

Spatial patterns in meiobenthic assemblages in intermittently open/closed coastal lakes in New South Wales, Australia

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Abstract

Intermittently closed and open lakes and lagoons (ICOLLs) are important features of the Australian coastline. Local authorities frequently open lakes by bulldozing or dredging the mouths, in an effort to improve water-quality and to reduce the risk of flooding and these interventions provided an opportunity to examine large-scale patterns in meiobenthos in relation to isolation from the sea. Even at a coarse level of taxonomic resolution (phylum, class and order), consistent differences between assemblages of meiobenthos in different reaches of the lakes and between open and closed lakes were revealed. The abundance of meiobenthos generally decreased with increasing distance from the sea. Multivariate analyses showed that nematodes, copepods and turbellarians were characteristic of assemblages near the mouths of lakes while polychaetes and oligochaetes characterised those in more isolated areas. Furthermore, assemblages in the inner reaches of open lakes also differed from those in closed lakes. Isolated localities were less diverse and more spatially variable. Differences in meiobenthos between natural lakes and those that are artificially opened became apparent when open and closed were analysed separately. Lakes that are kept open artificially are similar to naturally open lakes despite other impacts associated with human activities. These results are considered in the context of isolation and the implications of proposed changes in the way mouths are manipulated are discussed.

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1. Introduction

Coastal lakes and lagoons are important features of many coastlines and are among the world's most productive marine environments (Odum, 1971). Their highly variable geomorphology and hydrology make them ecologically complex (Roy et al., 2001) and this is compounded by the fact that many lakes are only intermittently open to the sea and exhibit great

variability in the frequency, timing and duration of opening. Despite their importance, few lagoons have been studied and our understanding of their ecology is limited. Intermittently open and closed coastal lakes and lagoons (ICOLLs) are common in Australia, with around 70 in New South Wales alone (Roy et al., 2001).

Australian coastal lakes have been described and classified on the basis of geomorphology (Roy, 1984; Pollard, 1994a; Roy et al., 2001). Aspects of nutrient dynamics and water-chemistry have been well-documented, notably in Lake Illawarra (Ellis et al., 1977; Qu et al., 2003), small lagoons near Sydney (Eyre and Ferguson, 2002) and the Tuggerah Lakes (King and

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Hodgson, 1995). There have been studies of seagrass (West, 1983; King, 1988; Udy and Dennison, 1997), phytoplankton (Eyre and Ferguson, 2002) and fish in coastal lagoons (Allen et al., 1985; Pollard, 1994b; Griffiths and West, 1999). Relatively little, however, has been published about macrobenthos in lagoons of NSW, apart from surveys of Gosford lagoons by Weate and Hutchings (1977), the Myall Lakes (Atkinson et al., 1981) and Smith's Lake by Robinson et al. (1983). No published information exists on the meiobenthos (animals between 0.032 and 0.5 mm (Soltwedel, 2000) of ICOLLs in Australia, although this group has been studied in estuaries (Hodda and Nicholas, 1985, 1986a,b; Stark, 1998) and mangrove systems (Nicholas et al., 1988; Alongi, 1988, 1989, 1990; Fisher and Sheaves, 2003).

Coastal lakes have been under pressure from urban development for many years and their benthic communities are subject to a variety of stresses arising from contamination, siltation and nutrient enrichment. Physical disturbances associated with construction, clearing of seagrass and wrack, recreational activities and dredging also impact negatively on the benthos (Pequegnat, 1975; Warwick and Clarke, 1993; Stark, 1998). A recent enquiry into the state of coastal lagoons in New South Wales concluded that most are severely degraded (Healthy Rivers Commission, 2002). One consequence of urban development is the practice of artificially opening lakes to increase flushing and reduce the threat of flooding. As a result, many lakes are maintained as open systems when, in fact, they would naturally be closed for long periods of time.

These interventions provided an opportunity to experimentally compare open and closed systems and to examine patterns of abundance and composition of benthos along estuarine gradients from marine to freshwater. The study focuses on meiobenthic assemblages in coastal lakes and is part of a larger programme aimed at enhancing our understanding of the role of isolation (or 'confinement' sensu Guelorget and Perthuisot (1992)) in the ecology of benthos in coastal lakes. Other papers will deal with patterns in macrobenthic assemblages and spatio-temporal variability in individual taxa of macro- and meiobenthos (Dye and Barros in prep.).

Meiobenthos is a ubiquitous, taxonomically diverse and numerous component of the fauna of marine sediments (Coull, 1999) with a fast turnover, producing several generations a year. These animals facilitate remineralization of organic material and enhance bacterial activity (Tenore et al., 1977; Tietjen, 1980). They are also important food for higher trophic levels (Gee, 1989; Castel, 1992). Meiobenthos are sensitive to anthropogenic disturbance and pollution (Warwick et al., 1990; Coull and Chandler, 1992; Warwick, 1993; Mirto et al., 2002) and their potential as indicators of environmental

condition is widely recognised (Moore and Bett, 1989; Kennedy and Jacoby, 1999; Schratzberger et al., 2000).

Meiobenthos in estuaries and lagoons are almost exclusively of marine origin (Warwick, 1971) and a number of studies have shown that their abundance and taxonomic diversity tend to decrease under conditions of great physical and chemical variability (Coull, 1999). While the penetration of macrobenthos into estuaries, for example, is known to be limited by their tolerance to reduced salinity (Carriker, 1967), this has not always been found to be the case for meiobenthos, where different taxa appear to respond to gradients in salinity in different ways (Capstick, 1959; Warwick and Gee, 1984; Warwick and Clarke, 1993). This is particularly relevant for ICOLLs where salinity regimes can be very different in open compared with closed lakes (Roy et al., 2001). Open systems often have clear gradients of salinity, which may result in changes in the composition and/or abundance of meiobenthos with increasing distance from the mouth. Closed lakes, in contrast, may have only slight gradients in salinity, but experience extended periods of either reduced or elevated salinity, depending on the relative strengths of freshwater inflow and evaporation (Guelorget and Perthuisot, 1992).

While the physical characteristics of sediments influence patterns of distribution of macrobenthos at various spatial scales (Whitlatch, 1981; Wu and Shin, 1997; Thrush et al., 2003), they also play an important role in structuring meiobenthic communities (Castel, 1992; Coull, 1999). Fine sediments, for example, trap clay and organic matter, excluding some taxa (Mirto et al., 2002), while limiting the depths to which meiofauna penetrate. In open systems tidal movement of water may scour sediments, removing fine material from mouths and establishing a gradient of decreasing particle-size with increasing distance from the sea. Such movements of water may also be important in dispersal of meiobenthos (Armonies, 1994).

Physical and chemical variability is typical of habitats that are not buffered by tidal incursions (Guelorget and Perthuisot, 1992). It may, therefore, be expected that increasing isolation from the sea will alter the structure of meiobenthic assemblages over time (McArthur et al., 2000), possibly through loss of species (Austen and Warwick, 1989) and/or changes in dominance. Assemblages of meiobenthos in open lakes, including those that are kept open artificially or are frequently opened, would therefore be expected to differ from those in closed lakes.

Anthropogenic disturbance is known to affect the structure and spatial distribution of meiobenthic communities. These disturbances include dredging (Essink, 1999), clam harvesting (Alves et al., 2003), beam trawling (Schratzberger and Jennings, 2002), aquaculture (Olafsson et al., 1995; Mazzola et al., 2000; LaRosa et al., 2001), eutrophication resulting from agriculture (Palacin et al., 1992) and pollution (Sandulli and de

Nicola-Giudici, 1990; Somerfield, 1994). Meiobenthos in urban lakes, which experience considerable anthropogenic disturbance, may therefore differ from that in less disturbed rural systems.

Many studies have also highlighted the importance of biotic factors in structuring benthic communities, including pre- and post settlement processes among macrobenthos (Olafsson et al., 1994; Hooker, 1995), bioturbation (Widdicombe et al., 2000) and interactions between macro- and meiobenthos (Dye and Lasiak, 1986; Olafsson and Elmgren, 1991; Austen and Widdicombe, 1998; Tita et al., 2000; Anneli and Olafsson, 2002). Differences in the composition and abundance of macrobenthos between open and closed lakes (Dye and Barros, in prep.), may alter the nature of these interactions, leading to differences in the meiobenthos.

Detection of spatial and temporal patterns in benthic communities is influenced by a number of factors, one of which is taxonomic resolution. Identifying meiofauna to a fine taxonomic resolution is a laborious and time-consuming process that requires considerable expertise (Heip et al., 1988). Several studies have, however, shown that differences in composition of meiobenthos, particularly in relation to disturbance, can be reliably detected, despite possible loss of resolution, using higher taxonomic levels (Heip et al., 1988; Herman and Heip, 1988; McArthur et al., 2000), including only phylum, class and order (Warwick and Gee, 1984; Gee et al., 1985; Warwick and Clarke, 1993). This classification was used in the present study, as one of the objectives was to determine whether consistent patterns in meiobenthos could be detected at a coarse taxonomic resolution. Such an approach enables examination of a large number of samples in a relatively short time and may also reduce noise in the data (Gee et al., 1992).

