko* and *Neoniphragus* n. sp. are possibly restricted to the lakes in the current study. Other alpine benthic species that occur in the littoral of these lakes, but were not specifically identified in this study, include the planarian *Spathula truculenta* and the caddis *Austrorheithrus dubitans* (Timms 1980). Dominant zooplankton are also either endemic to the Kosciuszko lakes (e.g., *Daphnia nivalis*) or upland in their distribution (e.g., *Boeckella montana*) (Bayly 1970; Benzie 1984). On the other hand, some common eubenthic chironomids (e.g., *Procladius villosimanus*, *Chironomus oppositus*?) (Timms 1980) and some uncommon littoral species (e.g., *Austropeplea tomentosa*, *Sternopriscus wehnekei*, and *Sclerocyphon basicollis*) are widespread.

Although biogeographically distinct, the Kosciuszko lakes have a similar species richness to the other highland lakes in Australia (Leonard and Timms 1974; Knott et al. 1978). However, they are not as species-rich as lowland lakes (e.g., Purrumbete – Quinn et al. 1996) or many lakes with rocky shorelines in the northern hemisphere (Macan and Maudesley, 1969; Barton and Hynes 1978). The low richness of the Kosciuszko lakes may be due in part to their relatively small size, since habitable area is approximately proportional to species richness (Macarthur and Wilson 1967).

Factors affecting distribution and abundance within the Kosciuszko lakes are hard to elucidate. Rock size appears to be important in the structure of macroinvertebrate communities, with species richness and abundance highest in sites dominated by cobbles compared with sites dominated by boulders. The nature of the substrate on which the rocks lie may also be important, for example, the phreatoicid *Metaphreatoicus australis* was more abundant in underlying gravel or sand than on underlying cobbles or pebbles. Other studies examining macroinvertebrates on the rocky shores of lakes have identified the nature of the rocky substratum (Leonard and Timms 1974) or exposure to wave action (Dall et al. 1984) as important in influencing community structure. The latter was shown to be significant for some species in Lake Purrumbete (Quinn et al. 1996), but since the Kosciuszko lakes are small, it seems not to be important in them.

Many authors (e.g., Macan and Maudsley 1969; Leonard and Timms 1974, Timms 1981, Quinn et al. 1996) claim that community composition changes with lake trophic status: insects dominate oligotrophic lakes while non-insects (crustaceans, molluscs) dominate lakes with increasing nutrient levels. Ultradilute water, particularly expressed as low concentrations of Ca, is thought to be the explanation for the scarcity of planarians, crustaceans and molluscs (Reynoldson 1966; Hutchinson 1994). While studies on four Tasmanian lakes (Leonard and Timms 1974; Knott et al. 1978) give some credence to this hypothesis, planarians are present and molluscs and crustaceans are abundant in most Kosciuszko lakes, whose waters are even more dilute than the Tasmanian lakes (Salinity: Tasmanian Lakes – 0.183 - 0.323 m-equiv/L; Kosciuszko Lakes – 0.0334-0.0407 m-equiv/L)

The presence of fish has also been identified as influencing which groups dominate. In the oligotrophic Tasmanian lakes introduced trout adversely impacts the syncarid *Anaspides tasmaniae* (Knott et al. 1978) and insects dominate if fish are present (Leonard and Timms 1974). While crustaceans are not as dominant in the littoral zone of the Kosciuszko lakes with fish (Blue and Club) they are still common. This may be explained by the preference of amphipods and isopods to live within the interstitial spaces of gravel and cobbles where they are probably not easily preyed on by fish. By comparison, syncarids behave very differently, tending to rest and feed on the top of rocks where they would be more prone to predation (Knott et al. 1978).

Confounding the relationship between trophic status and dominance of taxonomic groups is sampling method. In the Kosciuszko lakes, cobble picks suggest insects dominate in Blue and Club Lakes, but sweeps indicate crustaceans dominate in Club Lake and that molluscs and insects are of equal importance in Blue Lake. In Hartz Lake (Knott et al. 1980), dominance by crustaceans would likely have been clear had sweep sampling been used in addition to cobble picks. Macan and Maudsley (1969) only used rock picking to show that insects dominated in their lakes, but their method probably favoured collection of insects. If Quinn et al. (1996) had used sweeps as well as rock picking then insects may have appeared even less important, and gastropods more important in Lake Purrumbete. In addition, perceived dominance may be influenced by seasonal changes in faunal composition (insect emergence). In the Kosciuszko lakes, changes over the whole ice free period may have been greater than the observed differences between December and March. Clearly results need to be interpreted with caution, depending on methods used and seasonal variations.

In conclusion, substrate type is important in influencing macroinvertebrate community structure with cobbles supporting the highest species richness and abundance. Although results need to be interpreted with caution, it is evident that dominance by crustaceans, insects or molluscs can prevail in upland lakes in southeastern Australia, but in the presence of fish insects generally dominate.

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