State government policy now requires that artificial opening of lakes be phased out to restore more natural dynamics of mouths. Our ability to predict the consequences of this depends upon an understanding of how benthos responds to isolation. This study tested the hypotheses that the predicted patterns do indeed exist, that they are consistent among lakes and that differences in assemblages relate to their relative degree of isolation. The study compared meiobenthic assemblages in the mouth, middle and inner reaches of 8 ICOLLs chosen to represent two levels of isolation, i.e. mainly open or mainly closed. Within each of these categories two sub-categories were identified, 'managed' and 'natural'. The former are either kept open by training walls, etc., or are frequently opened by dredging or bulldozing. These lakes are also characterised by a considerable degree of development in their catchments and along their shorelines. Thus 'managed' refers to lakes that are impacted by human activities in a variety of ways that may include pollution and physical disturbance. 'Natural' refers to untrained lakes that are infrequently manipulated and

tend to be rural with extensive natural vegetation in their catchments.

2. Materials and methods

2.1. Study sites

The lakes (Fig. 1), which are shallow, with maximum depths between 3 and 5 m, and well-mixed by winds and/or tidal movements of water (Roy et al., 2001), were paired according to four entrance/management conditions, based on classifications in the NSW Department of Infrastructure, Planning and Natural Resources estuaries database (2002) and Ozestuaries database (Geoscience Australia, 2001). The pairs were: Durras/Wamberal (natural, mainly closed); Burril/Conjola (natural, mainly open); Illawarra/Narrabeen (managed, mainly open) and Curl Curl (Harbord)/Dee Why (managed, mainly closed). The last pair are opened artificially on a fairly regular basis (at least once per year), but the duration of opening is very short (1–6 days), due partly to low freshwater flows from their small catchments and rapid deposition by wave-action of sand at the mouths (Probst, 2002). As a result, they are considered closed despite managerial intervention. The lakes designated as being mainly open experienced less than one closure per year in the three years prior to the study (Table 1) and were open for an average of 360 days per year. Those designated as mainly closed, however, were opened for a total of between 20 and 77 days per year over this period.

Although the lakes differed considerably in surface area (Fig. 1) (from 0.13 km² for Curl Curl to 36 km² for Illawarra), their ratios of water area to catchment area were similar (0.03 for Curl Curl to 0.11 for Illawarra). All of the lakes except for Durras, in which there was some tidal exchange despite being classified as mainly closed, reflected their long-term open/closed classifications. In this study, Durras was treated according to the long-term classification.

Although the sampling sites supported a variety of macrobenthos (128 taxa were recorded overall), including polychaetes, oligochaetes, amphipods, bivalves, gastropods and nematodes, average density varied only from 7 through 18 to 22 individuals 100 cm⁻² in mouths, middle reaches and inner reaches respectively. In open lakes macrobenthos was dominated by polychaetes while in closed lakes oligochaetes predominated (Dye and Barros, in prep.).

2.2. Sampling

Four surveys were done, two approximately three weeks apart in March/April followed by two, also three weeks apart, in June/July 2002. This enabled an analysis

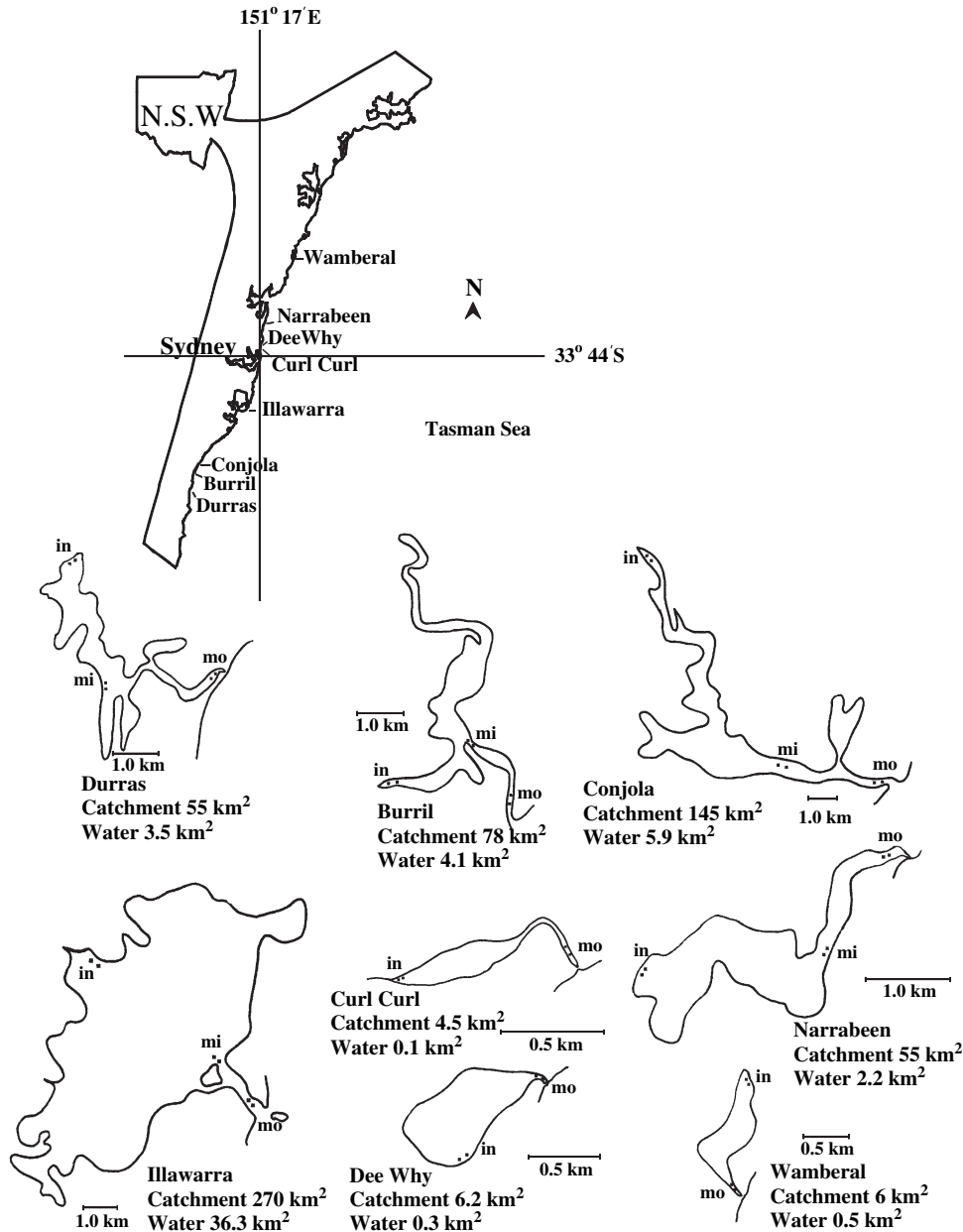


Fig. 1. Map showing locations of the lakes with their outlines indicating the positions of the sampling sites and the extent of their catchments and water bodies. mo=mouth, mi=middle reaches, in=inner reaches.

of variability at different temporal scales which will be reported elsewhere (Dye, in prep.) The emphasis in this report, however, is on the overall spatial patterns based on the combined data from the four surveys. Despite heavy rain, which raised water levels in the closed lakes, their mouths remained closed during the study. High water levels did, however, prevent sampling in the inner reaches of Wamberal on two occasions, while, on one occasion, stormy conditions prevented sampling in Illawarra. Winds were, however, generally light during the surveys.

On each occasion, samples of sediment were collected by hand-coring in shallow subtidal (approximately 1 m

depth), unvegetated sediments in the mouth and inner reaches of each lake. Samples were also obtained from the middle reaches of the open lakes and in Durras. The middle-reach localities were approximately half of the distance by water between the mouth and the inland limits of the lakes. Due to their small size and difficulty of access, only mouths and inner reaches were sampled in Curl Curl, Dee Why and Wamberal.

A nested sampling design was employed (Fig. 2) in which four replicate cores (2.7 cm diameter \times 10 cm depth) were taken from a 5 m \times 5 m block in each of two sites, 50 to 100 m apart, in each reach of a lake (mouth,

Table 1
Frequency, duration and time since last opening/closure and mean salinity and sediment characteristics of each lake

Lake	Mean annual frequency and duration of opening/closure ^a	Time since last opening/closure prior to this study	Reach	Salinity ± SE	Median grain size (µm) ± SE	Clay fraction (%) ± SE	Total organic (%) ± SE
Durras	<1 opening	14 days–opened remained open	mouth	39.2±2.1	395±11	1.1±0.2	2.2±0.3
			middle	39.0±2.3	336±45	5.4±0.8	5.5±1.0
			inner	38.8±2.8	293±54	37.9±7.1	6.8±0.4
Wamberal	2 openings × 10 days	11 months–opened for 10 days	mouth	17.8±3.2	390±2	0.8±0.1	0.3±0.03
			inner	10.0±3.0	202±19	16.5±1.0	5.1±0.3
Burril	0 closures	>3 yrs no change	mouth	38.8±1.7	366±2	1.2±0.2	0.7±0.1
			middle	36.5±1.8	351±2	3.0±0.7	3.3±0.6
			inner	39.8±2.4	356±33	8.1±1.8	8.8±1.6
Conjola	0 closures	>3 yrs no change	mouth	40.3±1.4	325±7	0.5±0.2	0.9±0.03
			middle	37.8±1.9	327±8	1.6±0.2	0.8±0.1
			inner	35.8±2.5	181±3	17.7±2.1	10.3±1.2
Curl Curl	12 openings × 3 days for 2 days	30 days–opened for 2 days	mouth	13.8±2.4	385±2	0.3±0.03	0.3±0.03
			inner	3.8±2.2	331±21	18.2±4.9	7.1±1.0
Dee Why	7 openings × 11 days	30 days–opened for 7 days	mouth	14.3±4.1	366±1	0.4±0.03	0.6±0.04
			inner	13.5±3.8	308±5	3.6±0.4	5.2±0.7
Illawarra	0 closures	>3 yrs no change	mouth	35.0±1.9	338±5	0.8±0.1	0.7±0.1
			middle	30.7±2.3	305±18	2.2±0.3	1.5±0.5
			inner	31.3±2.4	193±1	1.0±0.1	1.0±0.1
Narrabeen	<1 closure	16 months–closed for 14 days	mouth	37.0±0.5	412±6	0.8±0.04	1.5±0.2
			middle	34.0±2.2	251±10	1.2±0.1	0.5±0.02
			inner	32.8±2.1	200±7	6.2±1.1	3.9±0.6

N=32 except for Illawarra (N=24) and the inner reaches of Wamberal (N=16).

^a Average for the three years prior to this study. Data from NSW Department of Infrastructure, Planning and Natural Resources.

middle or inner reaches). The same sites were sampled on each occasion. The samples were preserved in 7% formalin. Two additional samples of sediment were obtained from each site for determination of particle size (dry sieving) and total organic content (loss on ignition at 500 °C for 12 h). These samples were frozen. Surface salinity was determined at each locality, but no measurements of temperature or oxygen were made as these are subject to considerable diurnal variation in coastal lakes (Haines et al., 2001; Wilson et al., 2002) and continuous recordings are required to relate these variables meaningfully to the benthos.

Meiobenthos was extracted from sandy sediments by decanting with tap water and washing through a 500 µm sieve suspended above a 45 µm sieve (McIntyre, 1969). Although some recent studies have used a lower limit of 32 µm for meiofauna, these are relatively few and a mesh size of 45 µm was used as this falls within the range of 40–65 µm characteristic of the majority of studies (Soltwedel, 2000). The material retained on the lower sieve was preserved in a mixture of 70% ethanol and 5% glycerol. A small amount of Rose Bengal was added to aid counting. Muddy sediments were first washed through the sieves and the fraction retained on the

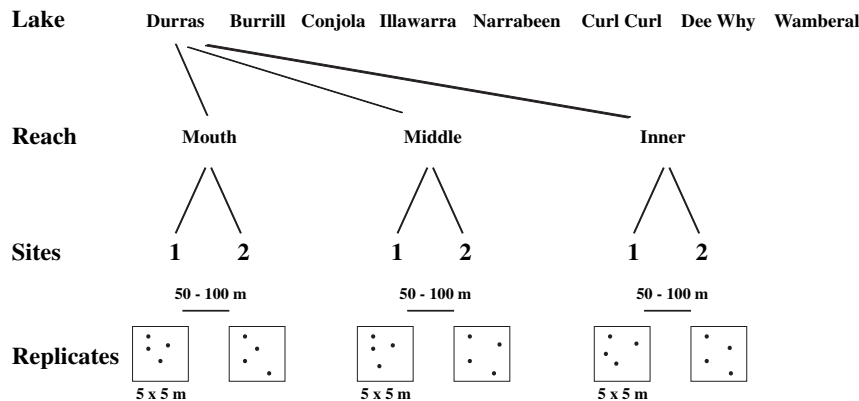


Fig. 2. Diagram of the sampling design used in each survey. No middle reaches for Dee Why, Curl Curl or Wamberal.

lower sieve was thoroughly mixed with Ludox HS40[®] (density 1.15) in a ratio of approximately 1 part sediment to 10 parts Ludox[®] (Somerfield and Warwick, 1996). The resulting suspension was then centrifuged at $4000 \times g$ for five minutes. The supernatant was washed through the 45 μm sieve with tap water and the material retained was preserved as above. All material was retained for further taxonomic study if required. Results are expressed per 10 cm^2 after multiplying the count from each core by 10 divided by the area of the core (5.73 cm^2).

2.3. Analyses of data

Abundances were analysed in terms of localities within lakes (mouths vs middle vs inner reaches), classification of the mouth (open vs closed) and managerial status (natural: open and closed vs managed: open and closed). Multivariate analyses on $\log(x+1)$ -transformed data from each survey were based on non-metric multi-dimensional scaling (MDS) ordinations derived from Bray-Curtis dissimilarity matrices. Tests for differences in structure of assemblages were based on one-way analyses of similarities (ANOSIM), a permutation test based on the R statistic (Clarke and Warwick, 2001), using ranks of Bray-Curtis dissimilarities. Multivariate dispersion analysis (MVDISP: Clarke and Warwick, 2001) was used to determine the spatial variability of assemblages. The significance of differences in spatial variability between localities was determined using nested analyses of variance to compare estimates of dissimilarity from each site. These were obtained by calculating percent dissimilarities between independent pairs of replicate cores, which gave two estimates for each site (Underwood and Chapman, 1998). Data from both sites in each reach were combined for subsequent one-way analyses of variance (open vs closed lakes and natural vs managed lakes) after transformation to arc sin.

The contribution of individual taxa to dissimilarities was determined from the combined data from the surveys by similarity percentage analysis (SIMPER; Clarke and Warwick, 2001). RELATE analyses from the PRIMER routines (Clarke and Warwick, 2001) were used to examine relationships between similarity matrices containing meiobenthos abundances and physical variables (Somerfield et al., 1995).

3. Results

A total of 14 meiobenthic taxa were identified in the study, comprising: Annelida (Oligochaeta, Polychaeta), Crustacea (Harpacticoida, other copepods, Cumacea, Ostracoda, Syncarida and Tanaidacea), Platyhelminthes (Turbellarians), Kinorhyncha, Gastrotricha, Echiura, Nematoda and Tardigrada. Over the entire study,

average total density of meiobenthos in the mouths of ICOLLs was $467 \pm 28 \times 10 \text{ cm}^{-2}$. In the middle reaches average total density was $314 \pm 35 \times 10 \text{ cm}^{-2}$, while in the inner reaches, the average number was $369 \pm 30 \times 10 \text{ cm}^{-2}$. Nematodes were numerically dominant at all sites followed, in variable order in different localities, by harpacticoid copepods, turbellarians, other copepods and polychaetes.

RELATE analyses across all lakes irrespective of their open or managed status, indicated significant correlations between the abundance of meiobenthos in the mouths of lakes and median particle-size ($\rho=0.25$, $P<0.03$) and organic content ($\rho=0.25$, $P<0.03$). In the middle reaches, meiobenthos correlated significantly with organic content ($\rho=0.51$, $P<0.007$) and clay ($\rho=0.61$, $P<0.003$). There were no significant correlations between meiobenthos and sediment attributes across inner-reach localities, but there was a significant correlation with salinity ($\rho=0.539$, $P<0.002$).

3.1. Open vs closed lakes

There was little difference in mean salinity between the mouths (38.2 ± 0.9), middle (34.8 ± 1.4) and inner reaches (35.9 ± 1.3) of open lakes (Table 1), but salinity was more variable towards the inner reaches. Salinity was much less and more spatially and temporally variable in closed than in open lakes and there were large differences between areas near mouths (15.3 ± 1.6) and inner reaches (9.1 ± 1.7).

There was considerable between-lake variability in characteristics of sediments (Table 1) and no clear patterns, or statistically significant differences, between sediments in open vs closed lakes were detected. Average median grain-size was $360 \pm 17 \mu\text{m}$ in the mouths of open lakes. In the middle and inner reaches, where sediment was less well sorted and contained varying amounts of silt and clay, shell fragments and stones, median grain-size was more variable (middle: $309 \pm 18 \mu\text{m}$, inner: $233 \pm 36 \mu\text{m}$). The average silt/clay content of sediments in the mouths of open lakes was $0.8 \pm 0.1\%$, rising to $2.0 \pm 0.3\%$ in the middle reaches and to $8.3 \pm 3.0\%$ in the inner reaches.

In closed lakes average median grain-size varied from $384 \pm 5 \mu\text{m}$ in the mouths to $284 \pm 24 \mu\text{m}$ in the inner reaches. Silt/clay content near the mouths was $0.7 \pm 0.2\%$ and $19.1 \pm 6.1\%$ in the inner reaches. Total organic content in sediments in open lakes ranged from an average of $1.1 \pm 0.2\%$ in the mouths to $1.5 \pm 0.5\%$ in the middle reaches and $6.0 \pm 1.9\%$ in the inner reaches. In closed lakes organic content was $2.5 \pm 1.3\%$ and $6.0 \pm 0.5\%$ in the mouths and inner reaches respectively.

Although there were no significant relationships between the abundance of meiobenthos and properties of sediment when open and closed lakes were compared, MDS ordinations indicate that assemblages in open

lakes were consistently different from those in closed lakes, particularly in the mouth and inner reaches (Fig. 3). In the middle reaches, clear differences were evident only in June, but this comparison should be treated with caution, as middle-reach data were available for only one closed lake (Durras). ANOSIM showed that the differences between open and closed lakes were nearly always significant (Table 2A), the single exception being in July when there was no difference between assemblages in the mouths of open and closed lakes. Analyses based on the combined data from the four surveys showed consistent differences between assemblages in open and closed lakes in all reaches.

The dissimilarity between assemblages in open and those in closed lakes generally increased with distance from the mouth (Table 2A), ranging from an average of 23% in mouths to 36% and 47% in middle and inner reaches, respectively. Although there were no statistically significant differences in spatial variability between open and closed lakes, indices of multivariate dispersion indicated that the mouths and inner reaches of closed lakes were always more variable than those in open lakes, while the opposite was true for middle reaches (Table 2A).

Within lakes, differences in the composition of assemblages were highest in comparisons between

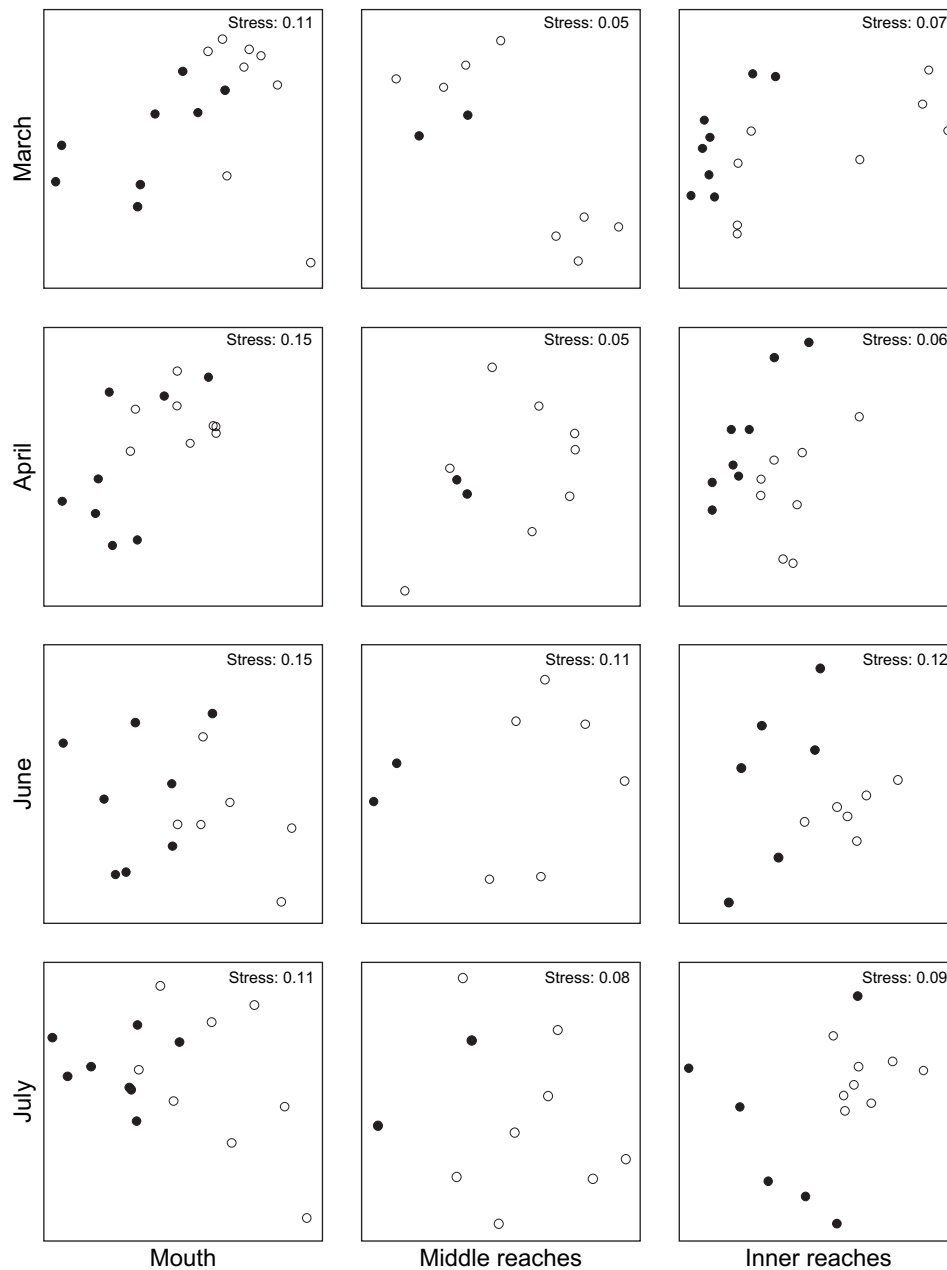


Fig. 3. MDS plots based on meiobenthos abundance on four occasions comparing assemblages in mouths, middle and inner reaches of open (open symbols) and closed lakes (solid symbols). Plots represent the centroids of replicate samples at each site.

Table 2

Results of one-way ANOSIM (R), Bray-Curtis percent dissimilarities (D) and indices of multivariate dispersion (IMD) on abundance data from each survey and on the combined data from the four surveys, comparing meiobenthic assemblages in (A) open and closed lakes and (B) reaches in open and closed lakes

		R	D	IMD	R	D	IMD	R	D	IMD
A		Mouth			Middle reaches			Inner reaches		
Open vs closed lakes	March	0.09**	29	0.21	0.02	38	0.35	0.15**	33	0.14
	April	0.10**	33	0.39	0.08	33	0.59	0.08**	54	0.08
	June	0.07*	22	-0.09	0.25*	40	0.18	0.16**	51	0.02
	July	0.02	34	0.06	0.24*	43	0.29	0.13**	54	0.38
	Combined	0.14**	23	0.30	0.22**	36	0.51	0.12**	47	0.03
B		Mouth vs Middle			Mouth vs Inner			Middle vs Inner		
Open lakes	March	0.22**	36	-0.52	0.58**	46	-0.50	0.10**	41	-0.03
	April	0.28**	42	-0.47	0.44**	54	-0.65	0.13**	49	-0.30
	June	0.45**	39	-0.59	0.58**	52	-0.69	0.06*	42	-0.26
	July	0.29**	42	-0.14	0.42**	51	-0.31	0.03*	40	-0.22
	Combined	0.28**	35	-0.55	0.24**	50	-0.56	0.05*	41	-0.05
Closed lakes [#]	March	0.68**	43	0.03	0.58**	53	-0.45	-0.10	38	-0.44
	April	0.61**	50	-0.51	0.44**	64	-0.48	-0.05	53	-0.77
	June	0.86**	50	-0.51	0.58**	59	-0.73	-0.16	39	-0.46
	July	0.72**	57	-0.35	0.42**	63	-0.59	-0.12	54	-0.34
	Combined	0.92**	43	-0.34	0.45**	53	-0.37	-0.06	42	-0.63

* $P < 0.05$, ** $P < 0.01$, [#]Data from middle reaches of Durras only.

mouths and either middle or inner reaches but close to zero between middle and inner reaches (Table 2B). There were no statistically significant differences between assemblages in sites within localities. Indices of multivariate dispersion indicated that spatial variability increased with distance from the sea in both open and closed lakes. Spatial variability was, however, significantly different only between mouths and middle reaches (ANOVA: $F = 12.49$, $P < 0.05$) and between mouths and inner reaches ($F = 12.47$, $P < 0.05$) of open lakes. There were no statistically significant differences in the mean number of taxa (S) per 10 cm² (all surveys combined) between localities within either open or closed lakes. Shannon-Wiener diversity H' was, however, significantly greater in the mouths of both types of lake than in the middle or inner reaches, which did not differ significantly (ANOVA: open lakes, H' : 1.1 vs 0.9, $F = 12.6$, $P < 0.0001$; closed lakes, H' : 1.1 vs 0.7, $F = 12.2$, $P < 0.001$). Furthermore, the difference was greater in closed than in open lakes.

Oligochaetes, copepods, polychaetes and harpacticoids accounted for most of the dissimilarities between assemblages in the mouths of open and closed lakes (Table 3A), while turbellarians also contributed significantly to dissimilarities between middle and inner reaches. A measure of the consistency with which a taxon distinguishes between assemblages is given by D/SD , where SD is the standard deviation associated with the average dissimilarity of all sample pairs in the analysis and higher values of the ratio indicate greater consistency (Clarke and Warwick, 2001). Oligochaetes and turbellarians distinguish most consistently between open and closed lakes in mouths and middle reaches, but no taxon

stands out in the inner reaches. Nematodes are the least consistent in distinguishing between assemblages.

Among open lakes, nematodes accounted for much of the dissimilarity between assemblages in mouths and middle reaches, while harpacticoids and other copepods accounted for most of the difference between mouths and inner and between middle and inner reaches (Table 3B). Harpacticoids and other copepods were also the most consistent taxa distinguishing between these assemblages. In contrast to open lakes, harpacticoids consistently accounted for most of the dissimilarity between mouths and middle reaches and between mouths and inner reaches of closed lakes (Table 3C). Assemblages in the middle reaches were distinguished from those in the inner reaches by other copepods and oligochaetes.

Nematodes, copepods and turbellarians were significantly more abundant in the inner reaches of open compared to closed lakes, but not in the other reaches (Fig. 4). Polychaetes and oligochaetes were significantly more abundant in the inner reaches of closed than of open lakes, but there were no significant differences in the abundance of other taxa. Copepods generally became more abundant with increasing distance from the mouth, while the other taxa tended to decline in abundance in this direction (Fig. 4).

The mean number of taxa per 10 cm² in the mouths of open lakes was significantly greater than that in closed lakes (6 vs 5, ANOVA: $F = 9.4$, $P < 0.003$), but there was no difference in diversity ($H' = 1.07$ vs 1.06). Although there was no significant difference in the number of taxa between the middle reaches of open and closed lakes ($S = 6$ vs 6), diversity was significantly

Table 3

Comparisons of Bray-Curtis percent dissimilarities (D)[#] and D/SD of meiobenthic assemblages in (A) reaches in open vs closed lakes and (B) reaches within open and closed lakes, due to individual taxa that contribute $\geq 5\%$ to total dissimilarity (based on SIMPER analyses)

	D	D/SD	D	D/SD	D	D/SD
	Mouth		Middle reaches		Inner reaches	
<i>(A) Open vs closed lakes</i>						
Nematoda	8	1.3	5	1.2	10	1.0
Oligochaeta	18	1.5	13	1.6	14	1.2
Copepoda	18	1.3	12	1.4	14	1.3
Harpacticoida	14	1.1	22	1.2	20	1.3
Polychaeta	17	1.4	15	1.3	12	1.4
Turbellaria	10	1.5	16	1.6	16	1.4
Cum. %	85		83		86	
	Mouth vs Middle		Mouth vs Inner		Middle vs Inner	
<i>(B) Open lakes</i>						
Nematoda	29	1.3	9	1.0	12	1.2
Oligochaeta	12	1.4	12	1.3	9	1.1
Copepoda	16	1.5	16	1.5	15	1.4
Harpacticoida	11	1.4	24	1.3	20	1.3
Polychaeta	5	1.3	11	1.3	14	1.3
Turbellaria	8	1.3	12	1.0	14	1.1
Cum. %	81		84		84	
	Mouth vs Middle		Mouth vs Inner		Middle vs Inner	
<i>(C) Closed lakes</i>						
Nematoda	–	1.3	5	1.4	8*	1.4
Oligochaeta	12*	1.5	14	1.3	16*	1.7
Copepoda	13*	2.1	18	1.6	16*	1.8
Harpacticoida	36*	3.1	28	1.7	19*	0.8
Polychaeta	9*	1.2	11	1.3	13*	1.4
Turbellaria	17*	2.0	13	1.4	14*	1.5
Cum. %	87*		89		86*	

Also shown are the cumulative percent contributions of the listed taxa. [#]Based on the combined abundance data from the four surveys. – taxa contributing $<5\%$ within a comparison. *Data from Durras only.

greater in the former ($H'=0.87$ vs 0.39 , $F=10.3$, $P<0.0001$). In the inner reaches, there were significantly more taxa in open than in closed lakes ($S=6$ vs 5 , $F=9.2$, $P<0.003$) while diversity was also significantly greater in open lakes ($H'=0.92$ vs 0.73 , $F=10.4$, $P<0.002$).

3.2. Natural vs managed lakes

As in the comparisons of open and closed lakes, there were no clear patterns, or statistically significant differences, between sediments in natural vs managed lakes. There were also no significant relationships between the abundance of meiobenthos and properties of sediment in natural vs managed lakes.

MDS ordinations indicated that meiobenthic assemblages do not differ as much between natural and managed lakes as they do between open and closed systems (Fig. 5). In the mouths of open lakes differences were evident only in June and July while in the inner reaches managed lakes appeared to differ from natural ones in April and July. Assemblages in the middle reaches of naturally open lakes did, however, differ more

consistently from those in managed systems, with the exception of March (Fig. 5). Assemblages in the mouths and inner reaches of naturally closed lakes differed from those in managed closed lakes in March and April, but not at other times.

Contrary to the above, ANOSIM indicated that, among open lakes, there were more consistent differences between managed and natural systems than was evident in the ordinations (Table 4). The only contrasts that were not significant were between assemblages in the mouths and middle reaches in March and between those in the mouths and inner reaches in June. In closed lakes, however, ANOSIM indicated fewer significant differences in meiobenthic assemblages in natural compared with managed systems. In the mouths of closed lakes meiobenthos differed between natural and managed systems in March, April and July, while in the inner reaches they differed in March and April. However, when data from all surveys were combined, consistent differences between managed and natural lakes were again revealed in all reaches (Table 4).

Dissimilarity between assemblages in natural vs managed lakes, like those in open and closed lakes,

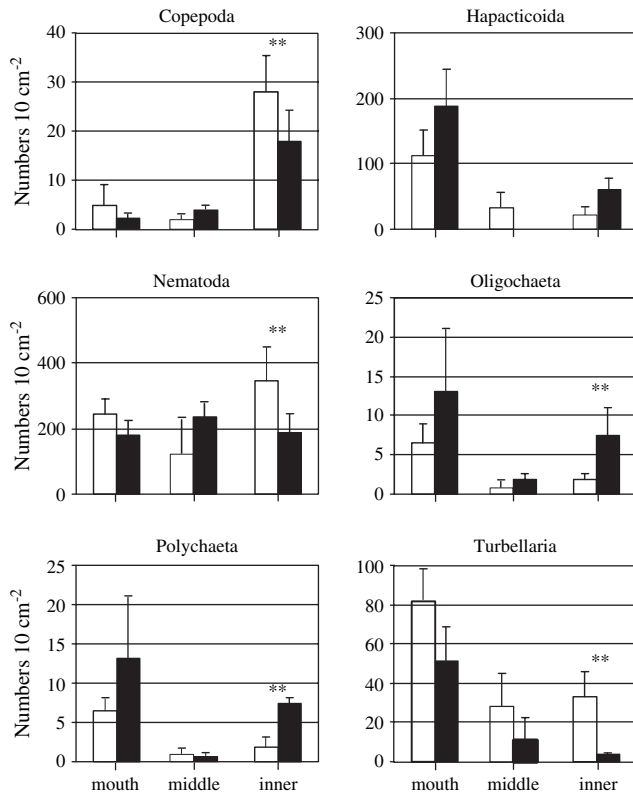


Fig. 4. Abundance (\pm SE) of individual meiofauna taxa contributing 5% or more to dissimilarities between assemblages (based on SIMPER analyses) in reaches of open \square and closed \blacksquare lakes. Asterisks indicate significant differences in abundance (one-way ANOVA: * $P < 0.05$, ** $P < 0.01$). Data for middle reaches of closed lakes from Durras only.

increased with distance from the mouth (Table 4). Indices of multivariate dispersion show that spatial variability was greater in the inner reaches than near the mouths. There were, however, no significant differences in spatial variability between reaches in relation to management. Assemblages in the inner reaches of naturally open lakes were, however, more variable than those in managed open lakes, but the opposite was true in closed lakes (Table 4).

There was a small, but significant difference in diversity between the mouths of natural and managed open lakes (H' : 1.14 vs 0.99, $F = 8.2$, $P < 0.007$), but there was no significant difference in mean number of taxa per 10 cm^2 . Neither diversity nor number of taxa was significantly different in the inner reaches of natural vs managed open lakes (H' : 0.94 vs 0.91; $S = 6$ vs 6). There were no significant differences in number of taxa or diversity between the mouths of natural and managed closed lakes. Diversity was, however, less in the inner reaches of managed closed lakes than in natural closed systems (H' : 0.58 vs 0.88, $F = 9.6$, $P < 0.004$), but the difference in mean number of taxa (6 vs 5) was not significant.

While there was no significant difference in the abundance of most taxa in the mouths of naturally

open compared with managed open lakes, polychaetes were more abundant in the latter (Fig. 6). In the middle reaches of open lakes polychaetes and harpacticoids were more abundant in natural than in managed systems, while turbellarians were more abundant in the latter. In the inner reaches, polychaetes were significantly more abundant in natural than in managed lakes, while nematodes and turbellarians were more abundant in managed systems.

In the mouths of closed lakes, harpacticoids and oligochaetes were more abundant in managed systems and polychaetes more abundant in natural systems (Fig. 6). Nematodes and copepods were more abundant in the inner reaches of natural than in managed closed lakes. Oligochaetes were, however, more abundant in the inner reaches of managed than in natural lakes.

The largest contributions to dissimilarities between assemblages in the mouths of natural vs managed lakes, irrespective of whether they were open or closed, were due to copepods, harpacticoids, polychaetes and oligochaetes (Table 5A), the last two being the most consistent discriminators. In the middle reaches, copepods and harpacticoids contributed most to dissimilarities, with copepods discriminating most consistently between these assemblages. Harpacticoids and turbellarians contributed most to dissimilarities and were among the most consistent discriminators between assemblages in the inner reaches of natural compared to managed lakes.

Among natural lakes, dissimilarities between assemblages in mouths compared to middle reaches and between mouths and inner reaches were due mainly to harpacticoids, which were also the most consistent discriminators (Table 5B). There was relatively little difference in the contributions of the major taxa to dissimilarities between middle and inner reaches. Differences between mouths and middle reaches of managed lakes were due mainly to harpacticoids and polychaetes (Table 5C). Differences between mouths and inner reaches and between middle and inner reaches were due to harpacticoids, oligochaetes and polychaetes, with the latter being the most consistent discriminator in both comparisons.

The above comparisons were of meiobenthic assemblages in natural vs managed lakes, irrespective of their open/closed status. However, since assemblages in open and closed lakes differ significantly, it is necessary to assess the possible influence of management on these types of lake separately. Among naturally open lakes harpacticoids, nematodes and turbellarians consistently accounted for most of the dissimilarities between mouths and middle reaches (Table 6A). Differences between mouth and inner reaches and between middle and inner reaches were due mainly to harpacticoids, turbellarians and copepods. Although nematodes discriminated between assemblages in middle and inner

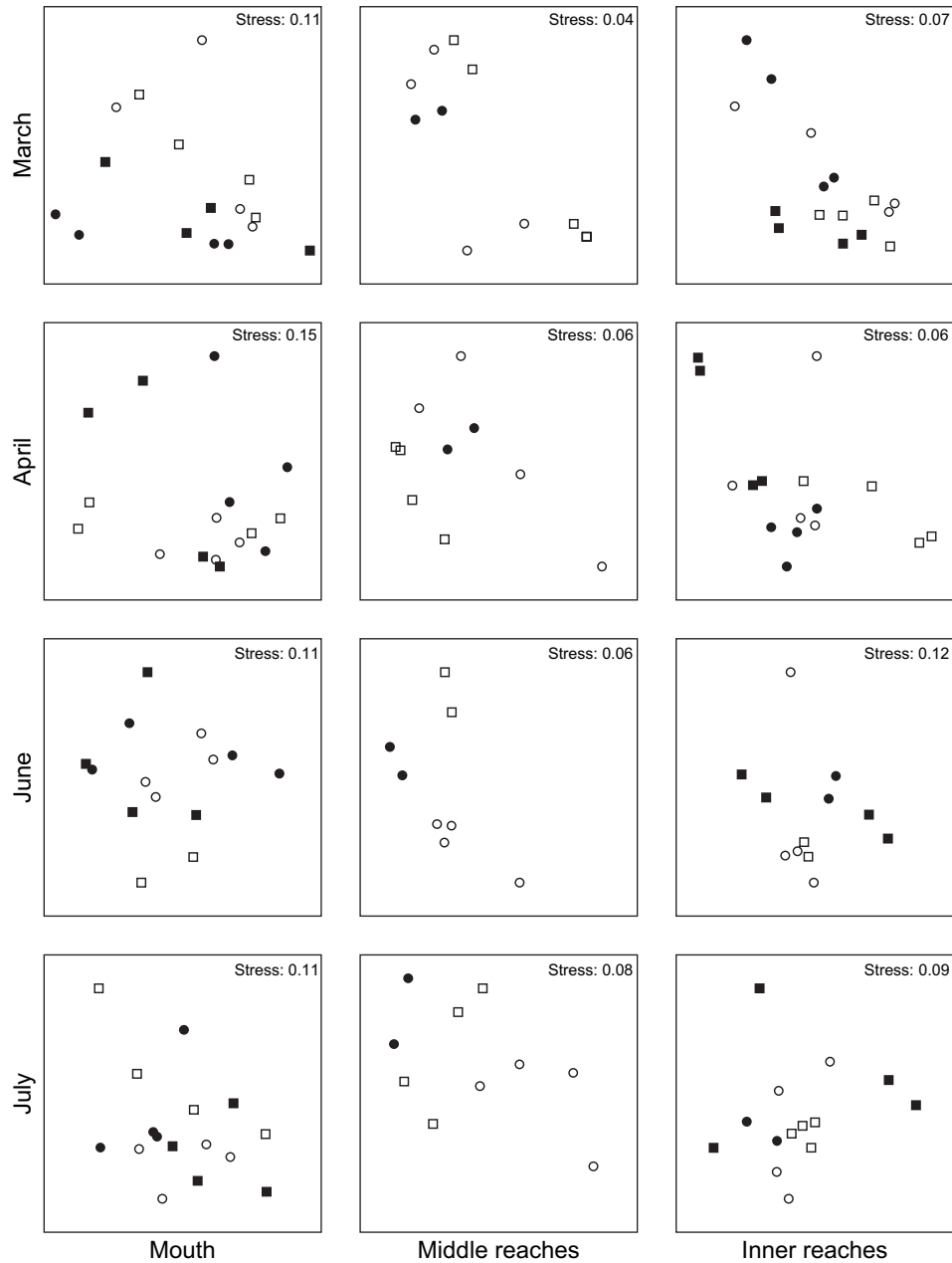


Fig. 5. MDS plots based on meiobenthos abundance on four occasions comparing assemblages in the mouths, middle and inner reaches of natural (circles) and managed (squares) open (open symbols) and closed (solid symbols) lakes. Plots represent the centroids of replicate samples at each site.

reaches with a high degree of consistency, they accounted for only 10% of the dissimilarity.

Within naturally closed lakes harpacticoids, nematodes and turbellarians accounted for much of the dissimilarity between mouths and middle reaches (Table 6B). Harpacticoids also consistently contributed most to differences between mouths and inner reaches. Assemblages in middle reaches were distinguished from those in the inner reaches primarily by nematodes and copepods, both with a high degree of consistency.

Differences in assemblages in the mouths and middle reaches of managed open lakes were due

mainly to nematodes, harpacticoids and turbellarians, which all consistently differentiate between them (Table 6C). Nematodes and copepods were the most consistent taxa differentiating between assemblages in middle and inner reaches. Turbellarians were also consistent in this respect but accounted for only 10% of the dissimilarity. The only comparisons that can be made between assemblages in managed closed lakes are between those in the mouths and inner reaches (Table 6D). In this case harpacticoids and oligochaetes accounted for most of dissimilarities between those assemblages.

Table 4

Results of one-way ANOSIM (R), Bray-Curtis percent dissimilarities (D) and indices of multivariate dispersion (IMD) on abundance data from each survey and on the combined data from the four surveys, comparing meiobenthic assemblages in reaches in natural and managed open and closed lakes

		Mouth			Middle reaches			Inner reaches		
		R	D	IMD	R	D	IMD	R	D	IMD
Natural vs managed open lakes	March	0.03	23	0.01	0.03	38	-0.05	0.27**	41	0.48
	April	0.12**	36	-0.56	0.17**	43	0.23	0.22**	70	-0.01
	June	0.53**	26	-0.34	0.53**	40	0.42	-0.17	49	0.70
	July	0.15**	37	0.37	0.27**	38	0.43	0.24**	58	0.52
	Combined	0.33**	27	0.17	0.26**	39	0.11	0.27**	52	0.47
Natural vs managed closed lakes	March	0.16**	24	-0.11	no comparison [#]			0.13*	37	-0.25
	April	0.08*	39	0.05	no comparison			0.55**	60	-0.40
	June	0.04	26	-0.14	no comparison			0.03	48	-0.69
	July	0.07*	36	0.35	no comparison			-0.00	58	-0.70
	Combined	0.11*	30	0.21	no comparison			0.32**	50	-0.40

* $P < 0.05$, ** $P < 0.01$, [#] only one middle reach in closed lakes.

4. Discussion

This study showed that there were greater differences in the structure of meiobenthos between reaches within lakes and between lakes than between sites within reaches. The differences were due to variations in

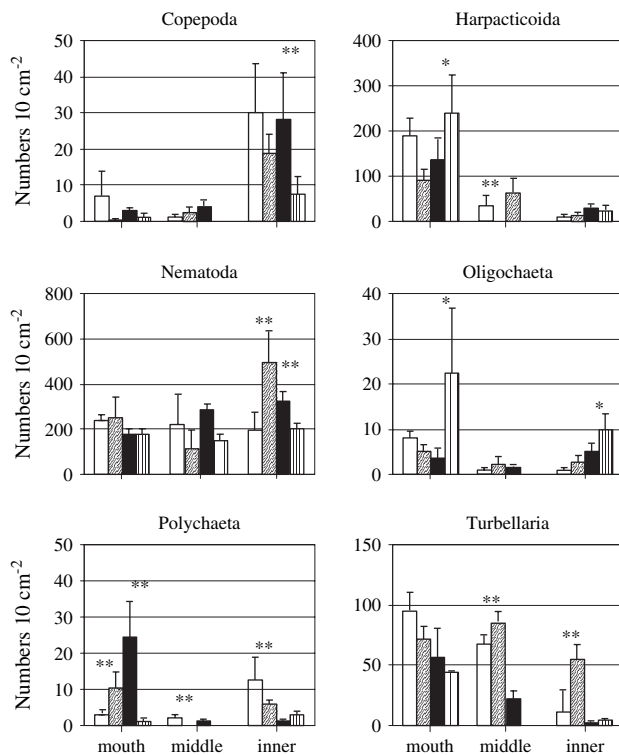


Fig. 6. Abundance (\pm SE) of individual meiobenthic taxa contributing 5% or more to dissimilarities between assemblages (based on SIMPER analyses) in reaches of natural \square and managed \boxtimes open lakes and in natural \blacksquare and managed \blacksquare closed lakes. Asterisks indicate significant differences in abundance (one-way ANOVA: * $P < 0.05$, ** $P < 0.01$). Data for middle reaches of closed lakes from Durras only.

abundance rather than variations in the number of taxa per unit area. In contrast to studies of macrobenthos, which indicate that the greatest variability is at the smallest spatial scales (Morrisey et al., 1992; Thrush et al., 1994; Chapman, 1998), these findings imply that, at the taxonomic resolution used in this study, there is a degree of spatial homogeneity within reaches. While small-scale (within site) variability was found to be the largest component of variance among nematode assemblages in three NSW estuaries (Hodda, 1990), other studies of meiobenthos have also shown that small-scale variability is often less than that at larger scales (Phillips and Fleeger, 1985; Montagna, 1991; Soetaert et al., 1994; Li et al., 1997). These apparently contradictory results imply that the degree of spatial variability that can be detected depends in part on taxonomic resolution. As resolution is increased, more small-scale patterns may become apparent. Whether this enhances ecological understanding, as opposed to simply creating 'noise' (Gee et al., 1992), depends on the objectives of the study. In the present case, the purpose was to determine whether consistent patterns could be seen at a coarse taxonomic resolution and the data indicate that they can.

In this study there were clear differences in the assemblages of meiobenthos in different parts of the lakes, irrespective of whether the lakes were open or closed, or subjected to different levels of management. Although harpacticoids and other copepods accounted for most of the differences, nematodes, turbellarians and polychaetes were also important. This is similar to what was found by McArthur et al. (2000) in an open lagoon in the Mediterranean, where nematodes, copepods, ciliates, turbellarians and ostracods accounted for around 80% of the dissimilarity between sites at mouths and in inner reaches. As in the present study, they also found a negative correlation between distance from the mouth

Table 5

Comparisons of Bray-Curtis percent dissimilarities (D)[#] and D/SD of meiobenthic assemblages in (A) reaches in natural vs managed lakes and (B and C) reaches within natural and managed lakes, due to individual taxa that contribute $\geq 5\%$ to total dissimilarity (based on SIMPER analyses)

	D	D/SD	D	D/SD	D	D/SD
	Mouth		Middle reaches		Inner reaches	
<i>(A) Natural vs managed lakes</i>						
Nematoda	7	1.2	6	1.5	9	1.0
Oligochaeta	18	1.3	11	1.2	12	1.2
Copepoda	17	1.2	17	1.5	14	1.4
Harpacticoida	14	1.1	24	1.3	21	1.3
Polychaeta	17	1.3	15	1.3	11	1.4
Turbellaria	9	1.4	12	1.3	18	1.5
Cum. %	82		85		85	
	Mouth vs Middle		Mouth vs Inner		Middle vs Inner	
<i>(B) Natural lakes</i>						
Nematoda	8	1.5	7	1.1	14	1.2
Oligochaeta	10	1.2	10	1.2	12	1.2
Copepoda	15	1.7	17	1.6	14	1.4
Harpacticoida	30	2.3	28	2.0	15	1.0
Polychaeta	10	1.3	10	1.3	14	1.5
Turbellaria	13	1.5	15	1.5	16	1.3
Cum. %	86		87		85	
	Mouth vs Middle		Mouth vs Inner		Middle vs Inner	
<i>(C) Managed lakes</i>						
Nematoda	7	1.2	7	1.3	8	1.3
Oligochaeta	17	1.3	17	1.3	14	1.2
Copepoda	13	1.4	17	1.5	16	1.5
Harpacticoida	29	1.1	25	1.4	26	1.3
Polychaeta	15	1.3	12	1.3	14	1.3
Turbellaria	10	1.3	9	1.3	10	1.4
Cum. %	91		87		89	

Also shown are the cumulative percent contributions of the listed taxa. [#]Based on the combined abundance data from the four surveys. – taxa contributing <5% within a comparison.

and abundance of meiobenthos. Nematodes dominated the meiobenthos, but copepods were proportionally more abundant in the inner reaches than near the mouths.

Many factors could contribute to the difference in composition of meiobenthos among localities within lakes. Among these are characteristics of sediments such as median particle-size and organic content (Castel, 1992; Coull, 1999). Meiobenthos are often more abundant and diverse in coarse sediments, because both burrowing and interstitial forms can coexist. Water also circulates more freely in coarse sediments, resulting in greater oxygenation and penetration of meiobenthos to greater depths. In fine sediments, interstices are small and, if the median particle size is 125 μm , interstitial forms are excluded (Coull, 1999). In the present study meiobenthos was most abundant in sandy sediments near mouths, but there were no significant correlations between meiobenthos and median grain-size.

Fine sediments contain larger amounts of clay and organic matter compared with coarse sediments. In the NSW lakes, there was substantially more clay and organic matter in sediments from the middle and inner reaches compared with mouths. Fenchel (1969) found

that 2–4% silt/clay was sufficient to exclude interstitial organisms. Clay and organic content have been found to influence the distribution of harpacticoids (Ivester, 1980) and turbellarians (Martens and Schockert, 1986). Organic enrichment is also known to reduce the abundance and diversity of meiobenthos (Castel, 1992; Mazzola et al., 1999; Mirto et al., 2002). In areas where oxygen penetrates only a centimetre or so, meiobenthos are restricted to the upper layers. Reduced diversity and abundance may also be a consequence of the restricted vertical distribution of animals, because fewer niches may be available under these conditions (Coull and Fleeger, 1977). This would suggest that meiobenthos may be less abundant in fine sediments and, while abundance did decrease towards the inner reaches in the present study, this was not correlated with characteristics of sediment. A similar lack of correlation between meiobenthos and sediment type in a Mediterranean lagoon was reported by McArthur et al. (2000), who concluded that other factors were responsible for the observed patterns of distribution.

Salinity is important in determining the composition and distribution of benthos in estuaries and lagoons (Coull, 1999). McArthur et al. (2000) found that

Table 6

Comparisons of Bray-Curtis percent dissimilarities (D)[#] and D/SD of meiobenthic assemblages in reaches within natural and managed open and closed lakes, due to individual taxa that contribute $\geq 5\%$ to total dissimilarity (based on SIMPER analyses)

	Mouth vs Middle		Mouth vs Inner		Middle vs Inner	
	D	D/SD	D	D/SD	D	D/SD
<i>(A) Naturally open lakes</i>						
Nematoda	25	7.8	10	1.1	10	6.4
Oligochaeta	7	1.4	9	1.2	9	1.2
Copepoda	10	1.9	13	1.3	13	2.7
Harpacticoida	27	5.3	27	1.5	24	1.3
Polychaeta	5	1.5	11	1.7	11	2.4
Turbellaria	19	6.2	14	1.2	14	2.3
Cum. %	93		84		81	
<i>(B) Naturally closed lakes</i>						
Nematoda	24*	4.4	–	–	39*	6.4
Oligochaeta	8*	1.3	11	1.3	–	–
Copepoda	–	–	20	2.3	22*	2.8
Harpacticoida	26*	4.6	28	3.1	9*	0.4
Polychaeta	10*	1.2	11	1.4	10*	1.5
Turbellaria	20*	4.4	16	2.0	10*	1.8
Cum. %	88*		86		90*	
<i>(C) Managed open lakes</i>						
Nematoda	28	8.1	7	1.3	39	8.8
Oligochaeta	9	1.7	18	1.5	–	–
Copepoda	6	1.1	16	1.6	22	2.4
Harpacticoida	21	3.9	29	1.4	9	1.7
Polychaeta	13	2.5	12	1.3	10	1.7
Turbellaria	20	6.2	9	1.3	10	7.4
Cum. %	97		91		90	
<i>(D) Managed closed lakes</i>						
Nematoda	no comparison**		7	1.6	no comparison**	
Oligochaeta	no comparison		18	1.4	no comparison	
Copepoda	no comparison		16	1.4	no comparison	
Harpacticoida	no comparison		29	1.4	no comparison	
Polychaeta	no comparison		12	1.5	no comparison	
Turbellaria	no comparison		9	1.3	no comparison	
Cum. %			91			

Also shown are the cumulative percent contributions of the listed taxa. [#]Based on the combined abundance data from the four surveys. – taxa contributing $<5\%$ within a comparison. *Middle reach data from Durras only. **No middle reaches for managed closed lakes.

meiobenthos were less abundant where seasonal fluctuations in salinity were greatest, in the inner reaches of a lagoon. The present study also indicated that diversity and abundance decreased with distance from the sea and were lowest where salinity would be expected to be most variable.

Many studies have shown that physical and chemical disturbance affects abundance and composition of meiobenthos in sediments (Coull and Chandler, 1992; Austen et al., 1994; Schratzberger and Warwick, 1998, 1999). Laboratory studies on nematode communities have shown that those from sandy substrata are more resilient to physical disturbance than those from mud (Schratzberger and Warwick, 1998). They found that communities from mud were most diverse at intermediate frequency of disturbance, which accords with the intermediate disturbance hypothesis (Connell, 1978). If this applies to meiobenthos in general, disturbance caused by intermittent opening could explain the greater

diversity among assemblages in the mouths of lakes, which was found in the present study.

The lower diversity within assemblages in middle and inner reaches of ICOLLs may, however, reflect the influence of at least two different processes, apart from the influence of physical factors. Mud-dwelling meiobenthos are known to be more sensitive to physical disturbance than those living in sand (Schratzberger and Warwick, 1998), although they can recover rapidly (Sherman and Coull, 1980). Disturbances such as re-suspension of sediment by wind-induced turbulence or movement of boats and bioturbation by macrobenthos (Widdicombe et al., 2000) may limit diversity in fine sediments, although the abundance of macrobenthos is relatively low (Dye and Barros, in prep.).

Alternatively, or perhaps additionally, competitive exclusion in the relatively stable inner reaches of lakes may also reduce diversity. Warwick and Gee (1984) concluded that this process was responsible for reduced

diversity among meiobenthos at some locations in the Tamar estuary. Further investigation of this possibility would, however, require finer taxonomic resolution and experimental manipulation.

4.1. Open vs closed lakes

Meiobenthos in closed lakes differed significantly from that in open systems. Because sediment may be an important factor in the differences in meiobenthos between localities within lakes, it is logical to expect that this may also be important in explaining differences between lakes. No significant correlations between sediment and meiofauna were, however, found. This implies that other factors related to the open/closed status of a lake may be responsible for the observed differences. Salinity could be one such factor. In three of the closed lakes, salinity was <50% of that in open lakes and there was a significant correlation between salinity and composition of meiobenthos across inner-reach localities. The lack of correlation in mouths and middle reaches, however, makes it difficult to draw conclusions about the role of salinity.

An alternative model to explain the differences in abundance and composition of benthos between mouths and remote localities in lagoons relates to the concept of isolation. The idea that isolation from the sea per se could be responsible for observed patterns in the distribution of benthos in coastal lagoons was first suggested by Guelorget and Perthuisot (1992) (quoted by Guelorget and Perthuisot, 1992). The central tenet of the idea is that the distribution of benthic fauna and flora is independent of factors such as surface area, salinity or shape of a lagoon, but is related to distance from the connection with the sea. The resulting patterns of distribution are characterised by progressively decreasing diversity, biomass and productivity with increasing distance from the sea, resulting from a reduced supply of 'vital elements of marine origin' (Guelorget and Perthuisot, 1992). While this idea has been vigorously debated, particularly in relation to macro-tidal estuaries (Barnes, 1994; Perthuisot and Guelorget, 1995), it has since been invoked in several studies of macrobenthos in coastal lagoons and has also been applied to the meiobenthos in these habitats (Castel, 1992; McArthur et al., 2000).

In this study, the localities with the smaller diversity and greatest spatial variability were those that were most isolated from the sea. These areas had greater proportions of copepods and oligochaetes compared to less isolated areas, where turbellarian flatworms were proportionally more abundant. While this may be due to isolation per se, it may also be a consequence of the greater variability in physical conditions characteristic of isolated areas. Meiobenthos in the mouths of open lakes may also experience some recruitment due to passive

transport of animals into the lakes by tidal currents, but this effect would diminish with distance from the mouth as currents slacken (Armonies, 1994).

4.2. Natural vs managed lakes

Differences in composition of meiobenthos between natural and managed lakes were less than those between open and closed lakes, except in the inner reaches, where the differences were greater. This is surprising given the differences between managed and natural systems. In managed lakes, there are localised disturbances associated with dredging or bulldozing in the mouths. Dredging often reduces diversity and abundance and increases spatial variability of benthos (Nichols et al., 1990) and effects can persist for up to 10 years, although some of these effects were probably due to occasional maintenance dredging (Pequegnat, 1975). Dredging also resuspends fine material that may be redistributed to adjacent areas. Furthermore contaminants, such as heavy metals, which are toxic to benthos, may also be released by dredging (Maurer et al., 1981). Meiobenthos were less diverse in the mouths of managed lakes and there was evidence of greater spatial variability, which may be a consequence of disturbance caused by artificial opening. There was, however, also greater spatial variability in the inner reaches of open and of closed managed lakes, which cannot be a consequence of disturbance in the mouths.

Managed lakes also have more urban development in their catchments and along their shorelines than do natural lakes and they are consequently subjected to more disturbance and receive greater loads of contaminants, pollutants and nutrients. These stressors can affect the abundance, diversity and spatial variability of benthos (Warwick and Clarke, 1993; Stark, 1998). In Port Hacking estuary, New South Wales, macrofaunal assemblages differed between sandy sediments in urban and non-urban areas (Lindgarth and Hoskin, 2001). Meiobenthos are sensitive to a wide range of pollutants. In the Bay of Naples, differences in the structure of meiobenthic assemblages reflected gradients in organic pollution (Sandulli and de Nicola-Giudici, 1990). Somerfield et al. (1994) found that changes in structure of assemblages of nematodes in the Fal estuary, southwest England, correlated closely with sediment concentrations of heavy metals. Assemblages near the mouths may thus be affected primarily by physical disturbances, while those in the middle and inner reaches may be responding to a suite of factors not directly related to artificial opening.

Despite potentially confounding factors, such as size of lake and catchment, degree of urbanisation, etc., this study shows that there are large-scale patterns in the composition, abundance and spatial variability of meiobenthos in coastal lakes in New South Wales and that

these patterns relate primarily to whether a lake is open or closed. Furthermore, the differences are greater between isolated localities with restricted connection with the sea, i.e. inner reaches and in closed systems. The influence of management (including the suite of anthropogenic impacts associated with urbanisation) becomes more apparent when open and closed lakes are considered separately. It appears that open lakes are different from closed lakes irrespective of whether they are naturally or artificially open. Because these differences are consistent in space and time, it is possible to predict how meiobenthos might change in response to increasing periods of isolation. For example, abundance would probably decrease and the meiobenthos would become more spatially variable. The relative abundance of copepods, polychaetes and oligochaetes would increase at the expense of harpacticoids and turbellarians, while there would be relatively little change in the abundance of nematodes.

Meiofauna mechanically break down detritus, are important in bioturbation and supply nutrients directly through exudates and faeces, while also representing an important source of food for higher trophic levels (Gee, 1989; Gaston, 1992; Coull, 1999). They also stimulate microbial activity (Gerlach, 1978). Changes in the abundance and composition of meiobenthos, such as those associated with prolonged closure of lakes, could therefore affect important estuarine processes.

Establishing that consistent patterns exist in the composition and abundance of meiobenthos and that these can be discerned at a relatively coarse level of taxonomic resolution, is an important step in understanding the ecology of ICOLLs. Experimental manipulations are now required to understand the processes that maintain the observed patterns and to assess how isolation may affect the functional role of meiobenthos in these systems.

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